The contribution of fog to the moisture and nutritional supply of *Arthraerua leubnitziae* in the central Namib Desert, Namibia

Tunehafo Ruusa Gottlieb

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Supervisors:

A. Prof Frank Eckardt, Department of Environmental and Geographical Science

A. Prof Michael Cramer, Department of Biological Sciences

Declaration

‘I know the meaning of plagiarism and declare that all of the work in the dissertation (or thesis), save for that which is properly acknowledged, is my own’.

Signed by candidate

Signature removed

Tunehafo Ruusa Gottlieb, October 2017

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Abstract

Fog is a key source of moisture to the diverse coastal Namib Desert biota, delivering five times more moisture than rain. Apart from the importance of fog as a source of water for plants, it is also associated with particulates that may contain essential nutrients for plants. Furthermore, dry deposition can be an important input of nutrients to many ecosystems, but without water, dust deposited on leaves or on soil is inaccessible for plant uptake. In other studies of coastal ecosystems (e.g. Strandveld), it has been found that this combined deposition of nutrients represents a major source of nutrients to terrestrial ecosystems. In the case of the Namib Desert, the range of *Arthraerua leubnitziae* is limited to those areas where fog occurs. This study was carried out at five meteorological stations in the gravel plains of the Namib Desert, along an east-west transect increasing in elevation inland. I hypothesised that marine-derived deposition contributes to moisture and nutrient supply of *Arthraerua leubnitziae,* an endemic shrub restricted to the fog zone of the central Namib Desert, and consequently determines its distribution. To test this hypothesis, two sub-hypotheses were developed and tested independently. The first sub-hypothesis was that fog contributed to the distribution range of *A. leubnitziae* in the central Namib Desert and the second was that fog deposition has a significant potential to supply moisture and nutrients to *A. leubnitziae* in the central Namib Desert. To test the first sub-hypothesis, I measured fog and rain volume, and plant morphological characteristics at the five sites. In addition, a fog map was derived using climatic variables from the five sites and used with climate and edaphic variables in MaxEnt model of the probability of occurrence of *A. leubnitziae*. The occurrence of *A. leubnitziae* was found to coincide with areas with high fog occurrence with fog contributing 36% to the modelled distribution of *A. leubnitziae* alongside precipitation, elevation and isothermality. In order to test the second sub-hypothesis, I measured nutrients deposited in fog water derived from wet and dry deposition (Ca, K, Mg, Na, Cl, Br, NO_3, PO_4 and SO_4) and plant essential nutrients in plant and soil samples (N, P, K, Ca, Mg, Mn, Fe, Cu and Zn). I also determined the nutrient uptake by stems of *A. leubnitziae*. During the period of Sep 2015 to Aug 2016, fog provided 92% of the yearly water input across the study sites. Over the course of the sampling cycle, the total annual nutrient content of fog and dust was dominated by Ca and Na. Most of the nutrients (K, Mg, Na, and S) were of marine origin. However, Ca enrichment factors (relative to seawater) were higher than 1, suggesting an input from dust. *A. leubnitziae* was found to be able to directly intercept and absorb some of the nutrients in the dust and fog via their stems. Even though plant and soil nutrients did not match each other, a contribution to plant nutrition from dust and fog was evident. The low nutrient concentrations in the soils of the Namib Desert and significant inputs from dust and fog suggests deposition is an important source of nutrients for *A. leubnitziae*. Although work is still required to better understand the importance of fog water uptake for nutrient provision, I have identified that water, nutrients and environmental stress alleviation should not be considered separately in studying the role of fog as a determinant of plant distributions.

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1. General introduction

1.1. Global Context

Fog is a major part of a number of coastal ecosystems globally (Burgess & Dawson, 2004; Cereceda, Larrain, Osses, Farías, & Egaña, 2008; Seely & Henschel, 1998; Vogelmann, 1973) and provides a significant portion of the water and nutrients to these ecosystems (Ingraham and Matthews, 1988; Soderberg, 2010; Templer et al., 2015). Fog is made up of water and dissolved ions which could be important for plant nutrition and growth (Gundel et al., 1994) and the daily occurrence of fog in fog ecosystems is important for providing moisture and nutrients to these fog ecosystem (Burgess and Dawson, 2004). Vegetation and soils capture the fog water and nutrients deposited to these coastal ecosystems, thus affecting the water balances and nutrient cycling of the ecosystems where fog is deposited (Azevedo and Morgan, 1974). In fog ecosystems, the occurrence of fog may, therefore, influence species composition, the character of soils and (Ewing et al., 2009).

Coastal fog, also called advected fog, is often the most common type of fog in coastal ecosystems. This type of fog is generally formed when warm, moist air passes over a cool ocean or terrestrial surfaces (Olivier, 1995). The fog contains small condensed water droplets that may be deposited onto surfaces such as vegetation. Fog water and nutrients in the fog water can be directly absorbed by vegetation, directly deposited onto soil surfaces or dripped to the soil as fog water droplets come in contact with leaf or stem surfaces (Bruijnzeel et al., 2011). Species that can use this atmospheric source of water and nutrients, might be more successful in inhabiting ecosystems in which fog is common.

Precipitation in many dryland ecosystems is so low relative to demand, that water availability is the main control of biological processes (McHugh et al., 2015). Fog is an especially important additional source of water in areas that receive more fog than rainfall (Fu et al., 2016). Species distribution, productivity, and nutrient cycling in these regions are commonly affected by the amount and timing of water delivery to ecosystems (Ewing et al., 2009). However, the frequency, duration and intensity of fog is important in determining the distribution of vegetation types (Hesse, 2012). The distribution of fog in a number of these ecosystems is seasonal and patchy (Ewing et al., 2012; Filonczuk et al., 1995; Fischer et al., 2016), but can provide an important portion of the yearly water budget (Oberlander, 1956). For example, in the coastal California redwood forest, 25-50% of the total water input each year is contributed by fog (Dawson and Vidiella, 1998). Fog creates a cloud belt in which vegetation (e.g. rosettes and cacti) thrive (Nicholson, 2011) and the use of fog water in areas that receive frequent fog is to be expected.

Fog deposited on the soil commonly evaporates quickly once the fog has lifted (Louw and Seely, 1982). In the Namib Desert, fog does not make a substantial contribution of moisture below the top 3 cm, which also dries up a few hours after fog deposition (Soderberg, 2010). This, therefore, makes the contribution of fog to subsurface water difficult to estimate and predict. However, in other fog ecosystems around the world, significant infiltration of fog water from fog dripping off vegetation has been shown (Burgess and Dawson, 2004; Byers, 1953; Carbone et al., 2013; Fischer et al., 2016). For example, seasonal fog contributed 30% of the total water precipitation in the broad-leaved coastal forest of Dhofar (Hildebrandt et al., 2007), in comparison to the estimated < 10% in arid lands (Martinez-Meza and Whitford, 1996). Fog can, therefore, increase soil water content by fog drip, by supplementing shallow water resources (Dawson, 1998; Liu et al., 2005).

Apart from fog as a source of moisture, fog water contains a variety of nutrients and ions that are important to ecosystems and can potentially be beneficial to terrestrial ecosystems (Ewing et al., 2012). The availability of nutrients in ecosystems is important in determining the plant growth and maintaining ecological processes. Fog formed over adjacent oceans contains nutrients, and pollutants, that are of both marine and terrestrial origin that may be important for ecosystem function (Weathers and Likens, 1997). Nutrients deposited to fog ecosystems via fog are either picked up over land as fog is blown inland or comes in with the fog from the sea where the fog originates. Nutrients over the land are formed in several processes that include dust that may be of local or regional origin. For example, Etosha Pan, Makgadikgadi Pans and ephemeral rivers (e.g. Kuiseb River) are identified as some of the dust sources in southern Africa (Dansie et al., 2017; Prospero, 2002; Washington et al., 2003). Atmospheric deposition can be an important source of nutrients to marine systems, and in many open oceans regions, atmospheric deposition contributes to the nutrient (e.g. Fe, N and P) input to the surface waters (Baker et al., 2016; Mahowald et al., 2005).

The inputs and losses of nutrients from ecosystems determine the availability of nutrients in an ecosystem Nutrients lost from ecosystems by processes such as fires, leaching and herbivory (Chapin III et al., 2002) need to be replaced (if nutrient pools are constant) into the ecosystem by additions from external sources. These sources may include atmospheric deposition, N_2 fixation, weathering (Vitousek et al., 1998), dry deposition (absorption of dust and gases on canopy surfaces and by the soil) and deposition of water vapour and associated dissolved nutrients onto canopy surfaces from clouds and fog (Perry et al., 2008). However, atmospheric wet and dry deposition are the most important sources of nutrients in areas with limited inputs from other sources such input of N from N_2 fixing plants and/or soil crusts (Belnap, 2003) and in areas with low nutrient bedrock (Chadwick, Derry, Vitousek, Huebert, & Hedin, 1999; Weathers, Lovett, Likens, & Caraco, 2000). The amounts and chemical forms of elements in the atmosphere determine the total potential input from the atmosphere as well as the proportion of that input represented by dry deposition.

The elements in wet or dry deposition may originate from local industrial pollution, fires, dust from agricultural lands and deserts (Bruijnzeel, 1991) and from long distance transport of dust, sea spray and pollution (Swank and Henderson, 1976). Elements contained in sea spray, primarily Cl, Na, K, and Mg (Chadwick et al., 1999) are carried from the ocean by air masses moving into terrestrial environments. In turn, dust and gases from surface soils, emissions from fires and pollen and organic emissions from vegetation are picked up by air currents and either deposited directly as dry deposition or entrained in the fog (Perry et al., 2008). For example, dust blown from the Sahara contributed *ca.* 1 kg ha^{-1} y^{-1} of P to the Amazon rainforest (Prospero, 1981). As some of the fog moving inland is captured by leaves of plants, the nutrients in dry deposition become available to the plants through the moisture. The moisture and nutrients may be absorbed directly by the leaf or drip onto the soil, thus supplying both water and nutrients either directly through the leaves or indirectly through the roots (Fig.1.1) (Ingraham and Matthews, 1995; Boyce et al., 1996). The degree to which plant canopies are exposed to clouds or fog and the larger scale patterns of air movement across the globe also influence the amount of deposition that can be captured (Prospero, 1981).

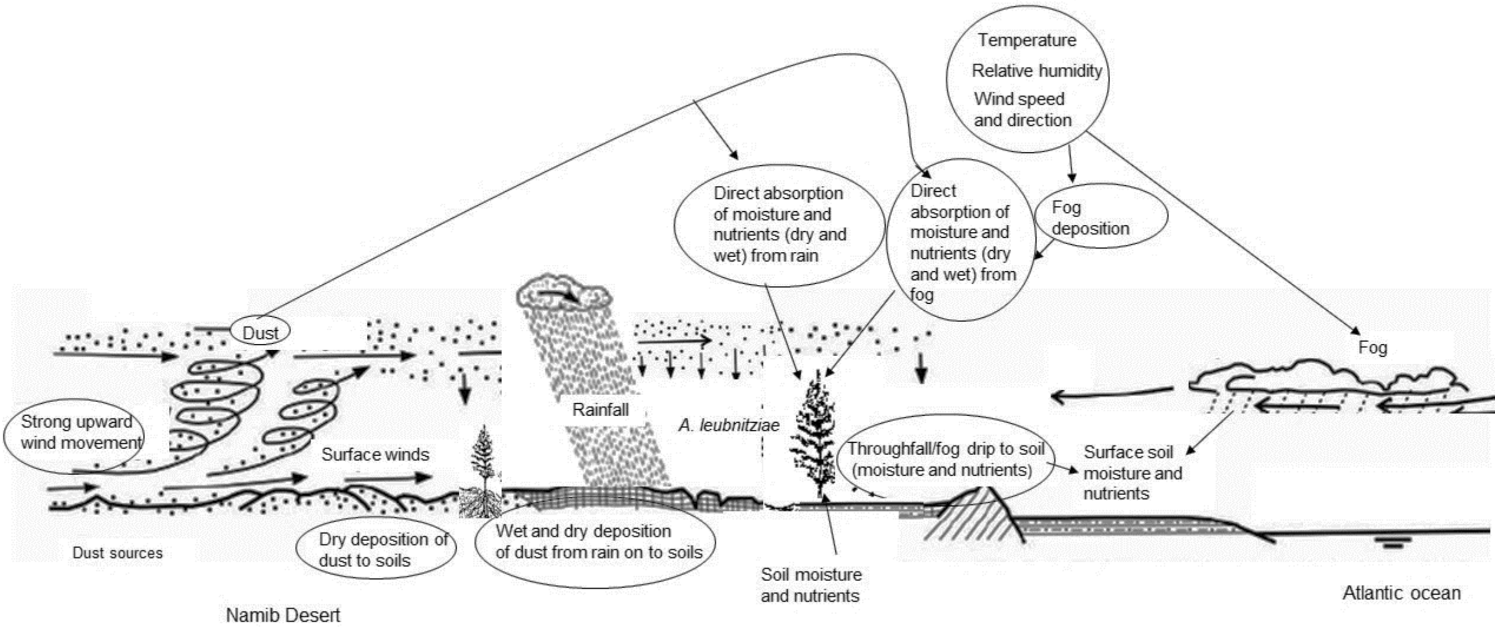


Figure 1.1: Schematic of the supply and transport of moisture, and nutrients from fog, dust and rain in ecosystems.

1.2. The Namibian context

The Namib Desert is a nutrient poor ecosystem (Jacobson, 1997), where fog is the most common and occurs more frequently than rainfall (Henschel and Seely, 2008). In this ecosystem, rainfall occurs in pulses that are important for many biogeochemical processes (Huxman et al., 2004; Jacobson and Jacobson, 1998; Seely, 1978). Fog is, however, a more reliable, major component of the climate and the main source of moisture in the western part of the desert (Pietruszka and Seely, 1985). In a course of a year, fog water collection at a local village in the Namib Desert exceeded 1 L $^{m-2}$ day^{-1} (Henschel et al., 1998). Once formed at the coast, fog is pushed up to a 100 km inland by northwesterly winds (Supp Fig. 1.1). The fog zone of the central Namib Desert is the area where the characteristics of advection fog impact the most (Olivier, 1995). This zone extends up to 150 km inland, between the Atlantic Ocean to the west and the Great Escarpment (a 5000 km long, semi-continuous mountain range in southern Africa) to the east (Heine and Walter, 1996; Viles and Goudie, 2013; Watson and Lemon, 1985). The escarpment is made up of most of southern Africa's major geological suites and separates the central plateaus from the arid coastal gravel plains (gravel Namib; Fig. 1.2) (Moore and Blenkinsop, 2006; White, 1983), but with a constant geomorphology of a plateau margin (van Zinderen Bakker Sr, 1983).

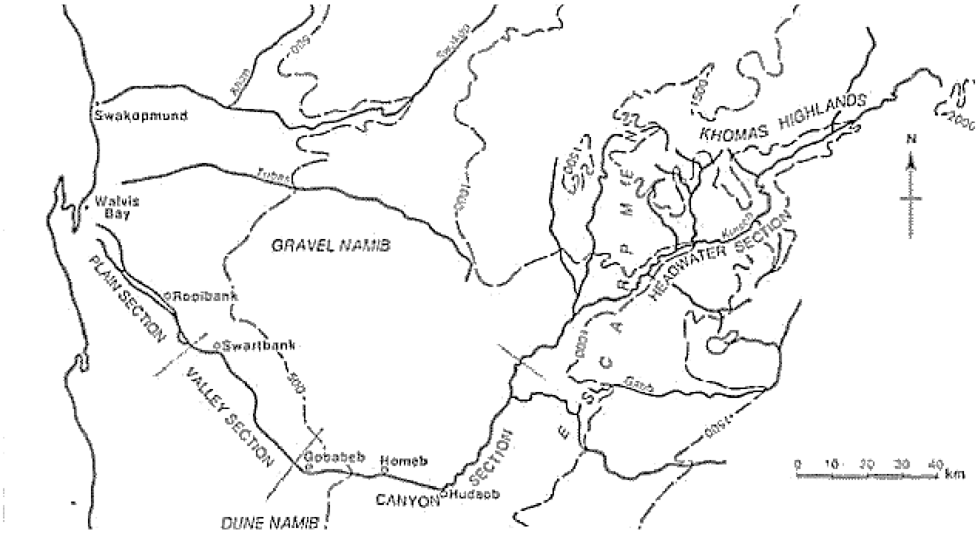


Figure 1.2: The location of the gravel plains (gravel Namib) in the central Namib Desert and the great escarpment. Adapted from, Marker, 1977.

The most common type fog in the Namib Desert is considered to be advection fog which is mainly driven by the Benguela current (Olivier, 1995; Seely & Henschel, 2001), forming in cool conditions at night and disappearing in the morning. Sea and high fog, that are both forms of advected fog, and occur separately from each other (Table. 1.1) (Seely & Henschel, 2001). Sea fog and high fog, however, deliver moisture differently to ecosystems. Sea fog mostly occurs during the afternoon, is blown inland by a southwesterly wind and condenses at a relatively low rate. On the other hand, high fog is blown inland by northwesterly winds (3–10 m s^{-1}), reaches the land at some distance from the coast and condenses at relatively high rates (Lancaster, Lancaster, & Seely, 1984; Seely & Henschel, 1998; Seely & Henschel, 2001). These fogs occur at different times and deliver water, and potentially nutrients, not only at different times but different rates and potentially influence the amount of water and nutrients received at different locations within the fog gradient. However, other types of fog (e.g. radiation and mixed) could occur in the Namib Desert (Eckardt et al., 2013; Kaseke et al., 2017).

Table 1.1: The properties of the of two common types of Namib fog, adapted from Seely and Henschel, 2001.

Fog type	Sea fog	High fog
Cloud altitude (m above mean sea level)	<200 m	200-500 m
Usual distance from coast (km)	0-15	20-60
Distance of peak precipitation (km)	5	30
Peak season	Mid winter	Early summer
Frequency (days/year)	70-200	30-120
Direction of cloud	SSW	NW
Direction on ground	SSW	NNE
Wind strength	Mild	Fairly strong
Condensation rate	Moderate	High

Due to the location of the Namib Desert along the highly productive Atlantic Ocean coast and the strong seasonal upwelling that occurs, a rich supply of nutrients (e.g. N, P, S) is supplied to the Atlantic Ocean (Hansell and Follows, 2008; Soderberg, 2010). While there have been some studies of the use of fog water by plants in the Namib Desert (e.g. Ebner et al., 2011; Roth-Nebelsick et al., 2012; Seely et al., 1977), little is known about the contribution of nutrients and pollutants by dry and wet deposition to the Namib Desert ecosystem. Some of the lowest aerosol chemical concentrations in the world are found in the Namib Desert (e.g. Pb of 0.6 ng/m^3) (Bollhöfer and Rosman, 2000) and S of 200 ng/m^3 (Annegarn et al., 1983). Fog and dust are both frequent in the Namib Desert. Dust contributes elements such as sulphur and calcium to the chemical composition of fog (Soderberg, 2010) and nutrients can be directly brought into the Namib Desert ecosystem from the ocean by the fog.

Based on studies from other coastal fog ecosystems where deposition of marine aerosols (containing base cations, N and P) influence the ecology of these areas (Dawson, 1998; Nyaga, 2013) it seems possible that nutrients are also an important contribution in the Namib Desert. For example in the west coast of South Africa, evidence of large fluxes of Na, and other base cations, N and P from marine systems to the coastal Strandveld ecosystem was found (Nyaga, 2013) and is therefore possible that, like the Strandveld, nutrients from fog are deposited to the fog zone of the Namib Desert.

1.4. The use of stable isotopes in plant water relations

The use of stable isotopes has become an important tool in investigating and understanding plant water use, different types of water sources, water utilisation processes and the ability to survive in arid environments has become an important tool (Deng et al., 2014; Liu et al., 2007; Yang et al., 2010). Due to the relative stability of evaporative fractionation for plants, the evaporative enrichment is important for determining the original source of desert plant water isotopes (Gat et al., 2007; Külls, 2000). Plant water can be extracted and used to identify the source of xylem water in plants. This is because the water in the xylem (non-photosynthetic part of the plant) does not significantly differ from the source water (White et al., 1985).

Through the use of D and ^{18}O stable isotopes, a few studies found that non-rainfall water (i.e. fog) contributed significantly to the water status of fog ecosystems (e.g. coastal forests in desert zones, fogged forests and mountain areas), sometimes more than rainfall (Corbin et al., 2005; Yang et al., 2010). For example, the use of fog water in the mountainous areas of northern Chile has been shown through the use of D and ^{18}O stable isotopes. Aravena et al., (1989) found that before stable isotope fracture, the isotopic composition of leaves is similar to that of fog under evaporative conditions and came to the conclusion that fog maintained plant growth in this ecosystem (Aravena et al., 1989). Stable isotopes have shown that the trees in this forest use fog water. Fog water is normally enriched in ^{18}O and ^{2}H isotopes in comparison to the source of the water (Dawson, 1998), therefore, stable isotope data with a focus on carbon (C), water (H2O), and nitrogen (N) are recently being used to further understand the relationship between fog and biota (Dawson et al., 2002).

In the Namib Desert, two early studies used tritiated water to demonstrate the ability, in situ, to take up fog water via surficial roots in a common dune grass, *Stipagrostis sabulicola* (Seely and Louw, 1980), and via leaves in a dune shrub, *Trianthema hereroensis* (Seely et al., 1977). Using the available “evapotranspiration lines”, which are a result of isotopic enrichment in the remaining water after evaporation and show the relative fractionation of ^{2}H and ^{18}O in the evaporation process for each species, Soderberg, (2010) confirmed that vegetation including *Arthraerua leubnitziae* (Kuntze) Schinz (Amaranthaceae), *T. hereroensis*, *S. sabulicola* and *Zygophyllum stapffii* use fog water in the Namib Desert. Fog contributed 5-20% to the plant stem (xylem) water of the shrubs in the gravel plains of the central Namib (Soderberg, 2010).

1.3. Study sites and species

The study was carried out in the fog zone of the hyper-arid central Namib Desert at 5 sites (Fig. 1.3) in an array of meteorological stations, and in 45 km transect inland from the coast.

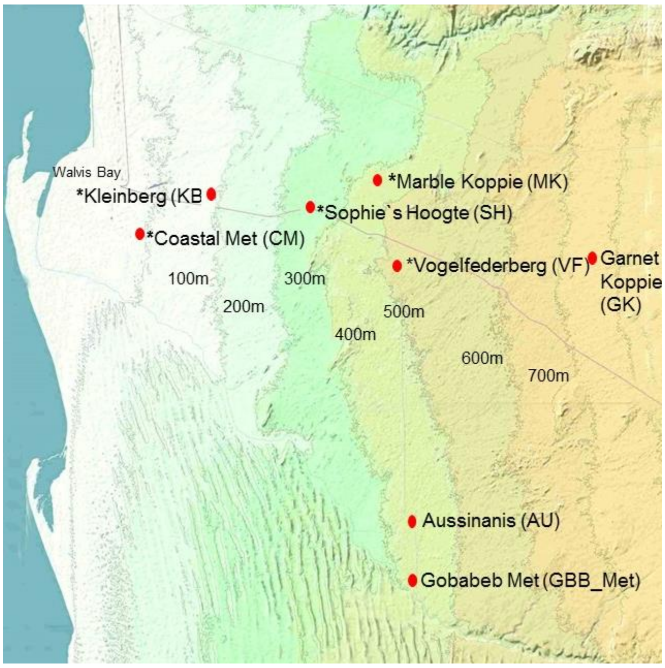


Figure 1.3: Location of the Gobabeb FogNet stations in the central Namib Desert. The different colours indicate elevation contours at 100 m increments. The red points are the locations of the stations. Station names marked with * indicate the five stations used in this study and are located at 15 km (CM), 25 (KB), 40 (SH), 50 (MK) and 60 km (VF) from the coast.

The regional weather patterns are strongly influenced by the cold Benguela current and the subtropical anticyclonic zone along the south-west coast of Africa. The weather of the central Namib Desert ranges from cool, foggy conditions at the coast to warmer and drier conditions inland (Fig.1.4). Situated on the southwestern edge of the summer rainfall zone, the study sites receive most of its rainfall during January and April (Hachfeld and Juergens, 2000; Lancaster et al., 1984). Relative humidity and temperature are higher at the coast and decreases (Fig. 1.4) as one moves inland while the wind is highest at the inland site (Supp Fig. 1.2). The most fog was measured at the inland site. Situated on the southwestern edge of the summer rainfall zone, the study sites receive most of its rainfall during January and April (Hachfeld and Juergens, 2000; Lancaster et al., 1984).

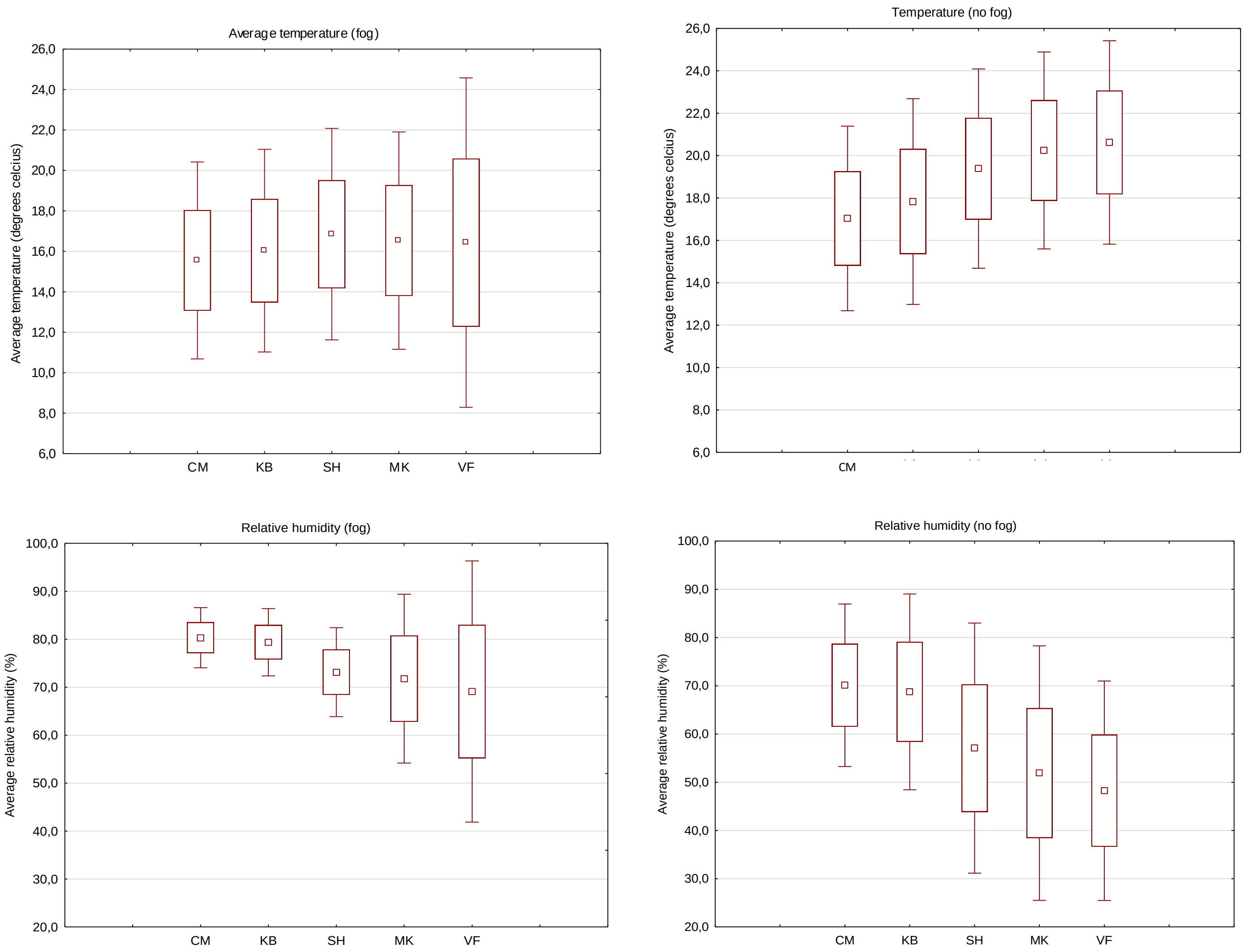


Figure 1.4: Monthly mean temperature and relative humidity at the different stations used in the study as of July 2014 – December 2016. The figures represent hourly mean temperature and relative humidity at the stations during fog events as well as when there was no fog.

The study area is characterised by low species richness and very low plant cover (ranging 3 and 7%) (Moisel and Moll, 1981). *A. leubnitziae*, commonly known as the pencil bush, is the only dwarf shrub growing at some of the study sites (i.e. Coastal Met, Kleinberg and Sophie`s Hoogte). However, other species of plants become more common from *ca.* 40 km from the ocean. A variety of lichens growing on rocks are, however, found at Kleinberg and other endemic species of plants such as *Z. stapffii*, and the non-endemic *C. capitata* are found at Marble Koppie and Vogelfederberg.

The gravel plains of the central Namib rise with ca. 1° inclination from sea level to about 1000 m above sea level (a.s.l) at the foot of the Great Escarpment (Heine and Walter, 1996).The extensive gravel plains of the central Namib Desert are dominated by gravel, gypsum, calcretes and extensive quartz pebble desert pavements (Eckardt et al., 2013). The gypsum is not present in the bedrock and is very likely to have originated from atmospheric deposition (Watson, 1987), whereby sulphur from the ocean that is deposited by fog in the soils that contain carbonate from aeolian input (Heine and Walter, 1996). Soils with gypsum are known to be poor in N and P in many parts of the world (FAO, 1990). In addition to the geology, a number of drainage lines and dry riverbeds (Huntley, 1985), as well as a network of shallow and low volume groundwater channels (Eckardt et al., 2013), occur in the gravel plains. A number of inselbergs, small furrows as well as erosion gullies (which disappear in the sand because of insufficient moisture) occur in the area, contributing to vegetation patterning.

1.3.1. A. leubnitziae

Arthraerua leubnitziae is a low growing, chlorophyllous stemmed (Fig. 1.5) and drought resistant shrub (Dinter, 2008) that traps wind-blown sand to form hummocks around it (van Damme, 1991). It is a xerophyte that is made up of a dense clustering of branches with comparatively short internodes and has inconspicuous, ephemeric leaves (Dinter and Haas, 2008) that lack hydathodes (Henschel and Seely, 2008). Leaves are shed during the early growth stages (Dinter and Haas, 2008), thus making the green stems the only photosynthetic organs of *A. leubnitziae* (Dinter and Haas, 2008). The shoots of *A. leubnitziae* have epicuticular wax (up to 180 mg/cm^2) (Dinter, 2008), with characteristics that showed the presence of polymeric aldehydes. A very dense arrangement of wax crystals (decreasing from the tips of the shoots to basal parts) are observed in the cavities, especially around the stomata (Dinter, 2008; Dinter and Haas, 2008). Stomata are hidden in longitudinal grooves at the base of the shoots in *A. leubnitziae*, therefore, creating a zone of still air and creating a microclimate within the epistomatal space (Dinter, 2008). In some instances, due to water stress, short internodes are formed in the shoots. The shoots and shoot tips occasionally dry out, as result of wind-borne sand particles. (Dinter and Haas, 2008).

The plants are usually < 1 m tall and < 2 m wide (Dinter and Haas, 2008). *A. leubnitziae* have an extensive root system that maintains normal metabolic activity even during periods of water scarcity (Dinter, 2008). Water storage is facilitated in the root cortex of *A. leubnitziae* and a significant amount of the water is needed and for root growth, thus making the above-ground parts of the plants to grow rather slowly (Dinter, 2008). These properties all act synergistically to improve the surface functions and are of importance in preventing water loss under the hostile environmental conditions of the Namib and in maintaining a sufficient water status of these plants (Dinter, 2008; Dinter and Haas, 2008).

A. leubnitziae is restricted to the fog zone of the Namib Desert (Juergens et al., 2013), regularly flowering and fruiting, thus indicating sufficient supply of water to maintain growth and photosynthesis in the hostile environmental conditions of the Namib Desert (Dinter and Haas, 2008; van Damme, 1991). These plants have the ability to actively absorb fog water and transporting this water downwards to the roots (Loris, 2004; Nel, 1995). *A. leubnitziae*, however, depends on rain for germination but fog enables the plant to grow and live for many years between the rainfall pulses (Seely and Henschel, 2001). *A. leubnitziae* was characterised as non-succulent sulphate halophyte due to its strangely high sulphate content, and because of this, the species requires a constant supply of water (Walter, 1973).

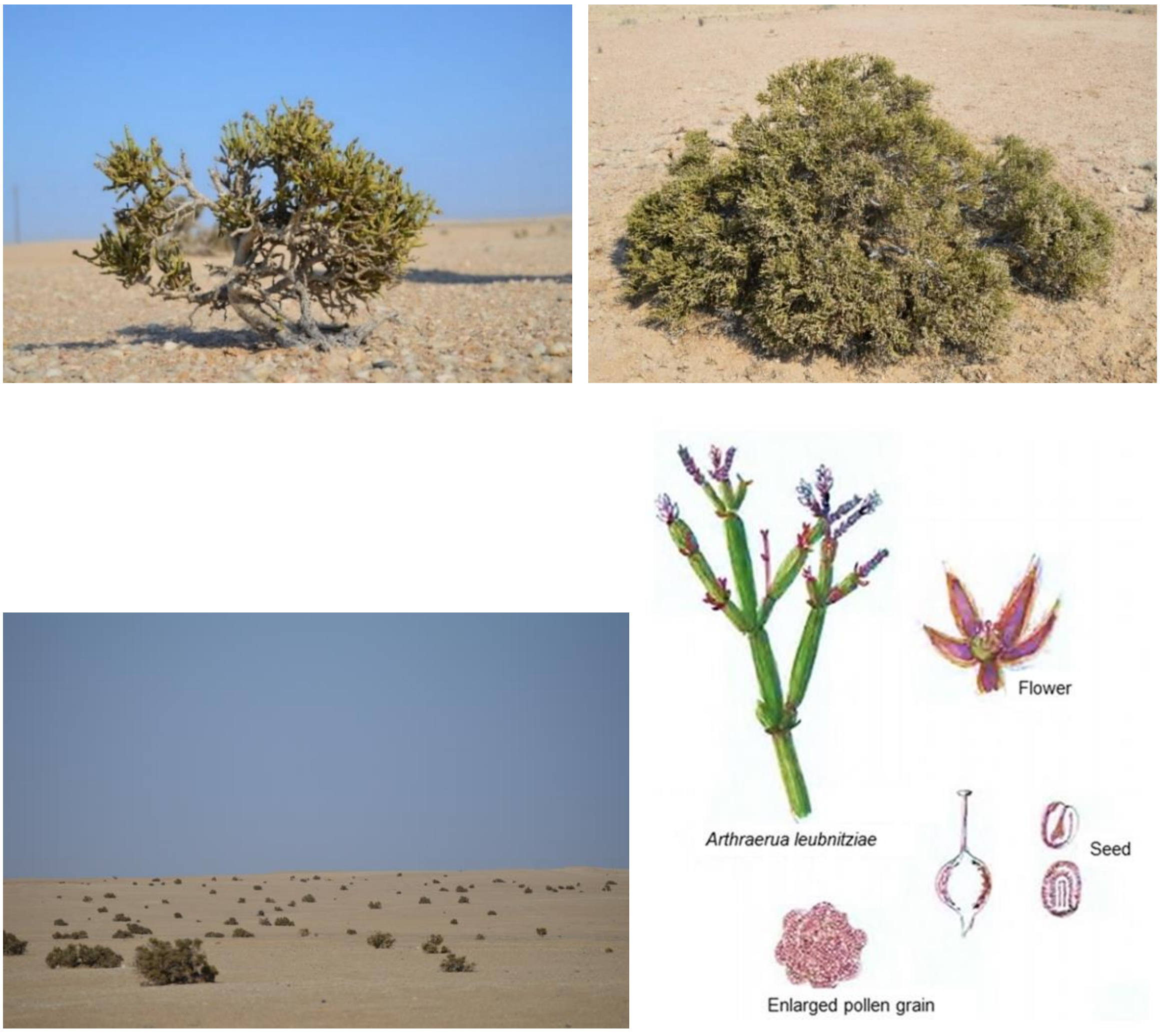


Figure 1.5: Some of the growth forms of *A. leubnitziae* in the Namib Desert, the landscape with *A. leubnitziae* and a drawing of the stem, flower, seed and an enlarged pollen grain of *A. leubnitziae*. Drawing adapted from Nel, 1995.

1.4. Hypotheses

I hypothesise that marine deposition contributes to the moisture and nutritional supply of *A. leubnitziae* in the central Namib Desert, and consequently determines its distribution. To test this hypothesis, the spatial and temporal characteristics of fog within the area were examined. I also examined the climatic and ecological characteristics of the study area. The ecological characteristics were examined in the context that they could be influenced by the climatic characteristics.

To be able to examine these characteristics in detail, 2 sub-hypotheses focusing on different aspects of the major hypotheses were developed and tested independently. The first sub-hypothesis was that fog contributed to the distribution range of *A. leubnitziae* in the central Namib Desert (Chapter 2) and the second was fog deposition has a significant potential to supply moisture and nutrients to *A. leubnitziae* in the central Namib Desert (Chapter 3).

To test the first sub-hypothesis, I measured fog and rain volume, and plant morphological characteristics at the five sites. In addition, a fog map using climatic variables from the "FogNet" sites, a MaxEnt model of the probability of occurrence was created, and the contribution of environmental variables to the occurrence of *A. leubnitziae* was determined. This was done with the prediction that fog contributed to the distribution of *A. leubnitziae* and that plant characteristics of *A. leubnitziae* are correlated to the fog.

And finally, to test the second sub-hypothesis, I measured nutrients deposited in fog water derived from wet and dry deposition (Ca, K, Mg, Na, Cl, Br, NO_3, PO_4 and SO_4^-) and plant essential nutrients in plant and soil samples (N, P, K, Ca, Mg, Mn, Fe, Cu and Zn). I also determined the stem nutrient uptake in *A. leubnitziae* and its ability to hold water. This was done with the prediction that fog contributed to the moisture and nutrients of *A. leubnitziae* in the central Namib Desert.

1.5. Thesis structure

The primary goal of this research was to elucidate whether coastal fog is important in supplying *A. leubnitziae* with moisture, and nutrients and whether this subsequently affects the distribution range of these plants. This thesis is partitioned into four chapters. The first chapter is the general introduction, that sets the scene of the ecological and climatic importance of fog, introduces the study sites and species, and introduces the hypotheses of this the thesis. The second chapter focuses on the contribution of fog to the distribution range and plant characteristics of *A. leubnitziae*. The third chapter focuses on whether fog contributes to the moisture and nutritional supply of *A. leubnitziae* in the central Namib Desert, while the fourth chapter discusses the thesis as a whole and draws linkages between the different components of the thesis.

1.6. References

Annegarn, H.J., Griekent, R.E. V, Bibby, D.M., Von Blotinitz, F., 1983. Background aerosol composition in the Namib Desert, South West Africa (Namibia). Atmos. Environ. 17, 2045–2053.

Aravena, R., Suzuki, O., Pollastri, A., 1989. Coastal fog and its relation to groundwater in the IV region of northern Chile. Chem. Geol. Isot. Geosci. Sect. 79, 83–91. https://doi.org/10.1016/0168-9622(89)90008-0

Azevedo, J., Morgan, D.L., 1974. Fog precipitation in coastal California forests. Ecology 55, 1135–1141.

Baker, A.., Kelly, S.., Biswas, K.., Witt, M., Jickells, T.., 2016. Atmospheric deposition of nutrients to the Atlantic Ocean. Geophys. Res. Lett. 30, 4. https://doi.org/10.1029/

Belnap, J., 2003. The world at your feet: desert soil crusts. Front. Ecol Env. Ecol Env. 1, 181–189.

Bollhöfer, A., Rosman, K.J.R., 2000. Isotopic source signatures for atmospheric lead: The Northern Hemisphere. Geochim. Cosmochim. Acta 64, 3251–3262. https://doi.org/10.1016/S0016-7037(00)00630-X

Boyce, R.L., Friedland, A.., Chamberlain, C.., Poulson, Simon, R., 1996. Direct canopy nitrogen uptake from 15N-labeled wet deposition by mature red spruce. Can. J. For. Res. 26, 1539–1547.

Bruijnzeel, L.A., 1991. Nutrient Input-Output Budgets of Tropical Forest Ecosystems : A Review. J. Trop. Ecol. 7, 1–24.

Bruijnzeel, L.A., Mulligan, M., Scatena, F.N., 2011. Hydrometeorology of tropical montane cloud forests: Emerging patterns, Hydrological Processes. https://doi.org/10.1002/hyp.7974

Burgess, S.S.., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): Foliar uptake and prevention of dehydration. Plant, Cell Environ. 27, 1023–1034. https://doi.org/10.1111/j.1365-3040.2004.01207.x

Byers, H.R., 1953. Coast redwoods and fog drip. Ecology 34, 192–193.

Carbone, M.S., Park Williams, A., Ambrose, A.R., Boot, C.M., Bradley, E.S., Dawson, T.E., Schaeffer, S.M., Schimel, J.P., Still, C.J., 2013. Cloud shading and fog drip influence the metabolism of a coastal pine ecosystem. Glob. Chang. Biol. 19, 484–497. https://doi.org/10.1111/gcb.12054

Cereceda, P., Larrain, H., Osses, P., Farías, M., Egaña, I., 2008. The climate of the coast and fog zone in the Tarapacá Region, Atacama Desert, Chile. Atmos. Res. 87, 301–311. https://doi.org/10.1016/j.atmosres.2007.11.011

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J., Hedin, L.O., 1999. Changing sources of nutrients during four million years of ecosystem development. Nature 397, 491–497.

Chapin III, S.F., Matson, P.A., Mooney, H.A., 2002. The ecosystem concept, in: Principles of Terrestrial Ecosystem Ecology. Springer-Verlag, New York: USA, p. 16.

Corbin, J.D., Thomsen, M.A., Dawson, T.E., D'Antonio, C.M., 2005. Summer water use by California coastal prairie grasses: Fog, drought, and community composition. Oecologia 145, 511–521. https://doi.org/10.1007/s00442-005-0152-y

Dansie, A.P., Wiggs, G.F.S., Thomas, D.S.G., 2017. Iron and nutrient content of wind-erodible sediment in the ephemeral river valleys of Namibia. Geomorphology 290, 335–346. https://doi.org/10.1016/j.geomorph.2017.03.016

Dawson, T., Vidiella, P.E., 1998. Plant-fog interactions in California and Chile, in: Conference on Fog and Fog Water Collection. Vancouver: Canada, pp. 225–228.

Dawson, T.E., 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117, 476–485.

Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., Tu, K.P., 2002. Stable isotopes in plant ecology. Annu. Rev. Ecol. Syst. 33, 507–559. https://doi.org/10.1146/annurev.ecolsys.33.020602.095451

Deng, Y., Kuo, Y.-M., Zhongcheng, J., Qin, X., Jin, Z., 2014. Using stable isotopes to quantify water uptake by Cyclobalanopsis glauca in typical clusters of karst peaks in China. Environ. Earth Sci. 74, 1039–1046. https://doi.org/10.1007/s12665-014-3780-x

Dinter, I., 2008. Untersuchungen zur Mikromorphologie und chemischen Zusammensetzung der Cuticularwachse bei den Gattungen Calicorema, Arthraerua und Leucosphaera (Amaranthaceae) in Namibia Dissertation zur Erlangung des Doktorgrades Fakultät Naturwissenschaften. Universität Hohenheim.

Dinter, I., Haas, K., 2008. Epicuticular wax and anatomical features of Arthraerua leubnitziae (Kuntze) Schinz (Amaranthaceae) related to the ecological conditions in the Namib Desert. Dinteria 30, 1–18.

Ebner, M., Miranda, T., Roth-Nebelsick, A., 2011. Efficient fog harvesting by Stipagrostis sabulicola (Namib dune bushman grass). J. Arid Environ. 75, 524–531. https://doi.org/10.1016/j.jaridenv.2011.01.004

Eckardt, F.D., Livingstone, I., Seely, M., Von Holdt, J., 2013. The surface geology and geomorphology around Gobabeb, Namib desert, Namibia. Geogr. Ann. Ser. A Phys. Geogr. 95, 271–284. https://doi.org/10.1111/geoa.12028

Eckardt, F.D., Soderberg, K., Coop, L.J., Muller, A.A., Vickery, K.J., Grandin, R.D., Jack, C., Kapalanga, T.S., Henschel, J., 2013. The nature of moisture at Gobabeb, in the central Namib Desert. J. Arid Environ. 1–13. https://doi.org/10.1016/j.jaridenv.2012.01.011

Ewing, H.A., Weathers, K.C., Lindsey, A.M., Templer, P.H., Dawson, T.E., Bradbury, D.C., Firestone, M.K., Boukili, V.K.S., 2012. Fog and soil weathering as sources of nutrients in a California Redwood Forest, in: Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers. U.S. Department of Agriculture, Albany, pp. 265–272.

Ewing, H.A., Weathers, K.C., Templer, P.H., Dawson, T.E., Firestone, M.K., Elliott, A.M., Boukili, V.K.S., 2009. Fog water and ecosystem function: Heterogeneity in a California Redwood Forest. Ecosystems 12, 417–433. https://doi.org/10.1007/s10021-009-9232-x

FAO, 1990. Management of Gypsiferous Soils. Rome; Italy.

Filonczuk, M.K., Cayan, D.R., Riddle, L.G., 1995. Variability of marine fog along the California Coast, Science (New York, N.Y.). https://doi.org/10.1126/science.84.2169.83

Fischer, D.T., Still, C.J., Ebert, C.M., Baguskas, S.A., Williams, A.P., 2016. Fog drip maintains dry season ecological function in a California coastal pine forest. Ecosphere 7, 1–21. https://doi.org/10.1002/ecs2.1364

Fu, P.L., Liu, W.J., Fan, Z.X., Cao, K.F., 2016. Is fog an important water source for woody plants in an Asian tropical karst forest during the dry season? Ecohydrology 9, 964–972.

https://doi.org/10.1002/eco.1694

Gat, J.R., Yakir, D., Goodfriend, G., Fritz, P., Trimborn, P., Lipp, J., Gev, I., Adar, E., Waisel, Y., 2007. Stable isotope composition of water in desert plants. Plant Soil 31–45. https://doi.org/10.1007/s11104-007-9321-6

Gundel, L.A., Benner, W.H., Hansen, A.D.A., 1994. Chemical composition of fog water and interstitial aerosol in Berkeley, California. Atmos. Environ. 28, 2715–2725. https://doi.org/10.1016/1352-2310(94)90443-X

Hachfeld, B., Juergens, N., 2000. Climate patterns and their impact on the vegetation in a fog driven desert: The central Namib Desert in Namibia. Phytocoenologia 30, 567–589.

Hansell, D.A., Follows, M.J., 2008. Nitrogen in the Atlantic Ocean, in: Nitrogen in the Marine Environment. pp. 597–630. https://doi.org/10.1016/B978-0-12-372522-6.00013-X

Heine, K., Walter, R., 1996. Gypcretes of the central Namib Desert, Namibia. Regensburg: Germany.

Heine, K., Walter, R., 1996. Gypcrete soils of the central Namib desert (Namibia) and their palaeoclimatological significance, Petermanns Geographische Mitteilungen.

Henschel, J., Mtuleni, V., Gruntkowski, N., Seely, M., Shanyengana, S.E., 1998. NAMFOG: Namibian Application of Fog-Collecting Systems Phase I: Evaluation of Fog Water Harvesting. Windhoek: Namibia.

Henschel, J.R., Seely, M.K., 2008. Ecophysiology of atmospheric moisture in the Namib Desert. Atmos. Res. 87, 362–368. https://doi.org/10.1016/j.atmosres.2007.11.015

Hesse, R., 2012. Spatial distribution of and topographic controls on Tillandsia fog vegetation in coastal southern Peru: Remote sensing and modelling. J. Arid Environ. 78, 33–40. https://doi.org/10.1016/j.jaridenv.2011.11.006

Hildebrandt, A., Al Aufi, M., Amerjeed, M., Shammas, M., Eltahir, E.A.B., 2007. Ecohydrology of a seasonal cloud forest in Dhofar: 1. Field experiment. Water Resour. Res. 43, 1–13. https://doi.org/10.1029/2006WR005261

Huntley, B.J., 1985. The Kuiseb environment : the development of a monitoring baseline.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. Oecologia 141, 254–268. https://doi.org/10.1007/s00442-004-1682-4

Ingraham, N.L., Matthews, R.A., 1995. The importance of fog-drip water to vegetation: Point Reyes Peninsula, California. J. Hydrol. 164, 269–285. https://doi.org/10.1016/0022-1694(94)02538-M

Ingraham, N.L., Matthews, R.A., 1988. Fog drip as a source of groundwater recharge in northern Kenya. Water Resour. Res. 24, 1406–1410. https://doi.org/10.1029/WR024i008p01406

Jacobson, K.M., 1997. Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in an arid grassland. J. Arid Environ. 35, 59–75. https://doi.org/10.1006/jare.1995.0140

Jacobson, K.M., Jacobson, P.J., 1998. Rainfall regulates decomposition of buried cellulose in the Namib Desert. J. Arid Environ. 38, 571–583. https://doi.org/10.1006/jare.1997.0358

Juergens, N., Oldeland, J., Hachfeld, B., Erb, E., Schultz, C., 2013. Ecology and spatial patterns of large-scale vegetation units within the central Namib Desert. J. Arid Environ. 93, 59–79. https://doi.org/10.1016/j.jaridenv.2012.09.009

Kaseke, K.F., Wang, L., Seely, M.K., 2017. Nonrainfall water origins and formation mechanisms. Sci. Adv. 3, 1–8. https://doi.org/10.1126/sciadv.1603131

Külls, C., 2000. Groundwater of the North-Western Kalahari, Namibia: Estimation of Recharge and Quantification of the Flow Systems. Julius-Maximilian University of Würzburg.

Lancaster, J., Lancaster, N., Seely, M.K., 1984. Climate of the central Namib Desert. Madoqua 16, 5–61.

Liu, W.J., Liu, W.Y., Li, P.J., Gao, L., Shen, Y.X., Wang, Y., Zhang, Y.P., Li, H.M., 2007. Using stable isotopes to determine sources of fog drip in a tropical seasonal rain forest of Xishuangbanna, SW China. Agric. For. Meteorol. 143, 80–91. https://doi.org/10.1016/j.agrformet.2006.11.009

Liu, W.J., Ping Zhang, Y., Mei Li, H., Hong Liu, Y., 2005. Fog drip and its relation to groundwater in the tropical seasonal rain forest of Xishuangbanna, Southwest China: A preliminary study. Water Res. 39, 787–794. https://doi.org/10.1016/j.watres.2004.12.002

Loris, K., 2004. Nebel als wasserressource für den strauch Arthraerua leubnitziae, in: Walter, H., Breckle, S.. (Eds.), Ökologie Der Erde: Spezielle Ökologie Der Tropischen Und Subtropischen Zonen. pp. 485–489.

Louw, G.., Seely, M.K., 1982. Ecology of desert ecosystems. Longman, London: United Kingdom.

Mahowald, N.M., Baker, A.R., Bergametti, G., Brooks, N., Duce, R.A., Jickells, T.D., Kubilay, N., Prospero, J.M., Tegen, I., 2005. Atmospheric global dust cycle and iron inputs to the ocean. Global Biogeochem. Cycles 19, 1–15. https://doi.org/10.1029/2004GB002402

Marker, M.M., 1977. Aspects of the geomorphology of the Kuiseb River, South West Africa. Madoqua 10, 199–206.

Martinez-Meza, E., Whitford, W.G., 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. J. Arid Environ. 32, 271–287. https://doi.org/10.1006/jare.1996.0023

McHugh, T.A., Morrissey, E.M., Reed, S.C., Hungate, B.A., Schwartz, E., 2015. Water from air: an overlooked source of moisture in arid and semiarid regions. Sci. Rep. 5, 1–6. https://doi.org/10.1038/srep13767

Moisel, A., Moll, E.., 1981. A Braun-Blanquet survey of the vegetation of the Welwitschia plain. Dinteria 15, 3–11.

Moore, A., Blenkinsop, T., 2006. Scarp retreat versus pinned drainage divide in the formation of the Drakensberg escarpment, southern Africa. South African J. Geol. 109, 599–610. https://doi.org/10.2113/gssajg.109.4.599

Nel, M., 1995. Rare and interesting plants of the Namib Desert. Veld Flora 14–15.

Nicholson, S.E., 2011. Dryland Climatology. Cambridge University Press, New York; USA.

Nyaga, J.M., 2013. Nutrional contribution of atmospheric deposition to the Strandveld vegetation of West Coast South Africa. University of Cape Town.

Oberlander, G.T., 1956. Summer fog precipitation on the San Francisco Peninsula. Ecology 37, 851–852.

Olivier, J., 1995. Spatial distribution of fog in the Namib. J. Arid Environ. 29, 129–138. https://doi.org/10.1016/S0140-1963(05)80084-9

Perry, D.A., Oren, R., Hart, S.C., 2008. Forest ecosystems. The Johns Hopkins University Press, Baltimore: USA.

Pietruszka, R.., Seely, M.., 1985. Predictability of two moisture sources in the Namib Desert. S. Afr. J. Sci. 81, 682–685.

Prospero, J.M., 2002. Environmental characterization of global sources of atmospheric soil dust identified with the NIMBUS 7 Total Ozone Mapping Spectrometer (TOMS) absorbing aerosol product. Rev. Geophys. 40, 1002. https://doi.org/10.1029/2000RG000095

Prospero, J.M., 1981. Eaolian transport to the world ocean, in: Emiliani, C. (Ed.), The Oceanic Lithosphere, The Sea. Wiley Interscience, New York: USA, pp. 801–874.

Roth-Nebelsick, A., Ebner, M., Miranda, T., Gottschalk, V., Voigt, D., Gorb, S., Stegmaier, T., Sarsour, J., Linke, M., Konrad, W., 2012. Leaf surface structures enable the endemic

Namib desert grass Stipagrostis sabulicola to irrigate itself with fog water. J. R. Soc. Interface. https://doi.org/10.1098/rsif.2011.0847

Seely, M.., de Vos, M.., Louw, G.., 1977. Fog imbition, satellite fauna and unusual leaf structure in a Namib Desert dune plant. S. Afr. J. Sci. 73, 169–172.

Seely, M., Henschel, J., 2001. Developing fog harvesting in Namibia, in: Developing Fog Harvesting in Namibia. Desert Research Foundation of Namibia, Windhoek: Namibia, p. 9.

Seely, M.K., 1978. Grassland productivity: the desert end of the curve. S. Afr. J. Sci. 74, 295–297.

Seely, M.K., Henschel, J.R., 1998. The climatology of Namib fog, in: 1st International Conference on Fog and Fog Collection. Vancouver: Canada, pp. 353–356.

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. J. Arid Environ. 3, 25–54.

Soderberg, K., 2010. The role of fog in the ecohydrology and biogeochemistry of the Namib Desert. University of Cape Town.

Swank, W.T., Henderson, G.S., 1976. Atmospheric input of some cations and anions to forest ecosystems in North Carolina and Tennessee. Water Resour. Res. 12, 541–546.

Templer, P.H., Weathers, K.C., Ewing, H.A., Dawson, T.E., Mambelli, S., Lindsey, A.M., Webb, J., Boukili, V.K., Firestone, M.K., 2015. Fog as a source of nitrogen for redwood trees: Evidence from fluxes and stable isotopes. J. Ecol. 103, 1397–1407. https://doi.org/10.1111/1365-2745.12462

van Damme, P., 1991. Plant ecology of the Namib Desert. Afrika Focus 7, 355–400.

van Zinderen Bakker Sr, E.., 1983. The late quaternary history of climate and vegetation in east and southern Africa. Bothalia 14, 369–375.

Viles, H.A., Goudie, A.S., 2013. Weathering in the central Namib Desert, Namibia: Controls, processes and implications. J. Arid Environ. 93, 20–29. https://doi.org/10.1016/j.jaridenv.2011.09.012

Vitousek, P.M., Hedin, L.O., Matson, P.A., Fownes, J.H., Neff, J., 1998. Within-System Element Cycles, Input-Output Budgets, and Nutrient Limitation, in: Successes, Limitations and Frontiers in Ecosystem Science. Springer-Verlag, New York: USA, pp. 432–433.

Vogelmann, H.., 1973. Fog Precipitation in the Cloud Forests of Eastern Mexico. Bioscience 23, 96–100.

Walter, H., 1973. Die Namib-Nebelwüste, in: Die Vegetation Der Erde in Ökophysiologischer Betrachtung. Fischer, Stuttgart: Germany, pp. 501–503.

Washington, R., Todd, M., Middleton, N.J., Goudie, A.S., 2003. Dust-storm source areas determined by the total ozone monitoring spectrometer and surface observations. Ann. Assoc. Am. Geogr. 93, 297–313. https://doi.org/10.1111/1467-8306.9302003

Watson, A., 1987. Desert gypsum crusts as palaeoenvironmental indicators: A micropetrographic study of crusts from southern Tunisia and the central Namib Desert. J. Arid Environ. 15, 19–42.

Watson, I., Lemon, R. &r, 1985. Geomorphology of a Coastal Desert: The Namib, South West Africa/Namibia. J. Coast. Res. 1, 329–342.

Weathers, K., Likens, G.E., 1997. Clouds in Southern Chile: An Important Source of Nitrogen to Nitrogen-Limited Ecosystems? environ. Sci. Technol 31, 210–213.

Weathers, K.C., Lovett, G.M., Likens, G.E., Caraco, N.F.M., 2000. Cloudwater inputs of nitrogen to forest ecosystem in southern Chile: Forms, fluxes, and sources. Ecosystems 5, 590–595. https://doi.org/10.1007/s100210000051

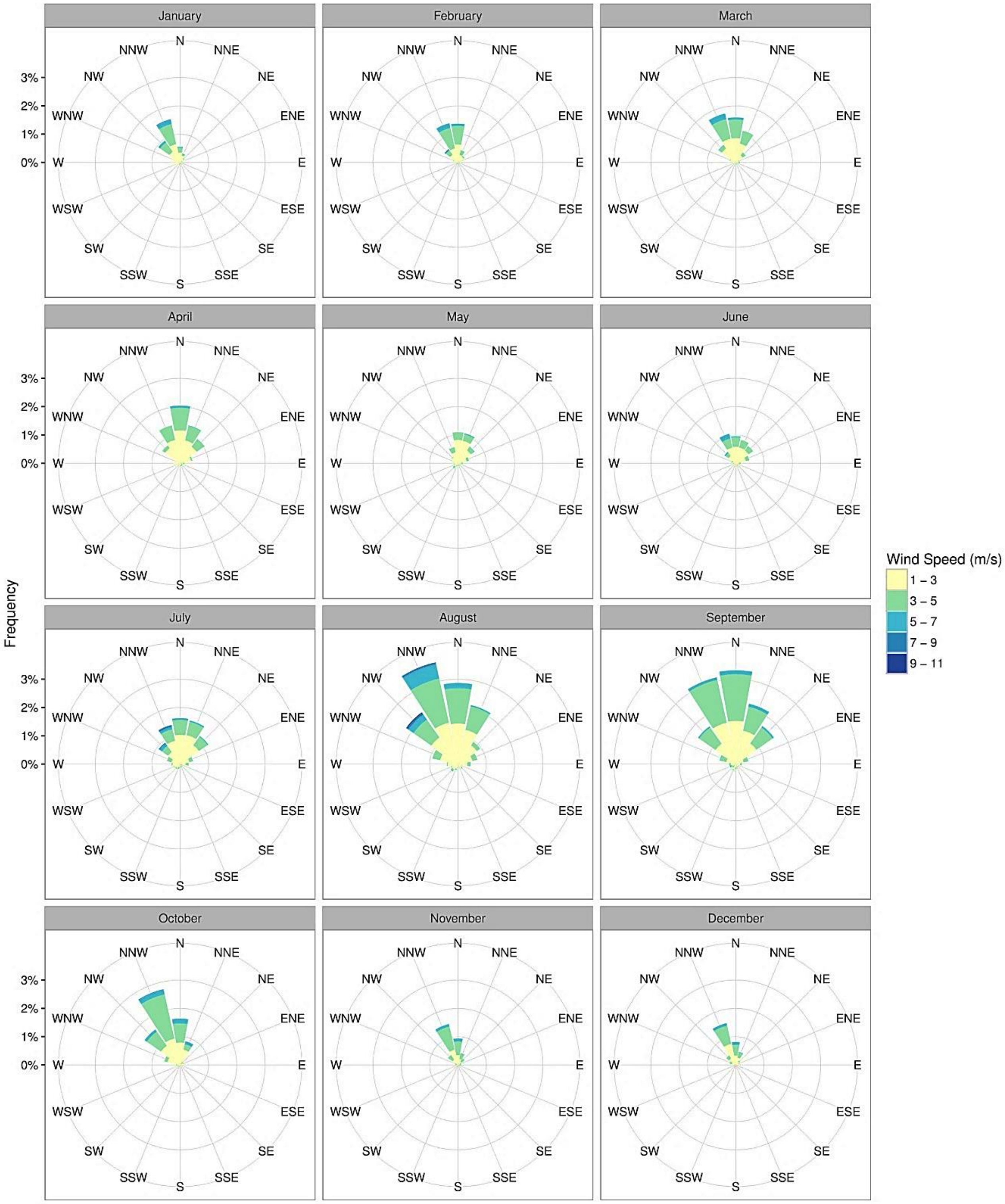
White, F., 1983. The vegetation of Africa: a descriptive memoir to accompany the

UNESCO/AETFAT/UNSO vegetation map of Africa, Natural Resources Research. https://doi.org/10.2307/2260340

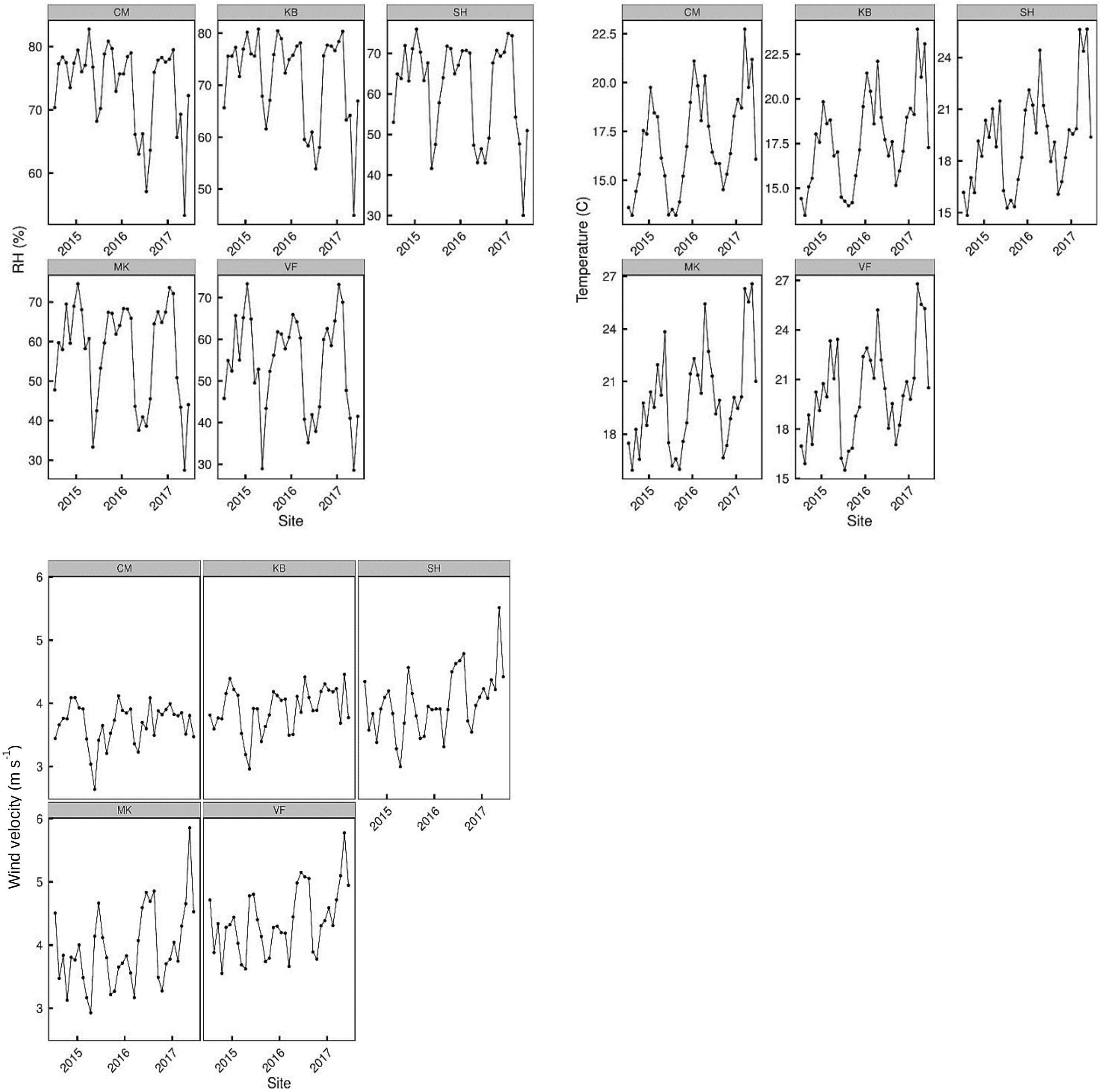
White, J.W.., Cook, E.R., Lawrence, J.R., Broecker, W.S., 1985. The D H ratios of sap in trees: Implications for water sources and tree ring D H ratios. Geochim. Cosmochim. Acta 49, 237–246. https://doi.org/10.1016/0016-7037(85)90207-8

Yang, Q., Xiao, H., Zhao, L., Zhou, M., Li, C., Cao, S., 2010. Stable isotope techniques in plant water sources: a review. Sci. Cold Arid Reg. 2, 112–122.

1.7. Supplementary



Supp Figure 1.1: Dominant wind directions associated with fog events and wind speed during fog events at all stations combined represented as a wind rose.



Supp Figure 1.2: Average monthly temperature, relative humidity (RH) and wind velocity at the five study sites for the period of July 2014 to June 2017. The station names as indicated at the top of each graph are CM (Coastal met), KB (Kleinberg), SH (Sophie`s Hoogte), MK (Marble Koppie) and VF (Vogelfederberg). Data from the five FogNet stations were used in this study.

2. Fog determines the distribution range of *Arthraerua leubnitziae* in the central Namib Desert.

2.1. Introduction

Fog has been recognised as an important determinant of the distribution of vegetation globally (Cavelier and Goldstein, 1989; Fischer et al., 2009; Hesse, 2012; Pinto et al., 2006; Williams et al., 2008). Fog is a major component of climatic conditions in a number of coastal ecosystems (Cereceda et al., 2008) and forms a considerable amount of the total water input in coastal areas with little to no rainfall (Burgess and Dawson, 2004; Dawson and Vidiella, 1998; Myers., 1968). For example, the 'lomas' formations of the Chilean-Peruvian desert (Hesse, 2012; Martorell and Ezcurra, 2002), tropical mountain rainforest types in Ecuador (Ingraham and Matthews, 1995) and the California redwood forest that are associated with the "California fog belt" (Ewing et al., 2009) dependent on the California Current oceanic upwelling zone (Johnstone and Dawson, 2010). The attributes of fog that are important for determining the distribution of vegetation types linked to fog include the frequency, duration and intensity of fog (Hesse, 2012).

Moisture is deposited into fog dependent ecosystems through direct absorption of fog water by leaf surfaces (Limm & Dawson, 2016; Eller et al., 2013; Limm et al., 2009 & Burgess & Dawson, 2004), fog condensate/deposition dripping off leaves onto soil below plants (Baguskas, 2014), and through direct deposition on soil surfaces on (Fig. 1.1). These types of fog deposition may provide a significant portion of the yearly water inputs (Ewing et al., 2009). Direct absorption of fog water has been recognised as the most common mechanism of acquisition of fog water (Burns et al., 2016; Eller et al., 2013 & Burgess and Dawson, 2004) especially for arid ecosystems where other types of precipitation are infrequent (Burgess and Dawson, 2004). In semi-arid montane environments, direct absorption could enable plants to avoid soil water uptake (Tognetti, 2015) and can moderate the negative effects of soil water shortages (Eller et al., 2013). Fog contributed up to 42% of total foliar water content in Brazil (Eller et al., 2013), while canopy drip contributed 66% of the water within the understory plants in coastal California redwood forest (Fischer et al., 2009; Hiatt et al., 2012; Li et al., 2016). In addition to these contributions, fog keeps the top layers of the soil wet and in some areas can provide water in the deeper soil layers for uptake by plant roots (Katata, 2014). However, in some ecosystems, fog is insufficient to directly wet the soil and must be intercepted by vegetation in order to enter the ecosystem (Stanton et al., 2014). For example, in the Namib Desert dune ecosystem, *Trianthema hereroensis,* has been shown to directly absorb water via its leaves by spraying tritiated water onto the leaves (Seely, de Vos, & Louw, 1977).

Apart from fog being a source of moisture, nutrients can also be deposited into ecosystems via fog and may affect nutrient cycling (Carbone et al., 2013). For example, the mineral nutrition of plant communities in Mediterranean coastal regions is influenced by summer fog (Azevedo and Morgan (1974). As fog is deposited onto by vegetation, the nutrients contained in the fog water are absorbed by the plants and may improve plant growth (Fu et al., 2016). The nutrients in fog water can also be available to the plant through root uptake when fog drips onto the soil (Vogelmann et al., 1968). Furthermore, dry aerosols that have previously been trapped on the plants can also be taken up in fog water on leaves (Nyaga et al., 2015) and washed off the leaves into the soil by the fog, providing nutrients that are then also absorbed by the plants through the soil (Fig. 1.1) (Ingraham and Matthews, 1995).

In addition to fog being a source of moisture and nutrients, fog can impact ecological processes by changing environmental properties in an ecosystem. Fog is a result of warm humid air that has been cooled over cold surfaces (e.g. ocean) and condenses. This means that fog is associated with cooler conditions that may also help in improving conditions for vegetation in fog ecosystems by altering important environmental conditions such as humidity and temperature (Supp Fig. 1.2) (Oberlander, 1956). Fog may thus reduce water loss from plants by suppressing daily water stress through shading (Burgess and Dawson, 2004), reducing air and leaf temperatures (Fischer et al., 2009; Rastogi et al., 2016) and improving photosynthetic rates by diffusing incoming radiation (Carbone et al., 2013). Fog deposition is, therefore, important in the providing water and nutrients and ameliorating harsh climatic conditions for vegetation, especially in semi-arid and arid regions (Ewing et al., 2009; Weathers et al., 2000).

The Namib Desert is hyper-arid in terms of total rainfall (< 20 mm year^{-1}), a large proportion of which is received as rainfall pulses that are ecologically important (Southgate et al., 1996). Plant survival between the rainfall pulses may be linked to the more frequent occurrence of fog which provides up to 60% of the moisture in this area (Eckardt et al., 2013; Seely & Henschel, 1998; Pietruszka & Seely, 1985 & Lancaster et al., 1984). The central Namib Desert is highly influenced by the cold Benguela Current of the Atlantic Ocean from where fog originates. Stratus and stratocumulus clouds penetrate up to 100 km inland into the Central Namib Desert from the Atlantic, advecting in moisture (Olivier, 1995; Lancaster et al., 1984). The frequency of occurrence of fog in the desert is known to decline from *ca*. 139 d year^{-1} at the coast to less than 117 d year^{-1} at 60 km from the coast (Supp Table. 2.1). Beyond that, the aridity of the Namib restricts the movement of fog inland (Henschel et al., 1998). The highest precipitation volume is 20–40 km inland, at altitudes of around 350 m above sea level and peaking during the winter months at the coast, and often in the second half of the year further inland (Lancaster et al., 1984). As a result of the coastal location, and as expected in a coastal desert, temperatures range from cool at the coast to hot further inland (Lancaster et al., 1984) and minimum and maximum temperatures do not vary much.

Perennial shrubs including *Arthraerua leubnitziae*, *Zygophyllum stapffii* and *Calicorema capitata* are common on the Namib Desert. Other studies have correlated the distribution of *Z. stapffii* and *A. leubnitziae* with fog occurrence (Hachfeld and Jürgens, 2000; Dinter & Haas, 2008). The use of fog water by the endemic *Trianthema hereroensis* and *Stipagrostis sabulicola* (Roth-Nebelsick et al., 2012; Ebner et al., 2011; Soderberg, 2010 & Louw & Seely, 1980) has also been studied. The distribution of *A. leubnitziae* extends only to 60 km east from the coast and the eastern distribution limit coincides with the transition to extremely low precipitation (Hachfeld 2000, Hachfeld & Jürgens 2000). *A. leubnitziae* germination requires rain events > 20 mm rain in order to germinate (Juergens et al, 2013), but once established, fog is thought to be important for survival (Henschel & Seely, 2008). The restriction of *A. leubnitziae* to the fog zone may indicate a dependence on fog (Hachfeld, 2000) for completion of its lifecycle (Dinter and Haas, 2008). Like other deserts (Rundel and Mahu, 1976), the central Namib Desert vegetation has low species diversity and density. Competitive interactions between vegetation and the little water available in the desert can cause plants to grow in spontaneous spatial arrangements or pattern formations (Borthagaray et al ., 2010). *A. leubnitziae* dominates these plains for the first 40 km from the coast whereas thereafter other species become more important (Juergens et al., 2013). The spatial distribution of *A. leubnitziae* within this region does appear to be regular, possibly suggesting competitive interactions between the individual plants.

In arid areas, water availability is assumed to be the main factor limiting the growth and distribution of plants. In other environments, however, other environmental factors may limit the distribution of plants (Kadmon and Danin, 2017). Fog is more frequent than rainfall in the Namib Desert and this has influenced the distribution of plants. I, therefore hypothesise that fog dictates the distribution of *A. leubnitziae* in the central Namib Desert and predict that the distribution of *A. leubnitziae* is correlated to the occurrence of fog. Another hypothesis being tested is that the plant characteristics of *A. leubnitziae* are correlated to the occurrence of fog within the study site. I predict that the plant characteristics of *A. leubnitziae* and occurrence of fog in the study area are correlated.

2.2. Methods and materials

2.2.1. *Climate data at study sites*

Climatic data from the Gobabeb "FogNet" sites was used in this study (http://www.gobabebtrc.org/index.php/research/atmospheric-sciences-and-meteorology).

The stations were set up in two orthogonal transects, from near the coast to 100 km inland at 1000 m elevation (seven stations) and four from Gobabeb research station northwards at between 400 and 500 m elevation (Fig. 1.3). Only five of the stations were used in this study because they are the only ones where *A. leubnitziae* is present. Fog and other meteorological variables were measured, including rain measured by a Young tipping bucket (Y52203, Young Company, Michigan, USA), air temperature (CS215, Campbell Scientific, Stellenbosch, South Africa), relative humidity (CS215, Campbell Scientific), soil temperature (CS5655, Campbell Scientific), and wind speed and direction (Y05103-5, Young Company) recorded on an hourly basis. Climate data were collected between July 2014 and June 2017.

2.2.2. *Derivation of a fog map*

Climate data acquisition and analysis was performed in the Google Earth Engine (Google Earth Engine Team, 2015) cloud computing platform for geospatial analysis. Air temperature (K), average surface skin temperature (K), potential evaporation rate [W m^{-2}], specific humidity (kg kg s^{-1}), rain precipitation rate (m^{-2} kg s^{-1}), total precipitation rate (m^{-2} kg s^{-1}), transpiration [W m^{-2}] and wind speed (m s^{-1}) were extracted from the Global Land Data Assimilation System (GLDAS) for each sampling point every day from 2010 to 2017. Data were aggregated to a daily minimum, maximum and mean values and these were used as descriptive variables for fog occurrence modelling. GLDAS precipitation, temperature and wind speed were all significantly correlated to SASSCAL station records ($p < 0.001$).

Random forest classification (RF) was used to model the change in fog occurrence (2010-2017) at the stations. RF is a learning algorithm which accommodates nonlinear responses between variables without making assumptions regarding their statistical distributions (Liaw & Wiener, 2002; Breiman, 2001). The fog occurrence RF model was trained using ground-based fog precipitation measurements from ground-based climatic data from the Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL) weather stations (www.sasscalweathernet.org) including Coastal Met, Kleinberg, Sophie's Hoogte, Marble Koppie, Garnet Koppie, Vogelfederberg, Station 8, Aussinanis and Gobabeb (measurements all started in July 2014). The GLDAS climatic variables were used as explanatory inputs in the model (Supp Fig. 2.1 *c.f.* 2.2) and produced a variety of decision trees that predicted a categorical response. The final output is therefore what results from a majority vote of the outputs of a large number of trees. The default RF model parameters were found to yield satisfactory results, and thus we set *ntree* to 500s trees and a *bag fraction* of 0.5 (Liaw & Wiener, 2002; Breiman, 2001). The model produced an overall classification accuracy of 90%, however, the consumer's accuracy (the number of correctly classified fog/no fog occurrences as a percentage of the total number for each category within the training dataset) was 89% for no-fog days and 75% for fog days (Supp. Fig. 2.1).

2.2.3. *Occurrence and environmental data for modelling A. leubnitziae distributions*

Occurrence data of *A. leubnitziae* were obtained from the National Herbarium of Namibia and iSpot produced by the South African National Biodiversity Institute (SANBI). Environmental variables were selected according to their relevance to plant survival and growth. Climate data were obtained from www.worldclim.org (accessed June 2017) at *ca.*1 km^2 resolution. Variables included 19 bioclimatic indicators that represented a range of temperature and precipitation summaries (e.g. trends, seasonality, and extremes). Additionally, normalised difference vegetation index (NDVI) data, which was corrected for molecular scattering, ozone absorption and aerosols, were obtained between 2001 and 2010 for southern Africa from eMODIS TERRA

(US Geological Survey Earth Resources Observation and Science Center). The dataset were averaged to obtain monthly and annual average values at a spatial resolution of 250 m. To calculate landscape slope, aspect and ruggedness index (quantifying the change in elevation within 3x3 pixel grid), elevation data from the 30 m resolution ASTER Global Digital Elevation Model (www.gdem.aster.ersdac.or.jp, accessed June 2017) were used in the *terrain* function in the library “raster” (Hijmans, 2015) in R. Potential evaporation (PET, mm) was obtained from Trabucco and Zomer (2009) and monthly PET subtracted from monthly precipitation to obtain an index of water availability (mm). Distance from the coastline (Natural Earth version 2.0.0., 2014; www.naturalearthdata.com) to the centre of each raster pixel (1 km^2) was estimated using the distance matrix tool in QGIS (Quantum GIS Development Team, 2014). The fog map derived from 2.1.2 was included in the model.

2.2.4. *MaxEnt Modelling*

MaxEnt (3.3.3 k; Phillips et al., 2004) was used to model the distribution of *A. leubnitziae* using the presence data and 10 000 random background points within the region of the plants obtained using the *gBuffer* function in the library “rgeos” (Bivandet al., 2017) in R with a width 0.65°. The modelling was initially with all variables and the function *VariableSelection* from the library “MaxentVariableSelection” (Jueterbock, 2015) was used in R to select the variables that were influential and not subject to collinearity. This optimisation procedure was run with the minimum contribution threshold = 5%, correlation threshold = 0.9 and stepped through a range of regularisation coefficients between 0.5 and 6 at intervals of 0.5. From this procedure, the optimal regularisation and influential predictors were retained. MaxEnt was run from the library “dismo” (Hijmans et al., 2011) implemented in R using a limited set of features (i.e. linear, quadratic, product) and variables with the optimised regularisation coefficients to prevent over fitting. Model development proceeded with 90% of locations, 10% being retained for model testing using the *evaluate* function to calculate the area under curve (AUC) scores. The models were used to produce predictions of *A. leubnitziae* probabilities using the *predict* function with both current and past climate data. Probabilities were compared between predicted distributions by subtracting one probability from another using the “raster” library (Hijmans, 2015) in R. I used the average predicted probability/suitability approach (Liu et al., 2005) to determine the critical likelihood threshold for each modelled result. See Supp Fig. 2.3 for integration of data used in 2.2.1 to 2.2.4.

2.2.5. *Plant morphology*

The morphological characteristics of *A. leubnitziae* were measured at the five study sites. Plant height and canopy size were measured for 100 individuals at each of the sites (Supp Fig. 2.3). Within an area, all individuals were measured. Distances between nearest neighbours were determined using GPS (MAP 62s, Garmin, Johannesburg, South Africa) coordinates taken at each individual plant in the sampling area with the *spDists* function in the library “sp” (Pebesma and Bivand, 2005; Roger et al., 2013) in R. The proportion living matter in the canopies was estimated by visually inspecting the canopy and allocating a percentage to the biomass that is alive for each of the individuals at the five sites. In order to determine the variation in the sizes of the stems of *A. leubnitziae* between the study sites, five replicates of stems were randomly collected from the study sites. The diameter of the stems was measured at five different places (for variation in the stem shape and size) of the five replicates from each of the study site.

2.3. Results

The yearly fog and rain varied considerably among the five sites (Fig. 2.1). The volumes of fog were the largest inland, while the rain volumes were the largest at the coast. The maximum amount of fog (471 mm) was observed at VF, as well as the minimum (15 mm) amount of rainfall. The minimum amount of fog (220 mm) was observed at MK, while the maximum (54 mm) rainfall was observed at CM.

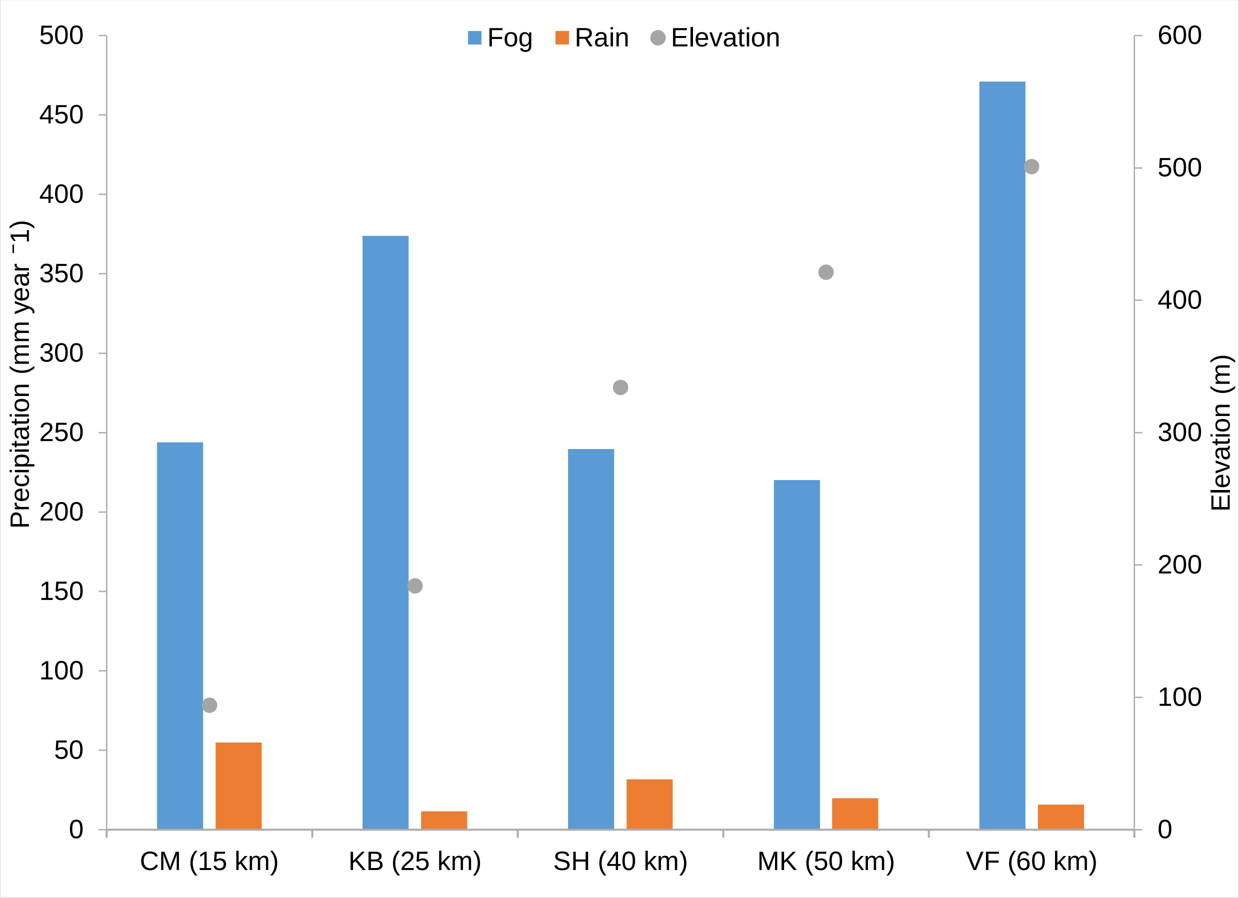


Figure 2.1: Yearly (Sept 2015 to Aug 2016) fog and rainfall at the five stations from the coast inland. The station names indicated on the x-axis are CM (Coastal Met), KB (Kleinberg), SH (Sophie`s Hoogte), MK (Marble Koppie) and VF (Vogelfederberg). The distance from the coast is given in parenthesis and elevation (meters above sea level) increased with distance from the coast as indicated with the grey dots on the y-axis.

Monthly fog and rain for July 2014 to June 2017 emphasised that fog is the main source of moisture across these study sites (Fig. 2.2). The monthly fog and rain measured varied seasonally and temporally. Maximum fog measurement occurred during winter (June-August) at the coastal sites (CM and KB), but SH, MK, VF differed and did not seem to have a pattern as to when the most fog is received. However, fog generally peaked during the second half of the year at the inland sites, VF and MK. Maximum rainfall measurement occurred during March 2015. All the sites, except CM, had a similar trend where rainfall peaked in March. Rainfall events of <10 mm month^{-1} were generally observed at CM, except for March 2017, when rainfall measured was > 90 mm month^{-1}. However, unlike CM, the other stations measured a number of rainfall events that were > 10 mm month^{-1} during the period of measurement.

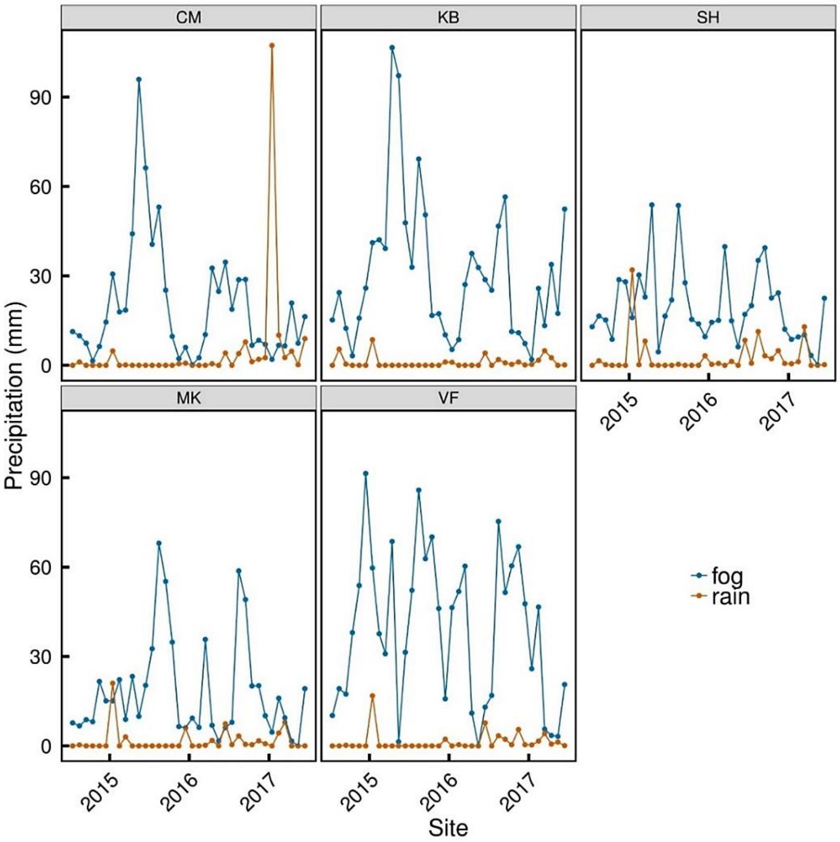


Figure 2.2: Average monthly fog and rain precipitation at the five study sites for the period of July 2014 to June 2017. The station names as indicated at the top of each graph are CM (Coastal met), KB (Kleinberg), SH (Sophie`s Hoogte), MK (Marble Koppie) and VF (Vogelfederberg).

The spatial distribution of fog frequency is restricted to the coastal area of the Namib Desert (Fig. 2.3). The highest frequency of predicted fog days was mainly in the central Namib Desert, adjacent to the coast, but also extended northwards and southwards along the coast in a narrow band. Notably, the main concentration of fog events is where collections of *A. leubnitziae* have been most common.

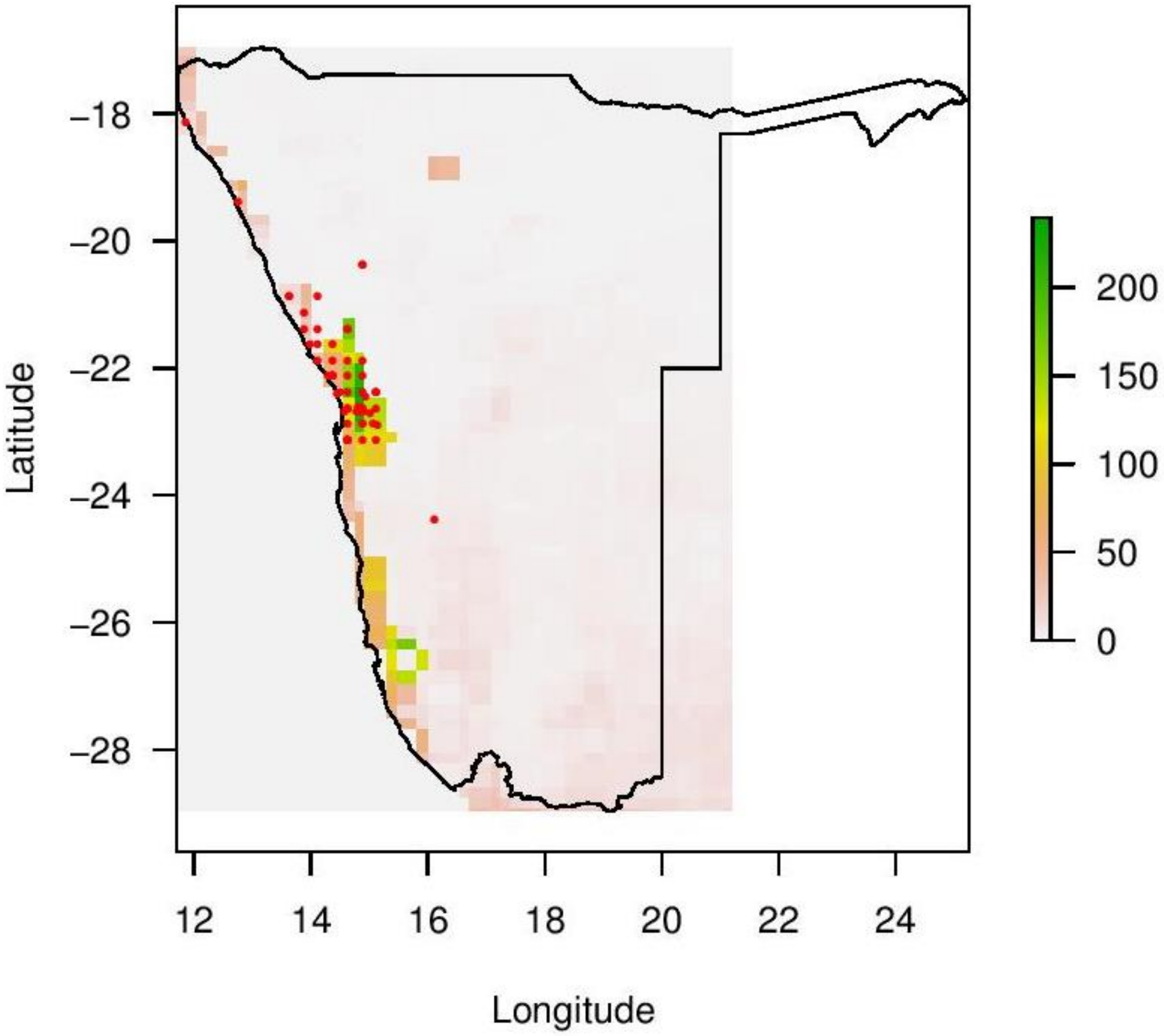


Figure 2.3: Map of yearly fog frequency (days per annum) in the Namib Desert modelled using random forest models, trained using ground-based fog precipitation measurements from SASSCAL weather stations. Cooler colours indicate a higher probability of fog days per annum. The locations of observed *A. leubnitziae* occurrences are shown as red points.

The MaxEnt modelled distribution of *A. leubnitziae* is restricted to the fog zone in the central Namib Desert (Fig. 2.3 *c.f.* Fig. 2.4) probability of occurrence decreasing with distance from the coast. The MaxEnt predictions of the occurrence of *A. leubnitziae* are tightly associated with the actual presence data of *A. leubnitziae.*

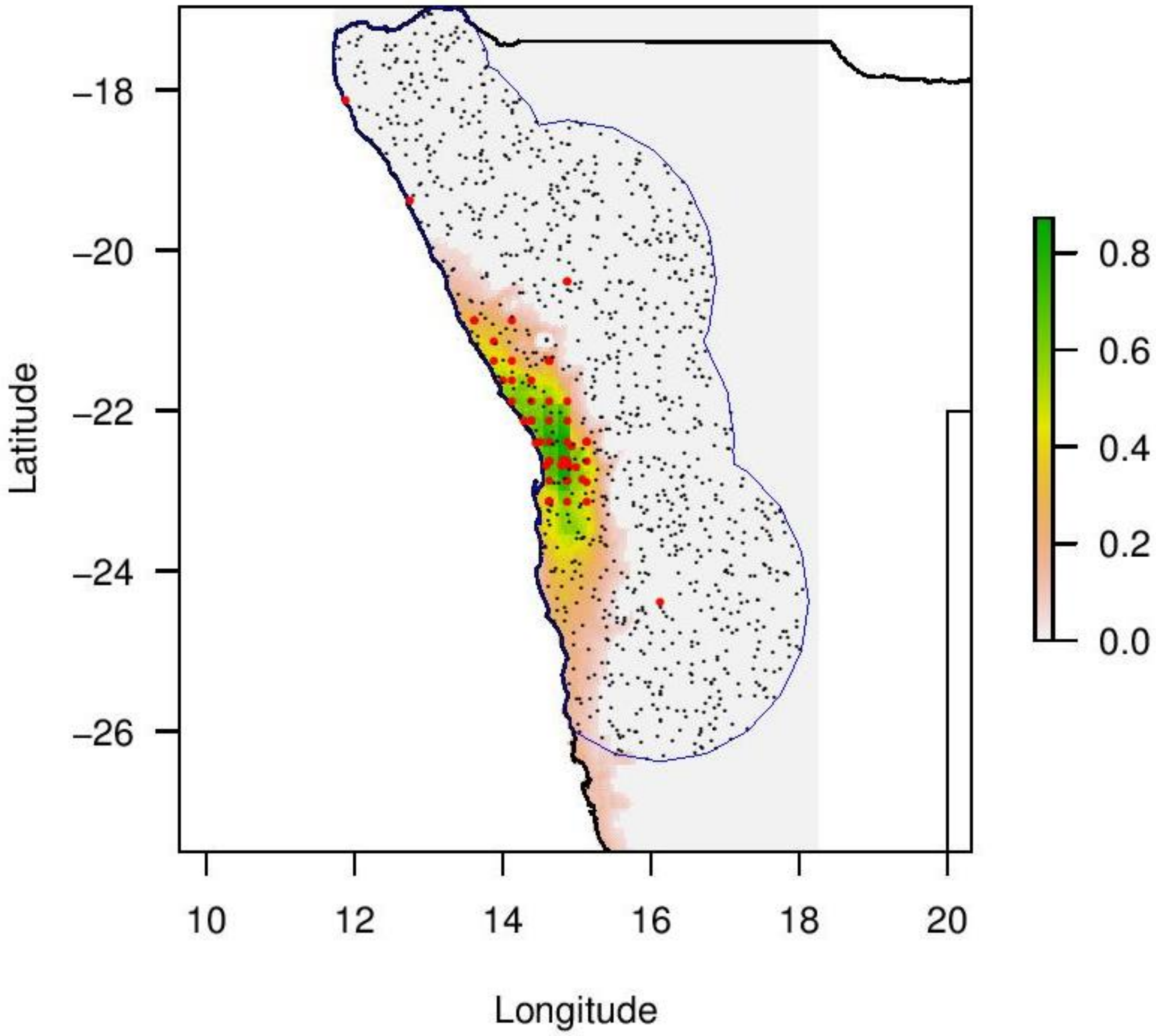


Figure 2.4: MaxEnt analysis was used to model the likelihood of the distribution of *A. leubnitziae* (cooler colours indicate a higher probability of distribution), using only predictors that contributed significantly to the model AUC score. The blue line represents the buffer area around known occurrences in which background points (black points) were randomly distributed. The red dots indicate the unique locations (n = 69) where *A. leubnitziae* was scored as being present.

The evaluation of percentage contribution of each variable to the model illustrated that four main predictors of *A. leubnitziae* occurrence were mean annual precipitation (MAP), fog, isothermality and elevation (Fig. 2.5). Mean annual precipitation was the strongest predictor of the distribution and had a steep decline, indicating that *A. leubnitziae* does not occur in areas with a mean annual rainfall of >200 mm. *A. leubnitziae* is also common (gentle increase of occurrence with fog) in areas with higher fog precipitation and at relatively low elevation (< 1000 m elevation). There was a steep increase in *A. leubnitziae* with an increase in the percentage of isothermality,

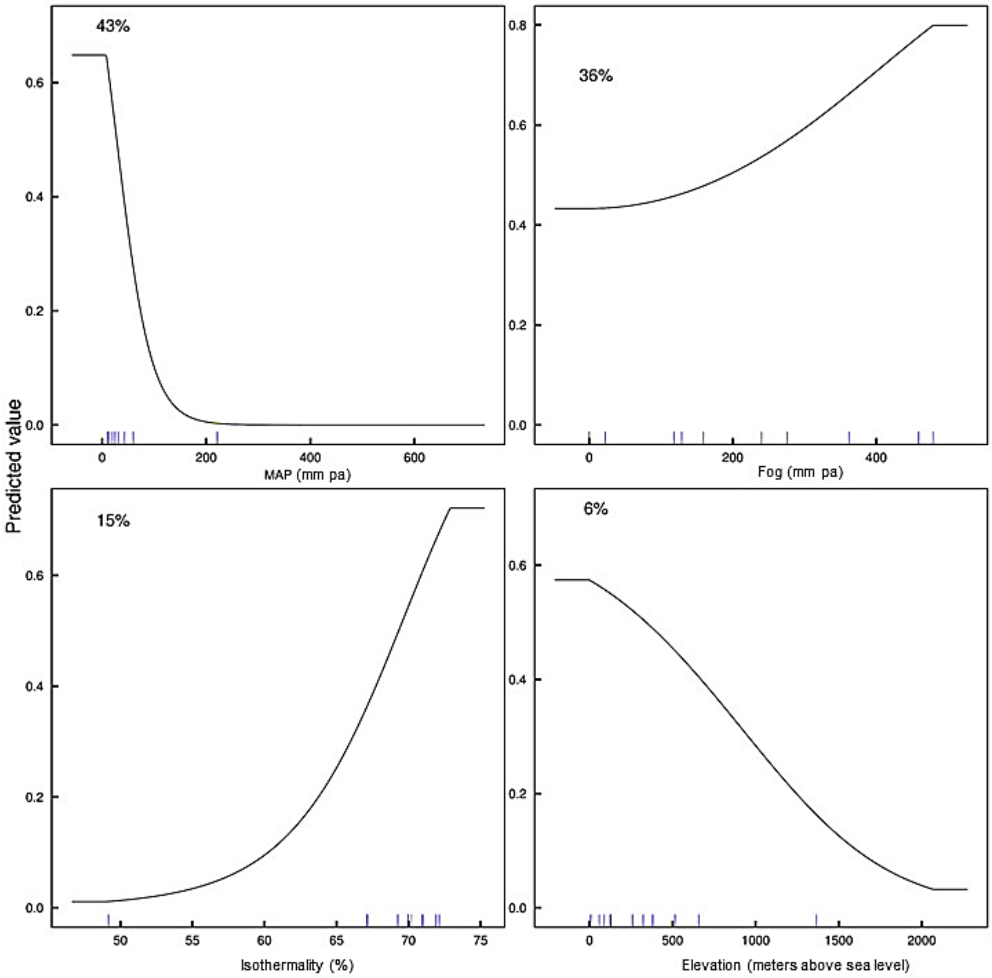


Figure 2.5: The relative influence of predictor variables for the distribution of *A. leubnitziae* in a MaxEnt model. Each variable`s influence on the model is a shown as a proportion of a cumulative 100%. The area under curve (AUC) was 0.92 and showing that the model was accurate and indicates that the model successfully discriminated between the occurrence and absence of *A. leubnitziae*.

The distance between the nearest neighbour, as a measure of spatial distribution, was associated with various climatic variables (Fig. 2.6). The distance between nearest neighbour increased with an increase in RH and air temperature at the first three sites, while it increased with an increase in soil temperature, rain and wind velocities at the first four sites from the coast. There did not seem to be a consistent relationship the distance to the nearest neighbour and the fog and rain volume at the sites.

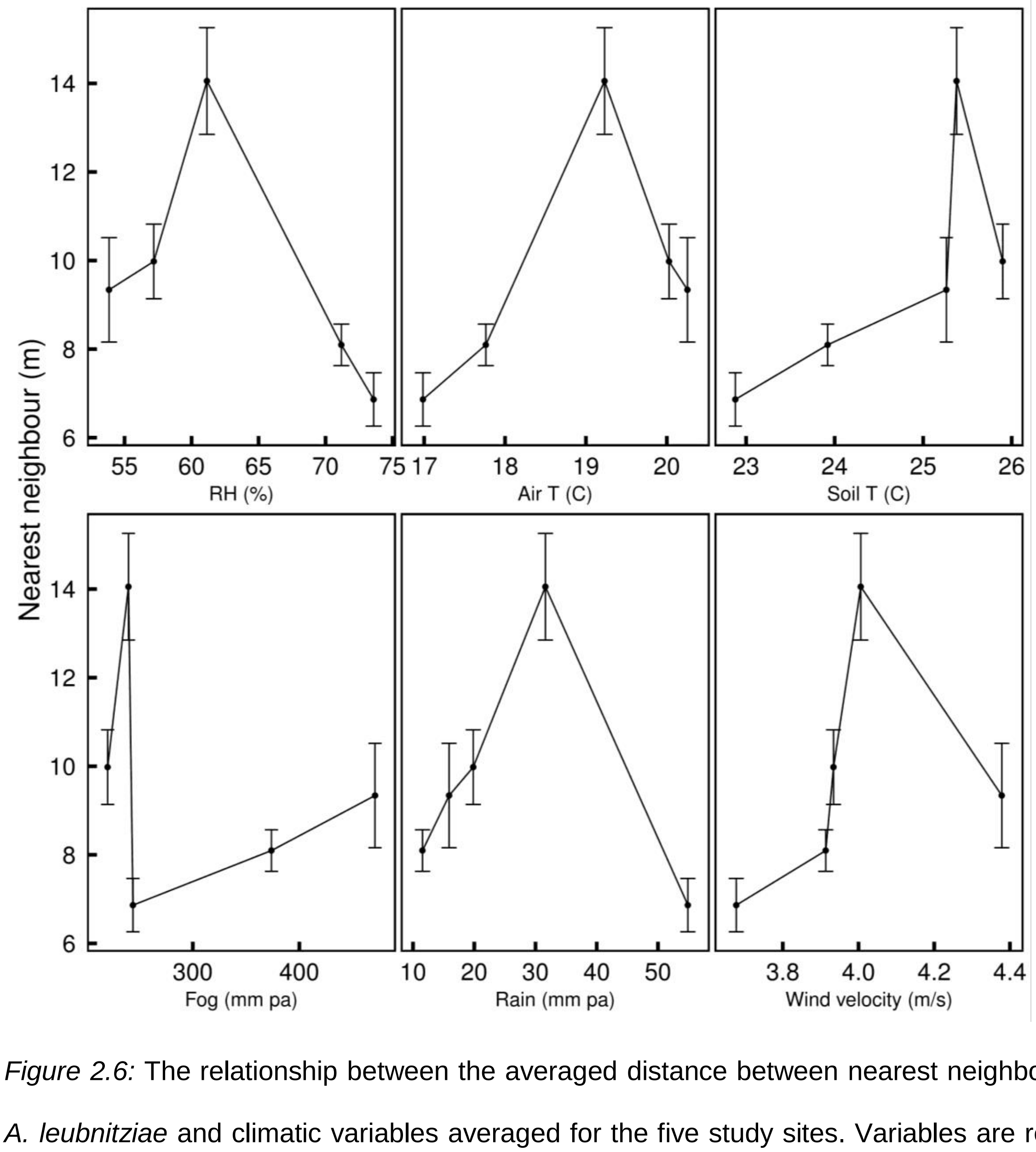


Figure 2.6: The relationship between the averaged distance between nearest neighbours of *A. leubnitziae* and climatic variables averaged for the five study sites. Variables are relative humidity (RH), air temperature, soil temperature, fog, rain and wind velocity. The graph was derived using plant characteristic as described in 2.1.5 and climatic data from the FogNet stations as described in 2.1.1 (Supp Fig. 2.3).

The proportion of living matter on the plants was associated with various climate variables. As RH increased, the proportion of living biomass decreased. In contrast, the proportion of living matter increased with an increase in air temperature and soil temperature. The proportion of living matter was highest at intermediate rainfall amounts and wind velocities. There did not seem to be a consistent relationship between fog volume and the proportion of living matter.

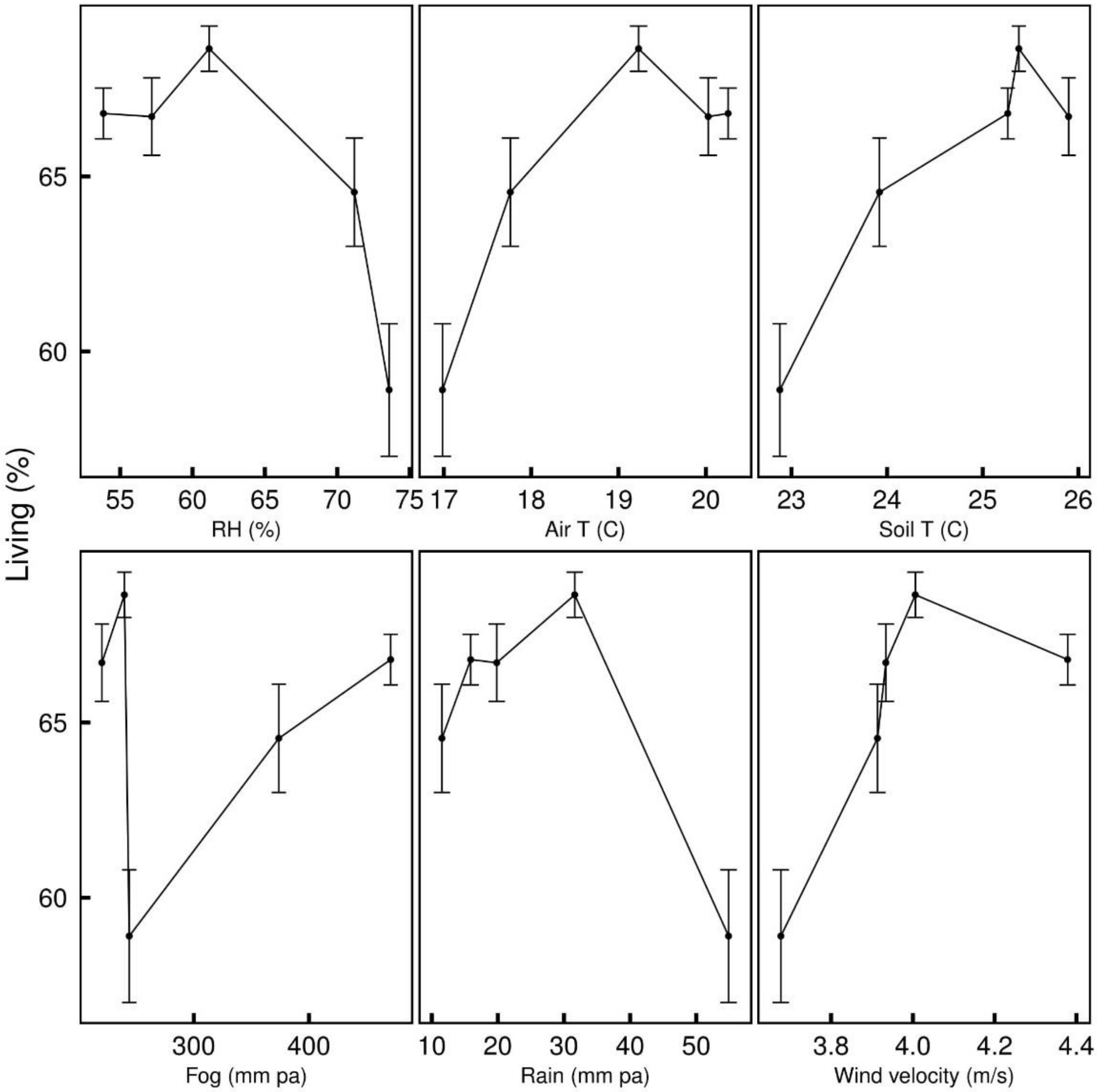


Figure 2.7: The relationship between the percentage living biomass averaged for the five study sites and environmental variables including relative humidity (RH), air temperature, soil temperature, fog and rain. The graph was derived using plant characteristic as described in 2.1.5 and climatic data from the FogNet stations as described in 2.1.1.

The stem diameter of *A. leubnitziae* was associated with various climate variables (Fig. 2.8). Stem diameter increased with an increase in RH and decreased with an increase in air temperature and wind velocities. There did not seem to be a consistent relationship between soil temperature, fog and rain volume and stem diameter.

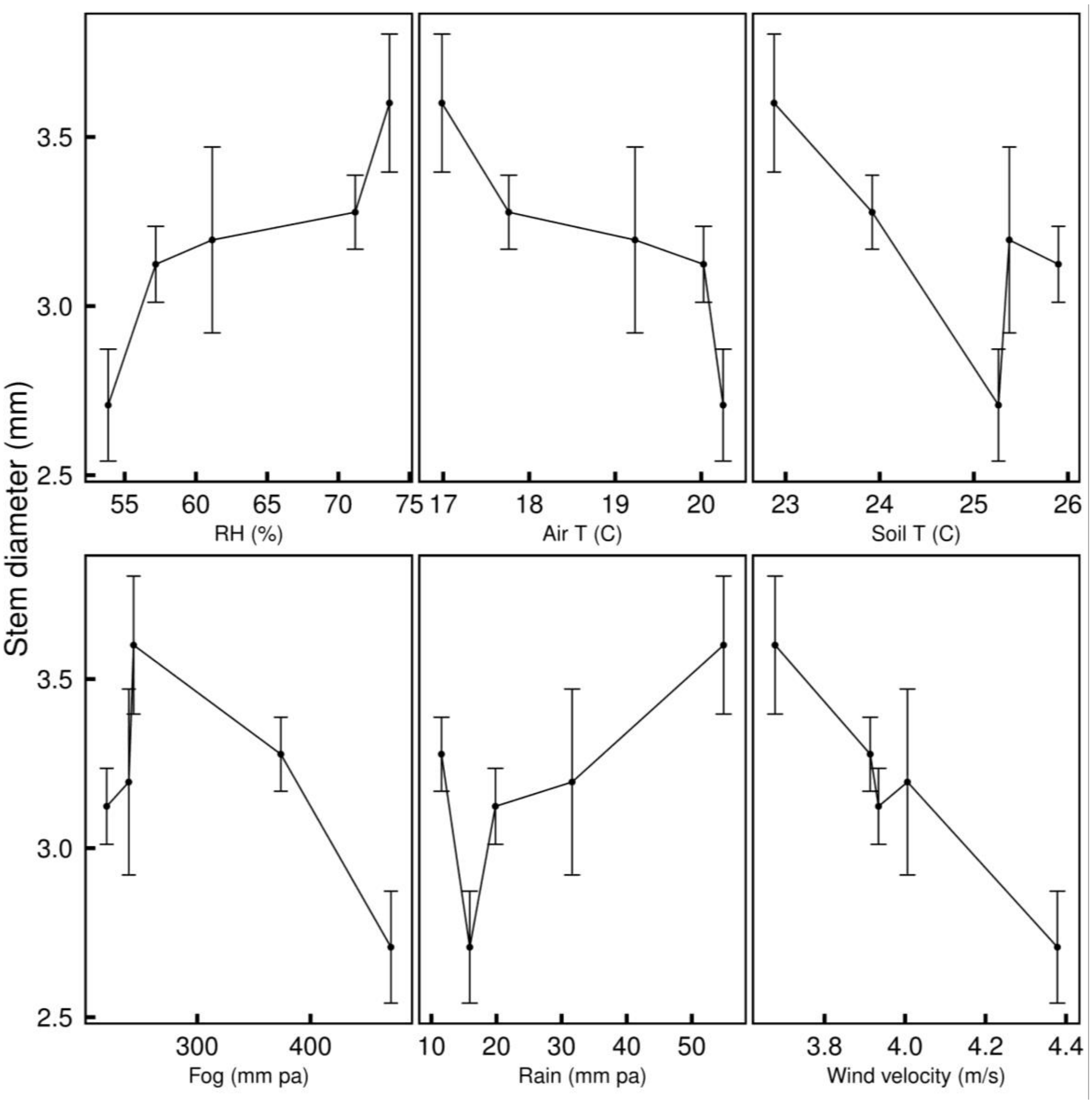


Figure 2.8 The relationship between the stem diameters averaged for the five study sites and environmental variables including relative humidity (RH), air temperature, soil temperature, fog and rain. The graph was derived using plant characteristic as described in 2.1.5 and climatic data from the FogNet stations as described in 2.1.1

2.4. Discussion

The distribution of *A. leubnitziae* is restricted to the fog belt of the Namib Desert, extending only up to 60 km eastward from the coast and only up to 501 m above sea level. The most common occurrence of *A. leubnitziae* overlaps with the highest frequency of fog days per year. This is also the beginning of the eastern minimum rainfall zone (Hachfeld, 2000; Hachfeld and Juergens, 2000), but had the most fog. *A. leubnitziae* is restricted to the gravel plains, is common in the soil type gypsum and the only vascular perennial plant species found on the gravel plains for the first 10-40 km from the coast. The confinement of this species to the fog belt may indicate a relationship between fog contribution to the water economy and distribution of these plants. Fog in the central Namib was observed to occur at some sites on more than 200 days in a year (Fig. 2.3). The occurrence and amount of fog, however, was strongly dependent on the site location and elevation (Fig. 2.1). Due to the condensation of fog at higher altitude, it was higher elevation sites that received more fog than lower elevation sites (Henschel et al., 1998), and this may, therefore, affect how species are distributed in this fog ecosystem.

Fog was the most abundant source of moisture in the region because it occurs throughout the year and contributed up to 92% of the total yearly water balance. The area between 20 and 60 km inland is known to receive the highest fog volume and fog day frequency (Seely and Henschel, 2001). Rainfall, on the other hand, is scarce in the Namib Desert. The MaxEnt model associated the distribution of *A. leubnitziae* with MAP, fog, isothermality and elevation in order of decreasing influence (Fig. 2.5). It is common for rainfall to be the main driver of large-scale distribution patterns plant species (e.g. Bongers et al., 1999; Maharjan et al., 2011) and it is likely these plants rely on MAP exceeding 20 mm for germination (Mary Seely, 2015, personal communication). However, as also concluded by Bongers et al., (1999), assuming that mean annual rainfall alone is the key water factor influencing the distribution of most species is not correct. In the case of *A. leubnitziae*, fog is likely to contribute since the MaxEnt model associated the distribution with fog (Fig. 2.5) and fog dominates the water input in the central Namib Desert. While *A. leubnitziae* may require in excess of 20 mm of rain to germinate, fog may enable the plants to survive for long periods between rainfall pulses and to live for many decades (Seely & Henschel, 2001).

The association of *A. leubnitziae* with fog seasonality is possibly related to its use of fog water. Fog water was found to have contributed 5-20% to the plant stem water of *A. leubnitziae* (Soderberg, 2010). Although the vegetation units of the Namib (Juergens et al., 2013) associate *A. leubnitziae* with the fog belt of the Namib Desert, on a finer scale (Fig. 2.4), the species is more common in parts of the of the fog belt with sufficient moisture, high fog intensity and where fog can frequently get to (Fig. 2.3). Similarly, the distribution and how far inland the *Tillandsia lomas* communities occur in Chile is determined by the intensity of fog, whereby fog decreases from north to south along the coast (Pinto et al., 2006). Vegetation in both areas is therefore distinctly distributed and follows a pattern that is associated with the occurrence of fog (Hesse, 2012; Ingraham and Matthews, 1995; Latorre et al., 2011; Pinto et al., 2006).

Isothermality contributed 15% to the model of the distribution of *A. leubnitziae* and the likelihood of *A. leubnitziae* increased in response to increased isothermality. The marine influence of the Atlantic Ocean on the climate of the Namib Desert buffers this ecosystem from extreme climate fluctuations. The occurrence of *A. leubnitziae* within the fog belt and association with isothermality may suggest that the probability of occurrence of *A. leubnitziae* is linked to buffered temperatures. Similarly, due to the occurrence of fog, the California coast has been buffered from big heat waves and droughts suffered by inland areas (Baguskas, 2014; Hamilton, 2013).

The decrease in the percentage of living biomass with an increase in relative humidity (Fig. 2.7) could be because in some plants, highly saturated air may have damaging impacts in that the growth of plants may be less than at lower humidity and sometimes, the morphology of plants can also be unusual as a result of disturbances in the hormonal balance (Nieman and Poulsen, 1967). There did not seem to be a consistent relationship between fog volume and the distance to the nearest neighbour, percentage living and the stem diameter of *A. leubnitziae*. This may suggest that other variables, other than climatic may affect the spatial patterning and characteristics of *A. leubnitziae*.

A. leubnitziae is one of the few species in the family Amaranthaceae with epicuticular wax (Engel and Barthlott, 1988), is made up of a dense clustering of branches with comparatively short internodes and has inconspicuous, ephemeric leaves (Dinter and Haas, 2008). This is important for the ecological conditions of the Namib Desert and in preventing water loss by acting as an effective barrier and reducing transpiration to a tolerable level (Haas and Schonherr, 1979). A decrease in the stem diameter of *A. leubnitziae* with an increase in temperature and wind velocities could be an adaptation mechanism to offset water loss and to increase the amount of heat that is transported away from the leaf or stem. Adaptation of *A. leubnitziae* to the hostile conditions of the desert may partly compensate the prevailing temperatures, especially further inland where it is warmer than near the coast.

2.5. Conclusion

Fog is a major source of moisture in the Namib Desert and the distribution of *A. leubnitziae* is constrained to the fog zone. Although also found in the northern and southern parts of the Namib Desert, high probability of species occurrence is confined to the central Namib Desert and to where the intensity and occurrence of fog is high. Other plant species in the Namib Desert have evolved in using both rain and fog as a source of moisture (Southgate et al., 1996). Based on this, the possibility of *A. leubnitziae* utilising both fog and rain as sources of moisture is high. The same low stratus clouds producing the fog may, however, reduce water loss by reducing net radiation, increase relative humidity and decrease air temperature. The water, nutrients from fog, and the maritime buffering of coastal ecosystems from extreme climate fluctuations may thus interact in determining and maintaining the stable distribution of *A. leubnitziae.*

2.6. References

Azevedo, J., Morgan, D.L., 1974. Fog precipitation in coastal California forests. Ecology 55, 1135–1141.

Baguskas, S., 2014. Influences of coastal fog on the physiology and distribution of Bishop pine on Santa Cruz Island, California. University of California.

Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K.O., 2017. CRAN - Package rgeos [WWW Document]. https://cran.r-project.org/web/packages/rgeos/index.html. URL https://cran.r-project.org/web/packages/rgeos/index.html

Bongers, F., Poorter, L., Van Rompaey, R.S.A.R., Parren, M.P.E., 1999. Distribution of twelve moist forest canopy tree species in Liberia and Côte d'Ivoire: response curves to a climatic gradient. J. Veg. Sci. 10, 371–382.

Borthagaray, A.I., Fuentes, M.A., Marquet, P.A., 2010. Vegetation pattern formation in a fog-dependent ecosystem. J. Theor. Biol. 265, 18–26. https://doi.org/10.1016/j.jtbi.2010.04.020

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324

Burgess, S.S.., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): Foliar uptake and prevention of dehydration. Plant, Cell Environ. 27, 1023–1034. https://doi.org/10.1111/j.1365-3040.2004.01207.x

Burns, E., Simonin, K.A., Bothman, A.G., Dawson, T.E., Burns, E., Kevin, L., Bothman, A.G., Dawson, T.E., 2016. Foliar water uptake : A common water acquisition strategy for plants of the Redwood. Oecologia 161, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Carbone, M.S., Park Williams, A., Ambrose, A.R., Boot, C.M., Bradley, E.S., Dawson, T.E., Schaeffer, S.M., Schimel, J.P., Still, C.J., 2013. Cloud shading and fog drip influence the metabolism of a coastal pine ecosystem. Glob. Chang. Biol. 19, 484–497. https://doi.org/10.1111/gcb.12054

Cavelier, J., Goldstein, G., 1989. Mist and fog interception in elfin cloud forests in Colombia and Venezuela. J. Trop. Ecol. 5, 309–322. https://doi.org/10.1017/S0266467400003709

Cereceda, P., Larrain, H., Osses, P., Farías, M., Egaña, I., 2008. The climate of the coast and fog zone in the Tarapacá Region, Atacama Desert, Chile. Atmos. Res. 87, 301–311. https://doi.org/10.1016/j.atmosres.2007.11.011

Dawson, T., Vidiella, P.E., 1998. Plant-fog interactions in California and Chile, in: Conference on Fog and Fog Water Collection. Vancouver: Canada, pp. 225–228.

Dinter, I., Haas, K., 2008. Epicuticular wax and anatomical features of Arthraerua leubnitziae (Kuntze) Schinz (Amaranthaceae) related to the ecological conditions in the Namib Desert. Dinteria 30, 1–18.

Ebner, M., Miranda, T., Roth-Nebelsick, A., 2011. Efficient fog harvesting by Stipagrostis sabulicola (Namib dune bushman grass). J. Arid Environ. 75, 524–531. https://doi.org/10.1016/j.jaridenv.2011.01.004

Eckardt, F.D., Soderberg, K., Coop, L.J., Muller, A.A., Vickery, K.J., Grandin, R.D., Jack, C., Kapalanga, T.S., Henschel, J., 2013. The nature of moisture at Gobabeb, in the central Namib Desert. J. Arid Environ. 1–13. https://doi.org/10.1016/j.jaridenv.2012.01.011

Eller, C.B., Lima, A.L., Oliveira, R.S., 2013. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, Drimys brasiliensis (Winteraceae). New Phytol. 199, 151–162. https://doi.org/10.1111/nph.12248

Engel, T., Barthlott, W., 1988. Micromorphology of epicuticular waxes in Centrosperms. Plant Syst. Evol. 161, 71–85. https://doi.org/10.1007/BF00936014

Ewing, H.A., Weathers, K.C., Templer, P.H., Dawson, T.E., Firestone, M.K., Elliott, A.M., Boukili, V.K.S., 2009. Fog water and ecosystem function: Heterogeneity in a California Redwood Forest. Ecosystems 12, 417–433. https://doi.org/10.1007/s10021-009-9232-x

Fischer, D.T., Still, C.J., Williams, A.P., 2009. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. J. Biogeogr. 36, 783–799. https://doi.org/10.1111/j.1365-2699.2008.02025.x

Fu, P.L., Liu, W.J., Fan, Z.X., Cao, K.F., 2016. Is fog an important water source for woody plants in an Asian tropical karst forest during the dry season? Ecohydrology 9, 964–972. https://doi.org/10.1002/eco.1694

Haas, K., Schonherr, J., 1979. Composition of soluble cuticular lipids and water permeability of cuticular membranes from citrus leaves. Planta 146, 399–403.

Hachfeld, B., 2000. Rain, fog and species richness in the Central Namib Desert in the exceptional rainy season of 1999/2000. Dinteria 113–146.

Hachfeld, B., Juergens, N., 2000. Climate patterns and their impact on the vegetation in a fog driven desert: The central Namib Desert in Namibia. Phytocoenologia 30, 567–589.

Hamilton, J., 2013. Fog and redwood: Demystifying the mist. Bay Nat.

Henschel, J., Mtuleni, V., Gruntkowski, N., Seely, M., Shanyengana, S.E., 1998. NAMFOG: Namibian Application of Fog-Collecting Systems Phase I: Evaluation of Fog Water Harvesting. Windhoek: Namibia.

Henschel, J.R., Seely, M.K., 2008. Ecophysiology of atmospheric moisture in the Namib Desert. Atmos. Res. 87, 362–368. https://doi.org/10.1016/j.atmosres.2007.11.015

Hesse, R., 2012. Spatial distribution of and topographic controls on Tillandsia fog vegetation in coastal southern Peru: Remote sensing and modelling. J. Arid Environ. 78, 33–40. https://doi.org/10.1016/j.jaridenv.2011.11.006

Hiatt, C., Fernandez, D., Potter, C., 2012. Measurements of fog water interception by shrubs on the California central coast. J. Coast. Conserv. 2, 525–531. https://doi.org/10.1007/s11852-016-0443-y

Hijmans, R.., 2015. Raster: Geographical data analysis and modeling. R Packag. version 2.4-15. https://doi.org/10.1186/1741

Hijmans, R.J., Phillips, S., Leathwick, J.R., Elith, J., 2011. Package “ dismo .” October 55. https://doi.org/10.1016/j.jhydrol.2011.07.022.

Ingraham, N.L., Matthews, R.A., 1995. The importance of fog-drip water to vegetation: Point Reyes Peninsula, California. J. Hydrol. 164, 269–285. https://doi.org/10.1016/0022-1694(94)02538-M

Johnstone, J.A., Dawson, T.E., 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. Proc. Natl. Acad. Sci. U. S. A. 1–6. https://doi.org/10.1073/pnas.0915062107

Juergens, N., Oldeland, J., Hachfeld, B., Erb, E., Schultz, C., 2013. Ecology and spatial patterns of large-scale vegetation units within the central Namib Desert. J. Arid Environ. 93, 59–79. https://doi.org/10.1016/j.jaridenv.2012.09.009

Jueterbock, A., 2015. `MaxentVariableSelection ’ vignette.

Kadmon, R., Danin, A., 2017. Distribution of plant species in Israel in relation to spatial variation in rainfall. J. Veg. Sci. 10, 421–432.

Katata, G., 2014. Fogwater deposition modeling for terrestrial ecosystems: A review of developments and measurements. J. Geophys. Res. Atmos. 119, 8137–8159. https://doi.org/10.1002/2014JD021669.Received

Lancaster, J., Lancaster, N., Seely, M.K., 1984. Climate of the central Namib Desert. Madoqua 16, 5–61.

Latorre, C., González, A.L., Quade, J., Fariña, J.M., Pinto, R., Marquet, P.A., 2011.

Establishment and formation of fog-dependent Tillandsia landbeckii dunes in the Atacama Desert: Evidence from radiocarbon and stable isotopes. J. Geophys. Res. Biogeosciences 116, 1–12. https://doi.org/10.1029/2010JG001521

Li, B., Wang, L., Kaseke, K.F., Li, L., Seely, M.K., 2016. The impact of rainfall on soil moisture dynamics in a foggy desert. PLoS One 11. https://doi.org/10.1371/journal.pone.0164982

Liaw, A., Wiener, M., 2002. Classification and Regression by randomForest. R news 2/3, 18–22.

Limm, E.B., Dawson, T.E., 2016. Polystichum munitum (Dryopteridaceae) varies geographically in its capacity to absorb fog water by foliar uptake within the redwood forest ecosystem. Am. J. Bot. 97, 1121–1128. https://doi.org/10.3732/ajb.l000081

Louw, G., Seely, M., 1980. Exploitation of fog water by a perennial Namib Dune grass, Stipagrotis sabulicola. S. Afr. J. Sci. 76, 38–39.

Maharjan, S.K., Poorter, L., Holmgren, M., Bongers, F., Wieringa, J.J., Hawthorne, W.D., 2011. Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. Biotropica 43, 552–561. https://doi.org/10.1111/j.1744-7429.2010.00747.x

Martorell, C., Ezcurra, E., 2002. Rosette scrub occurrence and fog availability in arid mountains of Mexico. J. Veg. Sci. 13, 651–662. https://doi.org/10.1658/1100-9233(2002)013[0651:RSOAFA]2.0.CO;2

Myers., J.N., 1968. Fog. Sci. Am. 76–83.

Nieman, R.., Poulsen, L.., 1967. Effects of salinity and atmospheric interactive humidity on the growth of bean and cotton plants. Bot. Gaz. 128, 69–73.

Nyaga, J.M., Neff, J.C., Cramer, M.D., 2015. The contribution of occult precipitation to nutrient deposition on the West Coast of South Africa. PLoS One 10, 1–21.

https://doi.org/10.1371/journal.pone.0126225

Oberlander, G.T., 1956. Summer fog precipitation on the San Francisco Peninsula. Ecology 37, 851–852.

Olivier, J., 1995. Spatial distribution of fog in the Namib. J. Arid Environ. 29, 129–138. https://doi.org/10.1016/S0140-1963(05)80084-9

Pebesma, E.., Bivand, R.., 2005. Classes and methods for spatial data in R, News 5(2).

Phillips, S.J., Dudík, M., Schapire, R.E., 2004. A maximum entropy approach to species distribution modeling, in: Twenty-First International Conference on Machine Learning. p. 83. https://doi.org/10.1145/1015330.1015412

Pietruszka, R.., Seely, M.., 1985. Predictability of two moisture sources in the Namib Desert. S. Afr. J. Sci. 81, 682–685.

Pinto, R., Barrı, I., Marquet, P.A., 2006. Geographical distribution of Tillandsia lomas in the Atacama Desert, northern Chile. J. Arid Environ. 65, 543–552.

Rastogi, B., Williams, A.P., Fischer, D.T., Iacobellis, S.F., McEachern, K., Carvalho, L., Jones, C., Baguskas, S.A., Still, C.J., 2016. Spatial and temporal patterns of cloud cover and fog inundation in coastal California: Ecological implications. Earth Interact. 20, 1–19. https://doi.org/10.1175/EI-D-15-0033.1

Roger, S., Bivand, R., Pebesma, E., Gómez-Rubio, V., 2013. Applied spatial data analysis with R, Second edi. ed, Springer. Springer New York, New York: USA.

Roth-Nebelsick, A., Ebner, M., Miranda, T., Gottschalk, V., Voigt, D., Gorb, S., Stegmaier, T., Sarsour, J., Linke, M., Konrad, W., 2012. Leaf surface structures enable the endemic Namib desert grass Stipagrostis sabulicola to irrigate itself with fog water. J. R. Soc. Interface. https://doi.org/10.1098/rsif.2011.0847

Rundel, P.W., Mahu, M., 1976. Community structure and diversity in a coastal fog Desert in

Northern Chile. Flora 165, 493–505. https://doi.org/10.1016/S0367-2530(17)31888-1

Seely, M.., de Vos, M.., Louw, G.., 1977. Fog imbition, satellite fauna and unusual leaf structure in a Namib Desert dune plant. S. Afr. J. Sci. 73, 169–172.

Seely, M., Henschel, J., 2001. Developing fog harvesting in Namibia, in: Developing Fog Harvesting in Namibia. Desert Research Foundation of Namibia, Windhoek: Namibia, p. 9.

Seely, M.K., Henschel, J.R., 1998. The climatology of Namib fog, in: 1st International Conference on Fog and Fog Collection. Vancouver: Canada, pp. 353–356.

Soderberg, K., 2010. The role of fog in the ecohydrology and biogeochemistry of the Namib Desert. University of Cape Town.

Southgate, R.I., Masters, P., Seely, M.K., 1996. Precipitation and biomass changes in the Namib Desert dune ecosystem. J. Arid Environ. 33, 267–280. https://doi.org/10.1006/jare.1996.0064

Stanton, D.E., Armesto, J.J., Hedin, L.O., 2014. Ecosystem properties self-organize in response to a directional fog-vegetation interaction. Ecology 95, 1203–1212. https://doi.org/10.1890/13-0608.1

Tognetti, R., 2015. Trees harvesting the clouds: Fog nets threatened by climate change. Tree Physiol. 35, 921–924. https://doi.org/10.1093/treephys/tpv086

Trabucco, A., Zomer, R.., 2009. Global aridity index (glo-bal-aridity) and global potential evapo- transpiration (Glo-bal-PET) geospatial database [WWW Document]. CGIAR Consort. Spat. Information. URL www.csi.cgiar.org.

Vogelmann, H.., Siccama, T., Leedy, D., Ovitt, D., 1968. Precipitation from Fog Moisture in the Green Mountains of Vermont. Ecology 49, 1205–1207.

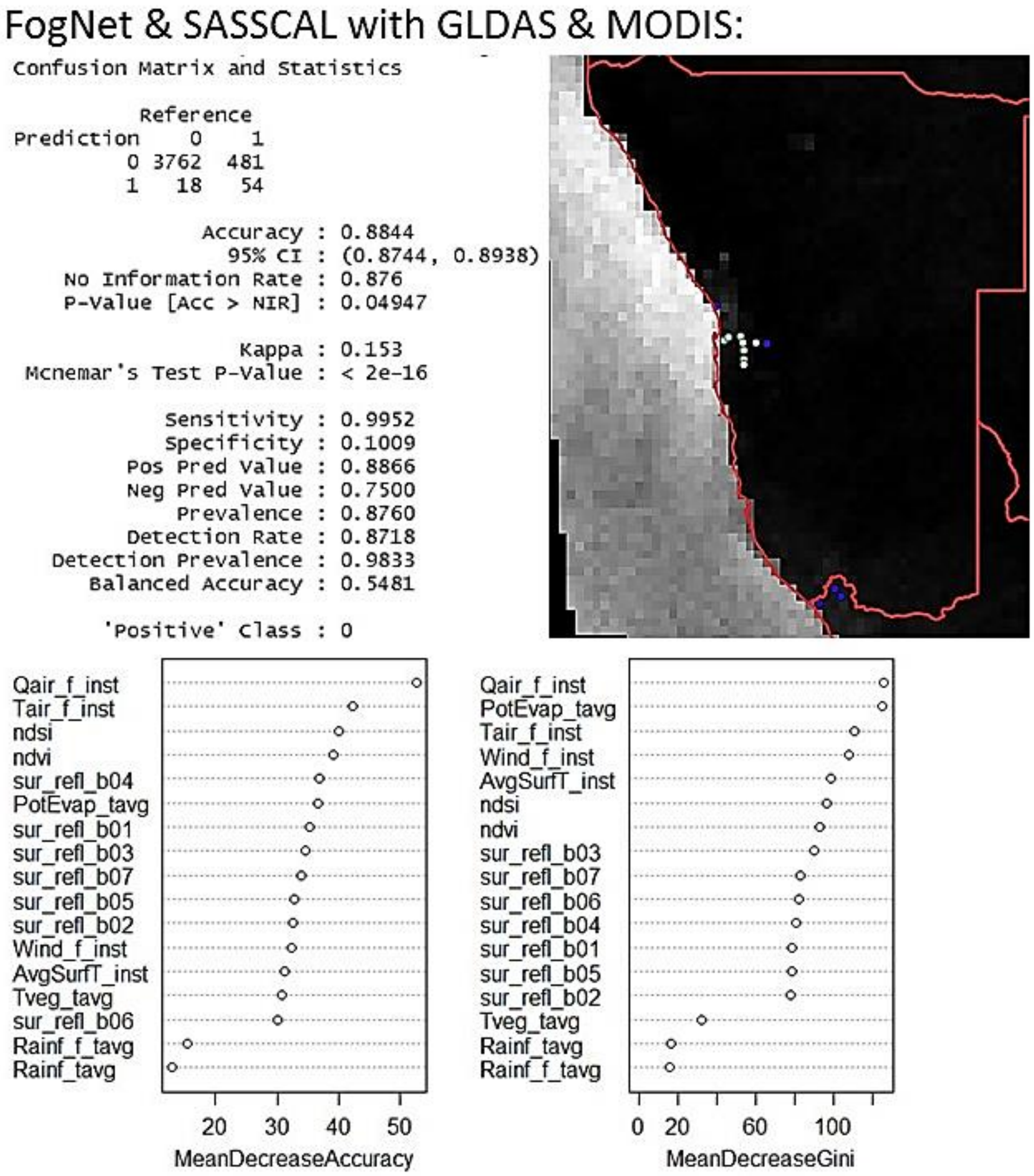
Weathers, K.C., Lovett, G.M., Likens, G.E., Caraco, N.F.M., 2000. Cloudwater inputs of nitrogen to forest ecosystem in southern Chile: Forms, fluxes, and sources. Ecosystems 5, 590–595. https://doi.org/10.1007/s100210000051

Williams, A.P., Still, C.J., Fischer, D.T., Leavitt, S.W., 2008. The influence of summertime fog and overcast clouds on the growth of a coastal Californian pine: A tree-ring study. Oecologia 156, 601–611. https://doi.org/10.1007/s00442-008-1025-y

2.7. Supplementary

Supp Table 2.1: Monthly mean number of days with fog during 2015.

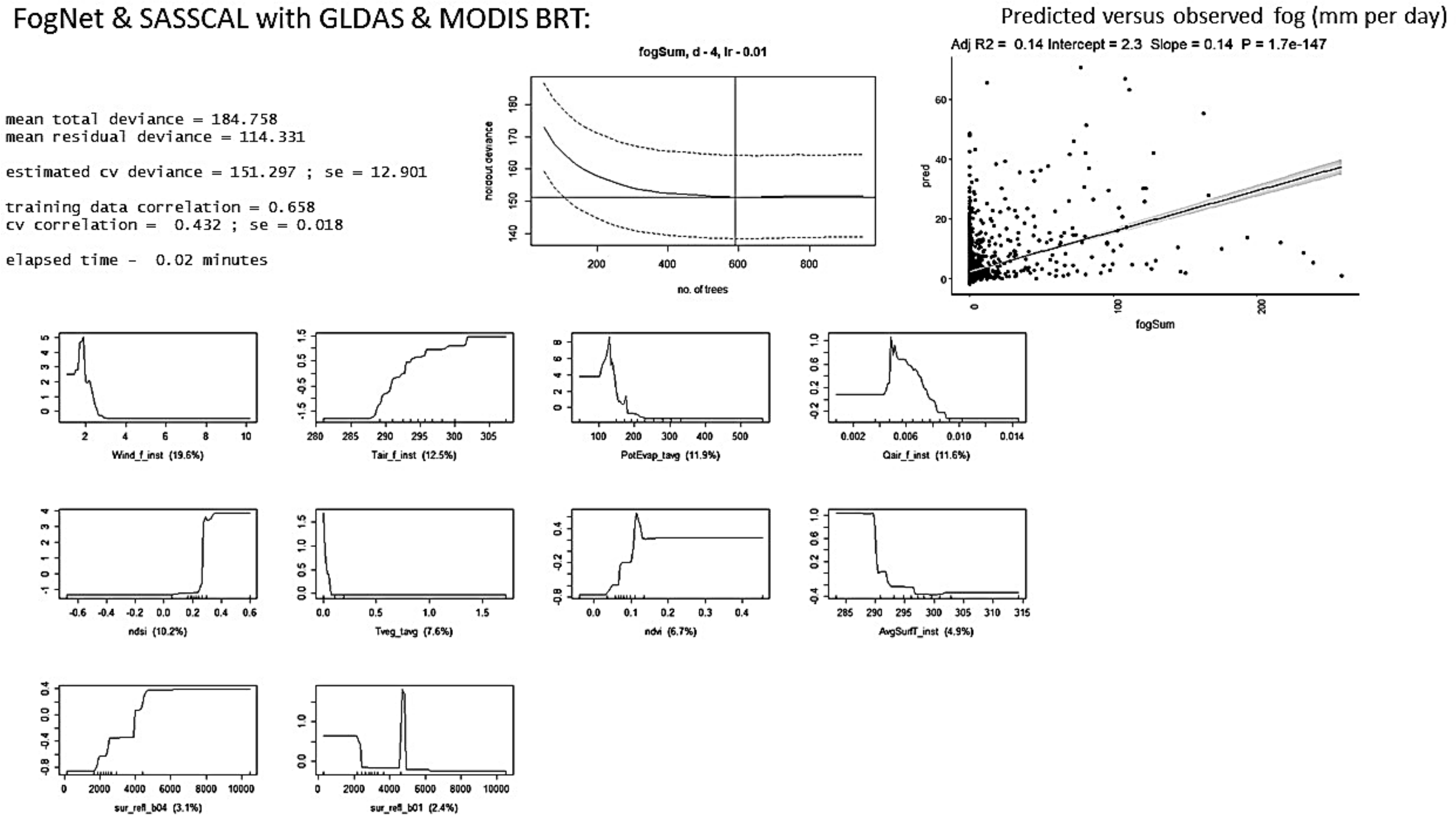
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Sum
CM	6	8	9	17	20	13	11	19	12	10	8	6	139
KB	15	11	6	14	16	14	11	11	9	4	9	8	128
SH	8	10	8	19	3	5	8	18	15	10	6	6	116
MK	9	10	5	10	1	5	7	15	15	14	5	5	101
VF	15	11	8	7	1	5	10	12	15	15	12	6	117



FogNet & SASSCAL with GLDAS & MODIS:

```
Confusion Matrix and Statistics

          Reference
Prediction    0    1
         0 3762  481
         1   18   54

               Accuracy : 0.8844
                 95% CI : (0.8744, 0.8938)
    No Information Rate : 0.876
    P-Value [Acc > NIR] : 0.04947

                  Kappa : 0.153
 Mcnemar's Test P-Value : < 2e-16

            Sensitivity : 0.9952
            Specificity : 0.1009
         Pos Pred Value : 0.8866
         Neg Pred Value : 0.7500
             Prevalence : 0.8760
         Detection Rate : 0.8718
   Detection Prevalence : 0.9833
      Balanced Accuracy : 0.5481

       'Positive' Class : 0
```

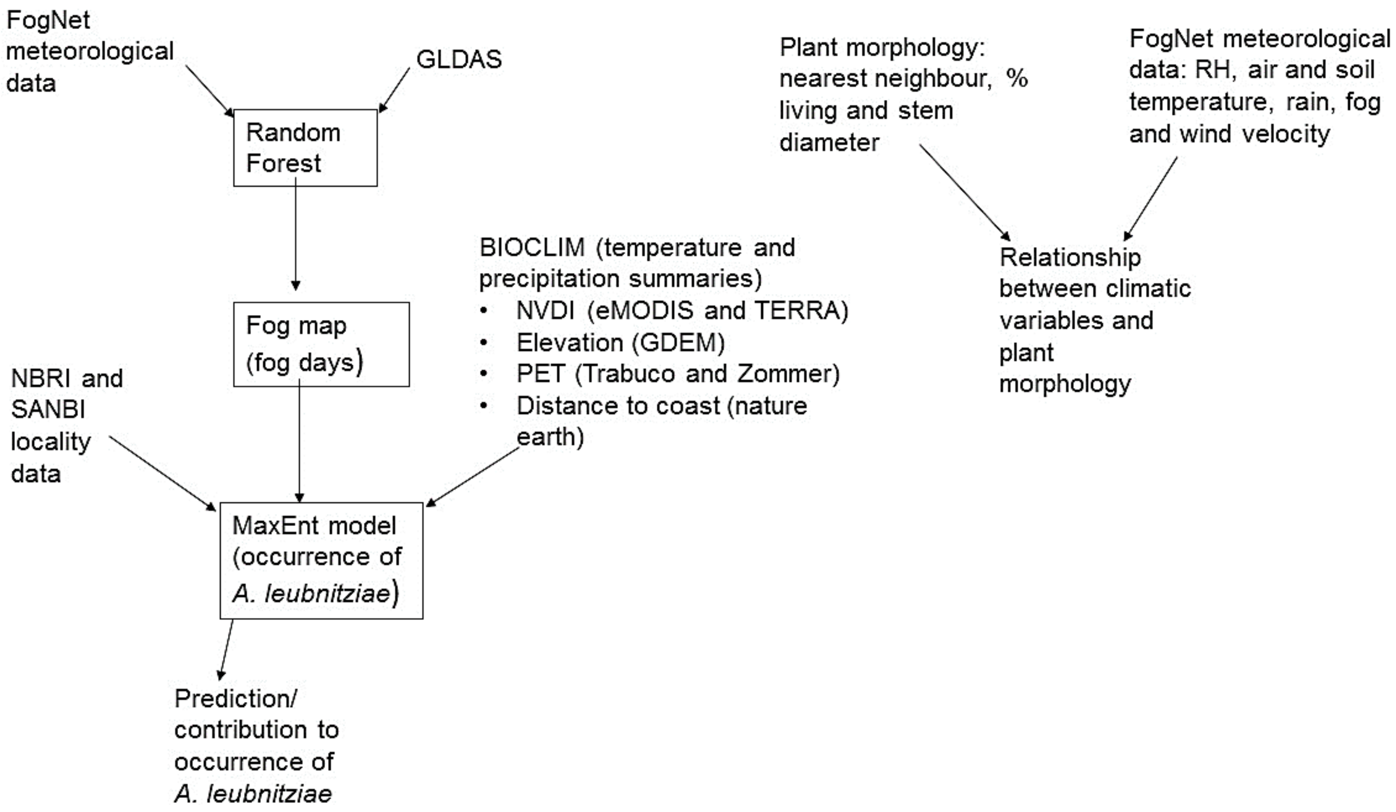
Supp Figure 2.3: Results of the final Random Forest model, whereby the strongest model included climate variables from GLDAS



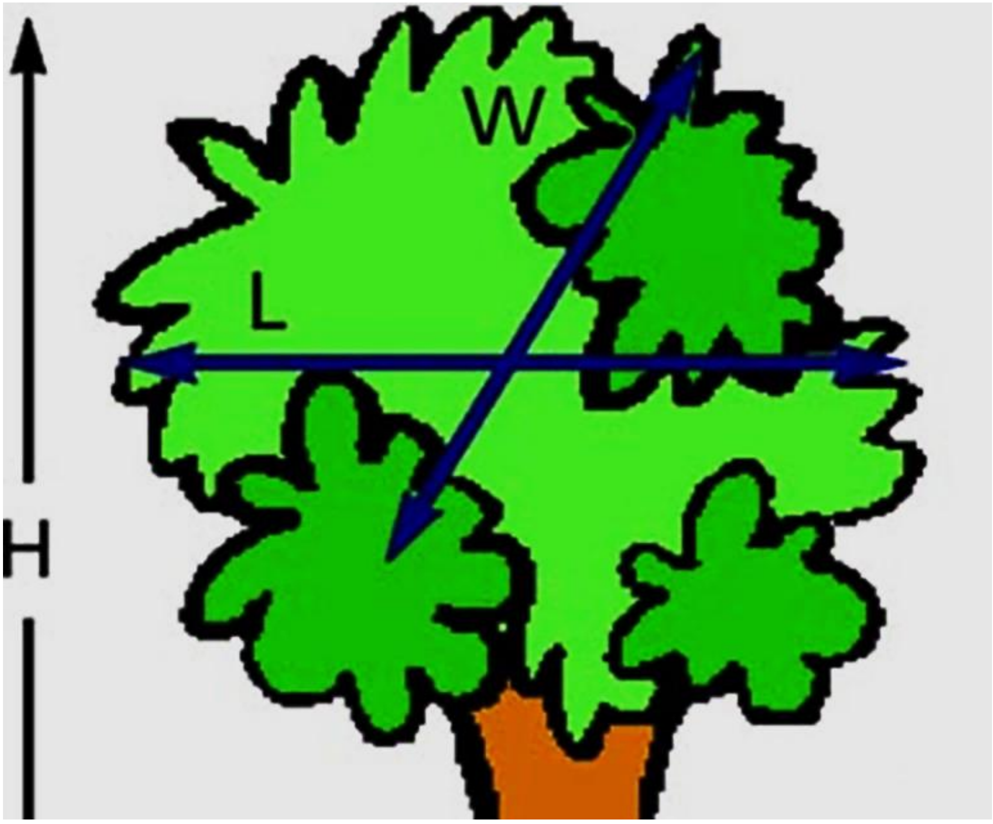
FogNet & SASSCAL with GLDAS & MODIS BRT:

```
mean total deviance = 184.758
mean residual deviance = 114.331

estimated cv deviance = 151.297 ; se = 12.901

training data correlation = 0.658
cv correlation =  0.432 ; se = 0.018

elapsed time -  0.02 minutes
```

Supp Figure 2.2: Results of the final Random Forest model of the FogNet sites with GLDAS and MODIS Boosted regression tree (BRT).



Supp Figure 2.4: The integration of data used in chapter 2 (Fog contributes to the distribution range of *A. leubnitziae*).



Supp Figure 2.4: An illustration of how the height and canopy of Arthraerua leubnitziae were measured at the different stations/study site.

3. Does fog contribute to the moisture and nutrient supply of *Arthraerua leubnitziae* in the central Namib Desert?

3.1. Introduction

Vegetation is generally sparse in the hyper-arid Namib Desert (Juergens et al., 2013; Moisel and Moll, 1981). Perennial shrubs including *Arthraerua leubnitziae, Zygophyllum stapffii* and *Calicorema capitata* are common on the gravel plains of the Namib Desert. *A. leubnitziae* dominates these plains for the first 50 km from the coast, but thereafter other species become more important (Loris, 2004). These extensive gravel plains (91% sand, 0.6% clay and 8.4% silt; Kaseke et al., 2017) are dominated by gypsum, gravel, calcretes and extensive quartz pebble desert pavements (Eckardt et al., 2013). The gypsum crusts are widespread, particularly in drier parts of this desert (Goudie and Viles, 2015), and form a cover of up 4 m thick at the coast that decreases with distance from the coast until only small patches are found in gypsum-free areas further inland (Martin, 1963). This distribution of gypsum coincides with the easternmost distribution of fog at 60 km from the ocean (Heine and Walter, 1996). The surface layers of soils with gypsum are known to be poor in N and P in many parts of the world (FAO, 1990). In arid regions, low soil water content and nutrient poor soils, predominantly N and P limits primary productivity (Lajtha and Schlesinger, 1988). Nutrient supply is often limited to the upper 5 cm and due to low decomposition and leaching rates, which in turn leaves the lower layers of the soil to be nutrient poor (Hadley and Szarek, 1981). In arid areas, nutrients are usually patchily distributed and strongly accumulated around individual plants (Garcia-Moya and McKell, 1970; Noy-Meir, 1985), thus limiting the availability of nutrients for plant establishment and growth of other plants in between the existing vegetation (Muller, 1953). Despite the low rainfall and nutrient poor soils (Jacobson, 1997) in the gravel plains of the central Namib Desert, plants survive (Pietruszka and Seely, 1985).

Although the geomorphology and geology of the Namib Desert are known (Eckardt et al., 2013; Ward, 2016; Watson and Lemon, 1985), little about the chemistry of the Namib Desert soils is known. Soils provide nutrients to plants and are important for capturing and retaining plant-derived carbon (Abrams et al., 1997). The relation between soil nutrient status and the plant communities associated with the status of nutrients has not been extensively studied in this ecosystem. Despite this, low nutrient levels have been reported, 1·53 µg g^{-1} maximum available P and a range of 0·013–0·062% of soil organic matter content (Jacobson, 1997). These astoundingly low values correspond with some of the most nutrient poor areas of the world (Cramer and Hoffman, 2015). In the arid regions of Australia, a combination of low decomposition rates, short periods of rapid growth (consumption of nutrients faster than they can be replaced) have been suggested to result in deficiencies of essential nutrients (Charley and Cowling, 1968).

Fog water deposition influences ecological functions of many coastal ecosystems and is not only known to provide moisture, but is also a major vector for nutrients into ecosystems around the world (Azevedo and Morgan, 1974; Derry and Chadwick, 2007; Hesse, 2012; Kennedy et al., 1998; Weathers et al., 2000). The relative importance of fog increases with decreasing annual amounts of rain (Ebner et al., 2011). Natural processes and human activities are some of the ways that nutrients enter the atmosphere, but in areas where a small portion nutrients are from anthropogenic activities, natural deposition can contribute the most to ecosystem nutrient budgets, predominantly in ecosystems that are nutrient poor and those where nutrients are lost faster than they are being replaced (Likens et al., 1996). For example, in the redwood forests of California where fog is the highest during summer, only 6% water input is delivered from fog. However, fog contributed 21% of the total N delivered by atmospheric deposition and canopy drip to the forest floor (Ewing et al., 2009). This suggests that even when small contributions to the water input came from fog, it could be an important path for nutrients and pollutants (Azevedo and Morgan 1974, Ewing et al. 2009). It is, therefore, to be expected that fog is predominantly of high importance for arid environments where fog occurs frequently.

The concentration of ions in the fog is influenced by the origin of the air mass (Thalmann et al., 2002). Fog interacts with aerosols in the marine boundary layer and may get enriched with nutrients with marine salts and organic matter (O’Dowd and de Leeuw, 2007). Nutrients and other elements are commonly more concentrated in fog than rain (Collett et al., 2002; Dasch, 1988;

Nyaga, Neff, & Cramer, 2015; Schemenauer, Banic, & Urquizo, 1995; Weathers, 1999; Weathers et al., 1986). Fog can, therefore, carry substantial amounts of Ca, Mg, K, and Na (Weathers et al., 1986) that may influence nutrient cycling, soil fertility, and plant growth (Azevedo and Morgan 1974, Weathers 1999, Weathers et al. 1986) by improving the availability of nutrients that are essential to vegetation (Ewing et al., 2012). Through time, the atmosphere has become an important source of the base cations, K, Ca and Mg (Chadwick et al., 1999), that may also be picked up during the transport of fog inland from the coast.

As the nutrient-rich fog is blown inland and intercepted by surfaces and vegetation, moisture is provided to the terrestrial ecosystem where fog is deposited and where it may improve the water balance and nutrient cycling (Dawson, 1998; Vogelmann, 1973). Nutrients and moisture may be trapped by both the leaves and soils. The soil and plant characteristics may also be affected, making fog important in determining the ecological and physiological characteristics of vegetation in fog ecosystems. Similarly to the water, as fog falls onto vegetation, the nutrients contained in the fog water are either absorbed directly by the plants or through root uptake when fog drips onto the soil (Vogelmann et al., 1968), consequently improving soil nutrient supply (Azevedo and Morgan, 1974). Evidence of plants directly absorbing nutrients through the leaves was found by Peuke et al. (1998) and Nyaga. (2015), whereby plants assimilated the same amounts of N in shoots and roots and took up NH_4^+ more readily than NO_3^- in the leaves. Nutrients may also be available to plants when aerosols that have previously been trapped on the plants are washed off into the soil by the fog, providing nutrients that are then also absorbed by the plants through the soil (Ingraham and Matthews, 1995) and when these nutrients are directly absorbed by the plants through their leaves and stem (Fig. 1.1).

The Namib Desert receives frequent and sufficient moisture from fog. Ecosystems neighbouring upwelling zones have been shown to benefit from moisture and nutrient input by this precipitation (Azevedo and Morgan, 1974; Weathers et al., 2000). I hypothesized that fog deposition has a significant potential to supply both moisture and nutrients to *A. leubnitziae* in the central Namib Desert. Since *A. leubnitziae* occurs in a narrow range along the Namibian coast, it is likely that the physical properties of the soils are relatively similar across this range. However, I predict that the variation in fog intensity (frequency and volume) and elemental composition across the range of *A. leubnitziae* is likely to influence both the soil and plant elemental composition. I also predict that *A. leubnitziae* is able to absorb elements on leaf surfaces from wet and dry deposition by direct uptake, especially when the plant surfaces are wetted by fog moisture. To test these predictions I studied five populations of *A. leubnitziae* across a fog gradient in the central Namib Desert and measured the elemental composition of fog, soils and plants. I also used $\delta^{15}N$ values to detect the influence of marine N-sources on plant and soil N. I applied tracers to stems of *A. leubnitziae* in order to determine the capacity of the stems for direct uptake of N (glycine, NO_3 and NH_4), K and Ca from stem surfaces. I found evidence for a role of fog in providing nutrients to *A. leubnitziae* and in enabling acquisition of those nutrients through direct uptake by stems

3.2. Methods and materials

3.2.1. Soil particle size analysis

Soil particle size distributions were analysed by means of laser diffraction using a Malvern Mastersizer 2000 (Malvern Instruments Ltd, Malvern, UK) attached to a Hydro 2000G wet sample dispersion unit. Five (1 mm) replicates of soil samples (bored from up to 30 cm below ground) from each study site were analysed. The samples were suspended in water and ultrasonically dispersed, stirred and introduced to the laser diffractometer. Each sample was subjected to 180 s ultrasonic dispersal to ensure that the particles were fully disaggregated. The particle size distribution is inferred from the instrument by the instrument software whereby it back-calculates from the diffraction pattern using appropriate models (Mie or Fraunhofer). The proportion of the soil particles in each size class were recorded and plotted. These size classes were then summed into categories representing clay, silt and sand, according to the Wentworth grain size chart (Williams et al., 2006).

3.2.2. Fog precipitation sampling

Five sampling sites running in an eastern direction from the coast, and at varying distances from the ocean (15, 25, 40, 50 and 60 km) were selected for this study. Fog water was collected monthly for 12 consecutive months (Sept 2015 to Aug 2016) using the so-called “Juvik” fog gauge (Frumau et al., 2006; Holwerda et al., 2011; Juvik and Ekern, 1978; Mcknight and Juvik, 1975) that is 40.6 cm long and has a cylindrical area of 500 cm^2 (Fig. 3.1). The entire setup was positioned at 1.5 m above the ground and consisted of the Juvik cylindrical gauge that was fitted onto a Young tipping rain gauge (Y52203, Young Company, Michigan, USA). The collectors were fitted with a cover (Fig. 3.1) to avoid contamination of samples from rain and birds. The fog gauges were connected to 2 L Schott bottles by a 6 mm ID tube (1 m long), and a loop was made in the pipe to form a moisture trap and wrapped in aluminium foil to reduce sample evaporation. A non-return valve was also inserted on the sampling bottles to further reduce evaporation. The sampling bottles were cleaned and rinsed multiple times with Millipore water prior and post-sampling. A biocide (200 mg of 2- isopropyl-5-methylphenol) was added to each of the bottles prior to sampling to minimize degradation of the sample from microbial activity (Cape et al., 2010). After the samples were removed, the fog gauge was washed with Millipore water, but this did not form part of the sample. The samples were stored at 4 ° C in 50 mL centrifuge tubes that were pre-rinsed with Millipore water. In addition to the fog water sampling, the amount of fog measured per day was also obtained from the five-meteorological stations used in this study.

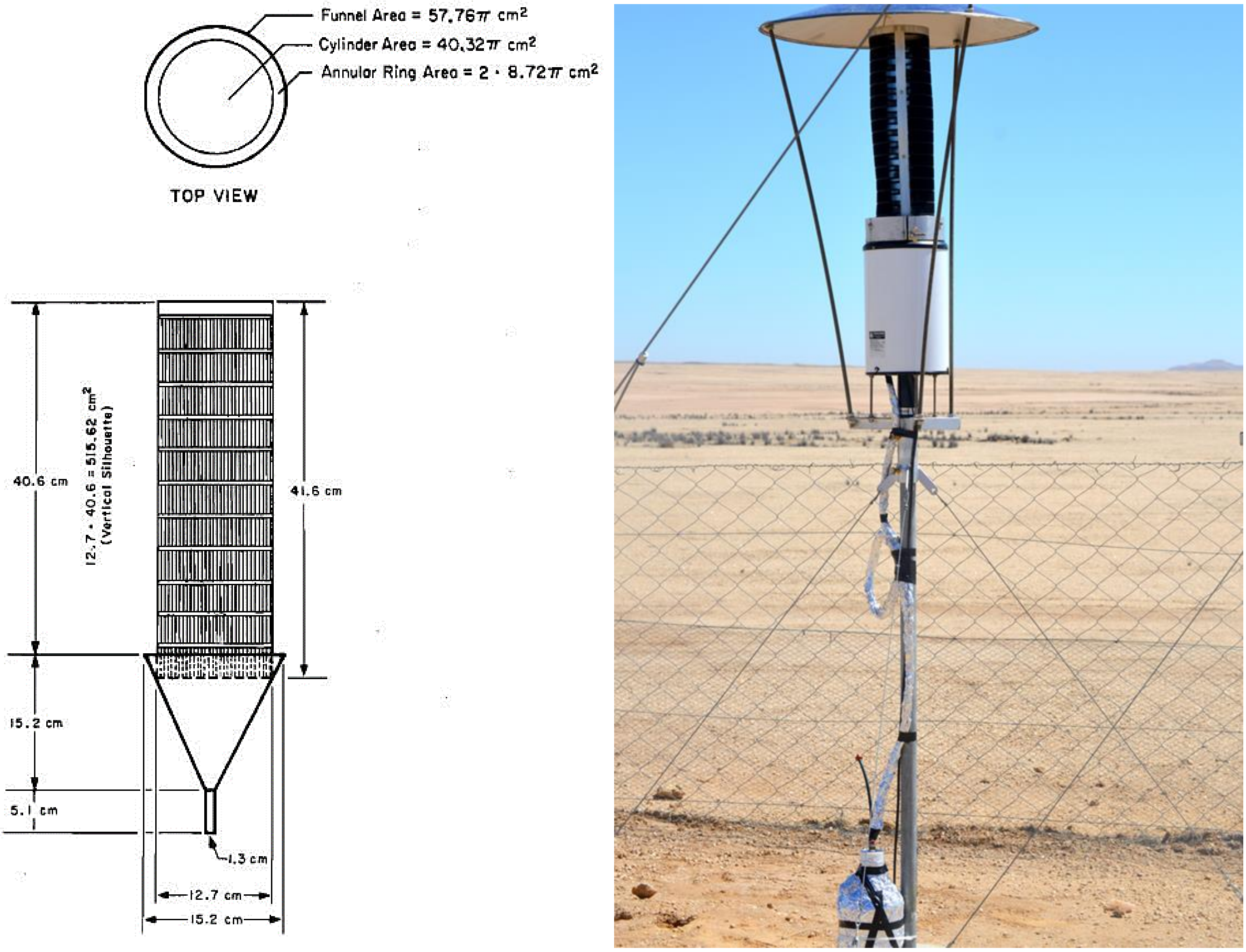


Figure 3.5: Schematic of the set-up of the Juvik fog gauge (Juvik and Ekern, 1978) and one of the gauges (set up at 1.2 m above ground) at the stations.

3.2.3. Ion chromatography

All fog water samples were diluted in Milli-Q water and analysed for Cl^-, NO_3^-, NO_2^-, Br^-, PO_4^{3-} and SO_4^{2-}. Samples were diluted 20 times before analysis and analysed by ion chromatography on a Waters 432 Conductivity detector (Microsep Pty Ltd, Johannesburg, South Africa), coupled to a Waters 717 plus autosampler and an Agilent 1100 series binary pump (Waldbronn, Germany). In addition, an IC-Pak A column was used with a Lithium Borate/Gluconate eluent, conductivity 240 µS, consisting of 20 ml Lithium Borate Gluconate concentrate (34 g Boric acid, 23.5 ml d-Gluconic acid, 8.6 g Lithium hydroxide monohydrate, 250 ml glycerin, filled up to 1litre with Milli-Q water), 10 ml n-Butanol, 120 ml Acetonitrile filled up to 1 litre with Milli-Q water. A 5 µl water sample was injected for analysis at a flow rate of 1.2 ml min^{-1}. The detection limits were 2 ppm for PO_4^{3-}, and SO_4^{2-}, 1 ppm for Cl^-, NO_3^-, NO_2^-, and Br^-.

3.2.4. ICP analysis

All fog water samples were analysed for Ca, K, Mg Na and S using Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES) on a Thermo ICap 6200 (Thermo Scientific, Johannesburg, South Africa). The accuracy percentage for the different elements were 99% for Ca, 95.6% for K, 96% for Mg, 96.8% for Na and 96% for S. The instrument was calibrated using NIST (National Institute of Standards and Technology, Gaithersburg MD, USA) traceable standards to quantify selected elements. A NIST-traceable quality control standard of a separate supplier than the main calibration standards were analysed to verify the accuracy of the calibration before sample analysis. The results were corrected for the dilution factor resulting from the digestion procedure where a sample has undergone a digestion step. Annual concentration was determined as the average of the monthly concentration of each element. Annual nutrient contents (mg day^{-1}) in horizontal precipitation for each site were calculated as the product of the total measured monthly precipitation volume (corrected for the wash water volume added) and concentration of the nutrient in the sample. Both annual concentration and contents were determined for the anion and cations. To identify the marine contribution fog, elemental enrichment relative to seawater was calculated, using the formula, $EF_{Cl^-}(X) = (X/Cl^-)_{fog} / (X/Cl^-)_{sea\ water,}$ where $(X/Cl^-)_{fog}$ is the ratio between substance X concentration and Cl- concentration in fog water; and $(X/Cl^-)_{sea\ water}$ is the ratio of substance X relative to Cl^- in sea water, reported elsewhere (Culkin and Cox, 1966; Eckardt, 1996; Morris and Riley, 1966). Enrichment factors were calculated for Ca, K, Mg, Na and S by comparing these ionic values over Cl with the equivalent ratio of the marine water average. The ratios of X/Cl seawater used were, Ca= 0.021, Mg= 0.067, Na= 0.55, K= 0.021, Cl: 1 and S= 0.14 (Kennish, 1989). Values greater than 1 indicate enrichment relative to seawater, whereas values smaller than 1 indicate depletion relative to seawater (Eckardt, 1996; Eltayeb et al., 1993).

3.2.5. Stem nutrient uptake

LiCl, as an analogue tracer for K and $SrCl_2$ as an analogue tracer for Ca, were separately dissolved in 1 L of distilled water to make up 0.2 mM solutions. Solutions (98% atom, Sigma-Aldrich, St. Louis Missouri, USA) of 8.104 µg ($NaNO_3$), 5.448 µg (NH_4Cl) and 7.606 µg glycine were also separately dissolved in 500 ml of distilled water to make up 0.01 mM. Each solution was applied to stems of 10 randomly selected plants at Marble Koppie (10 replicates per solution). The solutions were applied by brushing them on the stems with a paint brush and covering the stems with filter paper that was also soaked in the solutions. The label was left on the stems overnight. The treated stems were excised and washed twice in a 1 mM $CaSO_4$ solution to remove the excess label on the surface of the treated leaves. Untreated stems were also removed from a separate section of the plant and these were treated as the controls. The treated stems and the control stems were dried in an oven at 60°C for 48 h and then milled to a fine powder (Mixer Mill MM400, Retsch GmbH, Haan, Germany).

In order to determine $\delta^{15}N$ of the treated samples by mass spectrometry, samples were sent to the Archaeology Department Stable Isotope Facility at the University of Cape Town (see "Plant and soil ^{15}N analyses" below). The ^{15}N enrichment was expressed as the difference between the ^{15}N values measured in the treated stems compared to the control stems. The Li and $SrCl_2$ concentration in the stems were analysed (see 3.2.3) at the Central Analytical Facilities (University of Stellenbosch). The enrichment was expressed as the difference in Li and $SrCl_2$ in the treated and untreated stems.

3.2.6. Plant and soil elemental analysis

Five replicates of soil (bored to 30 cm below ground) and plants were collected from the five study sites. The soil samples were sieved (<1 mm) and left to air dry for two weeks, while the plant samples were rinsed with deionised water and dried in the oven at 60°C until the weight was constant. Both the soil and plants were milled to a fine powder (Mixer MillMM400). The plant and soil powder were put in sample cups with a polypropylene bottom and analysed in a Spectroscout energy-dispersive X-ray Fluorescence (XRF) analyser (SPECTRO Analytical Instruments, Kleve, Germany). Each filter was set to sample for a 100 s for each of the Pd, Mo and Ta filters and 100 s without a filter. Elemental concentrations obtained from NOAA Technical Memorandum NOS ORCA 68 (1992) were used to calibrate the instrument was by using a certified standard GBW07312 (National Research Center for CRMs, Beijing, China). The elements measured (all above detection limit in all samples) were Na, Mg, Al, P, K, Ca, Ti, V, Cr, Mn, Fe, Ni, Cu, Zn, Ga, As, Se, Br, Rb, Sr, Y, Zr, Ba, W, Hg, Tl, Pb, Bi and Th. However, for the purpose of this study, only the plant essential elements (P, K, Ca, Mg, Mn, Fe, Cu and Zn) were included in the data analysis.

3.2.7. Plant and soil ^{15}N analyses

In order to determine δ^{15}N signatures of the plant and soil samples by mass spectrometry, five replicates of soil (surface to a depth of 30 cm below ground) and plant samples were collected from each study site. The soil samples were sieved (<1 mm) and left to air dry for two weeks, while the plant samples were rinsed with deionised water and dried in the oven at 60°C until the weight was constant. The soil and plant samples were then milled to a fine powder (Mixer Mill MM400, Retsch GmbH, Haan, Germany) and sent to the Archaeology Department Stable Isotope Facility (University of Cape Town).

The soil samples, including those with the ^{15}N label, were weighed into tin cups to an accuracy of 1 microgram on a Sartorius M2P microbalance, compressed to enclose the sample and combusted in a Thermo scientific Flash 2000 organic elemental analyser. The plant samples (2.8–3.0 mg) were weighed in 5 × 9 mm tin capsules (Santis Analytical AG, Teufen, Switzerland) and analysed for N isotopes by Thermo scientific Flash 2000 organic elemental analyser (*Thermo Fisher Scientific* Inc, Korea, Japan). The gases are passed to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer (IRMS) via a Thermo scientific Conflo IV gas control unit. The analysis was done using three machines made by Thermo Scientific, Bremen, Germany. Nitrogen values were expressed as a value relative to atmospheric nitrogen and carbon values were expressed as a value relative to Pee-Dee Belemnite. All the in-house standards (Valine - DL-Valine purchased from Sigma) have been calibrated against IAEA (International Atomic Energy Agency) standards, either by the department of archaeology or by other labs. Delta ($\Delta^{15}N$) was calculated as the result of the soil minus plant ^{15}N (soil $\delta^{15}N$- plant $\delta^{15}N$).

3.2.8. Statistical analysis

Fog elemental concentrations were not analysed statistically since there were only 5 sites, with considerable spatial variability, that were sampled monthly. As a consequence, the annual elemental concentrations and contents are provided for all 5 sites. All statistical analyses were conducted in R (R Core Team, 2017). The data used for principal component analysis (PCA) was logged and then transformed using the function *preProcess* in the package "caret" in R using the BoxCox method to centre and scale the data. The *prcomp* function in "stats" package in base R was used to run the PCA on the transformed data. For the PCA of fog, the elemental concentrations included were Ca, K, Mg, Na, S, Cl, NO_3 and SO_4. For the PCAs of plant and soil elements N, Mg, P, K, Ca, Mn, Fe, Cu and Zn were included.

A multiple linear model of $\delta^{15}N$ was developed against plant $\delta^{13}C$ and the PC1 of fog. The model initially included both linear and quadratic terms and was simplified on the basis of the AIC scores following the protocol outlined by Crawley, (2006). One-way analysis of variance (ANOVA) was conducted on plant and soil data where there were replicate measurements and followed by post-hoc Tukey tests to separate means.

3.3. Results

3.3.1. Soil particle size

The substrates at the five stations in the gravel plains of the Namib Desert did not show a significant difference in the particle size (Fig. 3.2). The results show a remarkable homogenous distribution and show clear bimodal distribution, with higher percentages of sand particles and correspondently less clay at all the sites but show no significant soil textural differences in the size of the particles at the five sites.

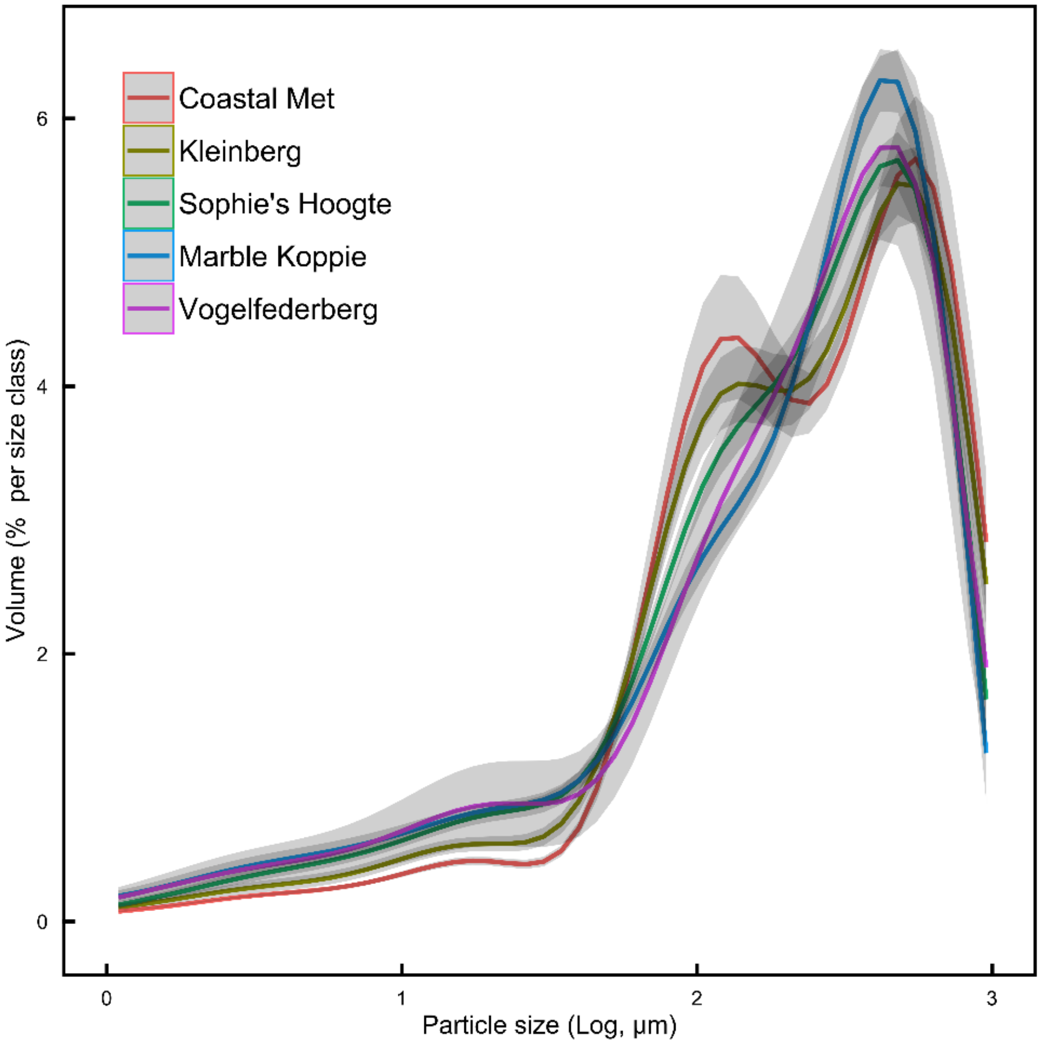


Figure 3.6: Logarithm of the variation in soil particle size of sieved (<1 mm) soil from the five sites used in the study. Values are a representative of the average for each particle size fraction (n=5) and the grey band indicate the 95% confidence interval.

3.3.2. Moisture and nutrient deposition from fog

During the study period (Sept 2015 to Aug 2016), the fog precipitation varied among the five sites (Fig. 3.3). The maximum amount of fog (9.2 L) was observed at VF while MK received the least amount of fog.

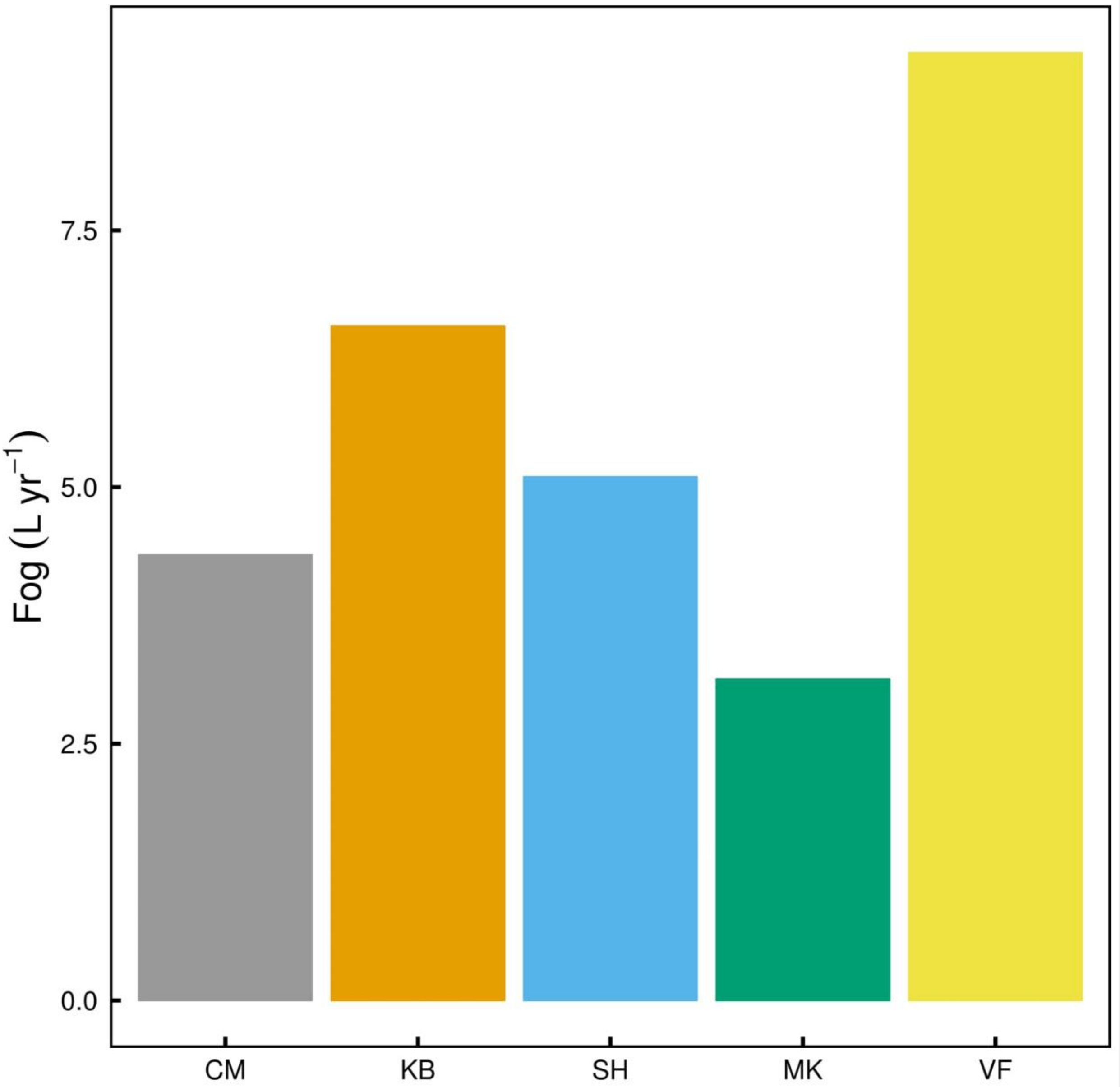


Figure 3.3: The variation in total annual fog at the five stations in a transect inland from the coast between Aug 2015 and Sept 2016. The station names as indicated on the x-axis are CM (Coastal Met), KB (Kleinberg), SH (Sophie`s Hoogte), MK (Marble Koppie) and VF (Vogelfederberg). The sites are located at; CM (15 km), KB (25 km), SH (40 km), MK (50 km) and VF (60 km) from the coast.

Over the course of the annual sampling cycle, average element concentrations between sites varied widely (Fig. 3.4). The site nearest to the coast had higher concentrations of most elements apart from Br and PO^{-}_{4} and was particularly heavily influenced by deposition. Very low concentrations of Br and PO^{-}_{4} were recorded at most of the sites. Cl, Na and SO^{-}_{4} were the dominant elements present in fog samples. The highest concentration recorded was for Cl^- and this varied from 1820 mg L^{-1} at CM to 465 mg L^{-1} at VF. The annual concentrations of Ca, K, Mg, Na, Cl and SO^-_4 decreased with distance inland and were the lowest at the inland site, even though this site had the most fog deposition.

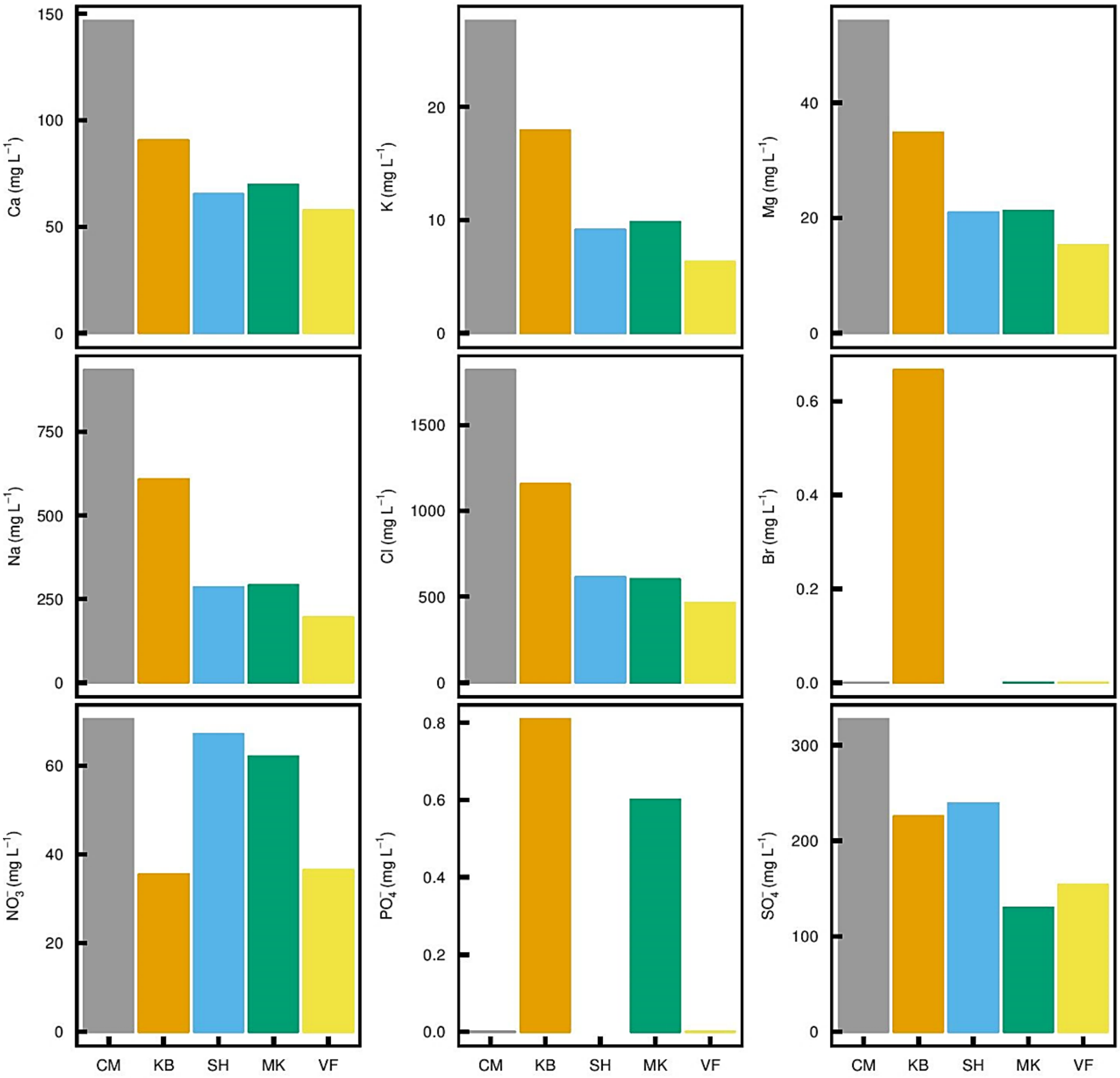


Figure 3.4: Annual concentration of major ions in fog water that was collected monthly at the five stations during the period Aug 2015 to Sept 2016. Annual nutrient concentrations (mg L^{-1}) were calculated as the average of the monthly concentrations for each element.

Over the course of the annual sampling cycle, total element contents (i.e. the product of concentration and volume) also varied widely between the sites (Fig. 3.5). The total annual nutrient content of fog was dominated by Cl and Na. However, the highest contents of Ca, K, Mg, Na and Cl were recorded at KB. These nutrients declined at SH and MK and then increased VF where the highest volume of fog was received (Fig. 3.5). The highest contents of Br, NO^-_3, PO^-_4 and SO^-_4 were recorded at SH but did not exhibit trends with the transect of sites inland.

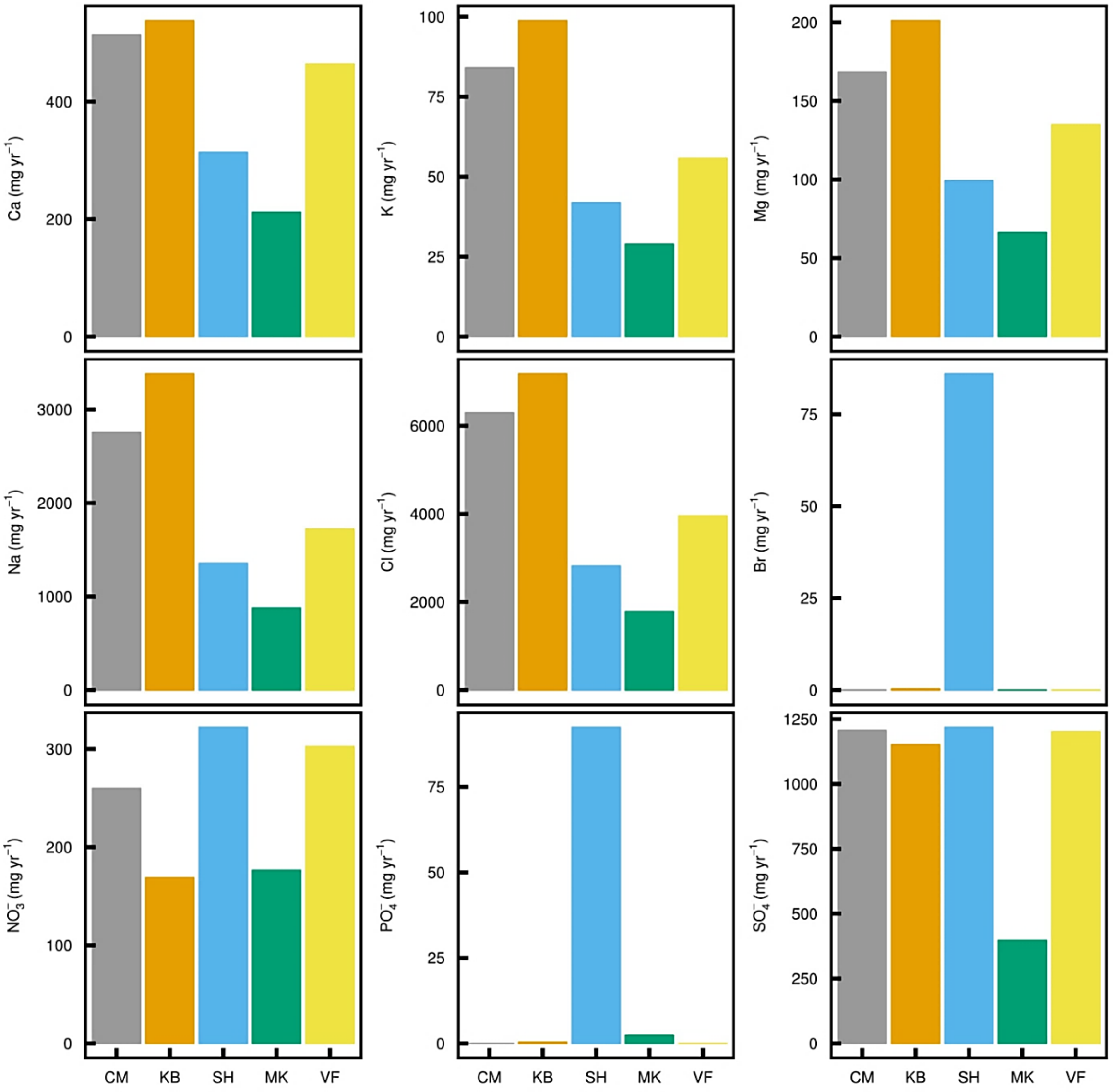


Figure 3.5: Deposition contents (mg year^{-1}) of elements measured in fog precipitation collected monthly at the five sites between Aug 2015 and Sept 2016. Annual nutrient contents (mg year^{-1}) in fog for each site were calculated as the product of the total measured monthly fog volume and concentration of the nutrient in the fog sample.

Enrichment factors showed that marine inputs dominated the fog nutrient composition at the five sites except for Ca for which there was a clear terrestrial contribution. Consistent with this, there was a trend of increasing Ca with distance inland. Na at CM also exceeded marine levels and followed a decreasing trend further inland (Fig. 3.6).

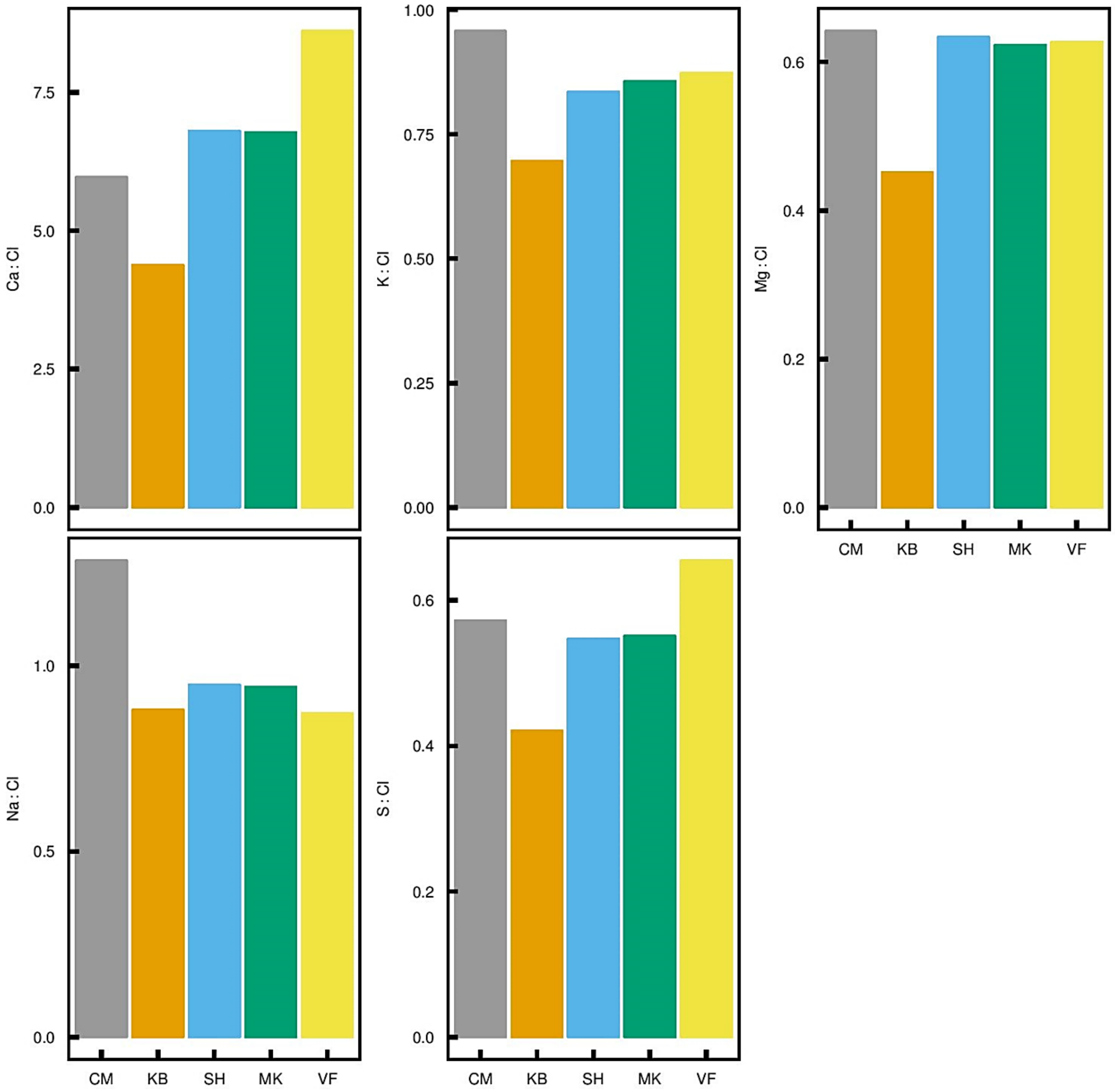


Figure 3.7: Enrichment factors of Ca, K, Mg, Na and S relative to chlorine (used as an index of marine origin) in fog water samples collected from the five study sites between Sept 2015 and Aug 2016. The source of elements in the fog water could be examined through the use of enrichment factors (EF_{Cl^-}) as described by (Ahmed et al., 1990). Values greater than 1 indicate enrichment relative to seawater, whereas values smaller than 1 indicate depletion relative to seawater (i.e. most likely seawater).

3.3.3. Foliar nutrient interception and uptake

A. leubnitziae absorbed ^{15}N–compounds in the form of glycine, $NaNO_3^-$ and $NO_3NH_4^+$ when these were applied to the stems of the plants. These plants also took up $SrCl_2$ and LiCl through foliar surfaces, thus demonstrating that *A. leubnitziae* had the capacity of absorbing nutrients through their stems (Fig. 3.7). Uptake of nutrients by the stems was significantly different among control and the plants that were applied with the ^{15}N labelled compounds, Sr and Li.

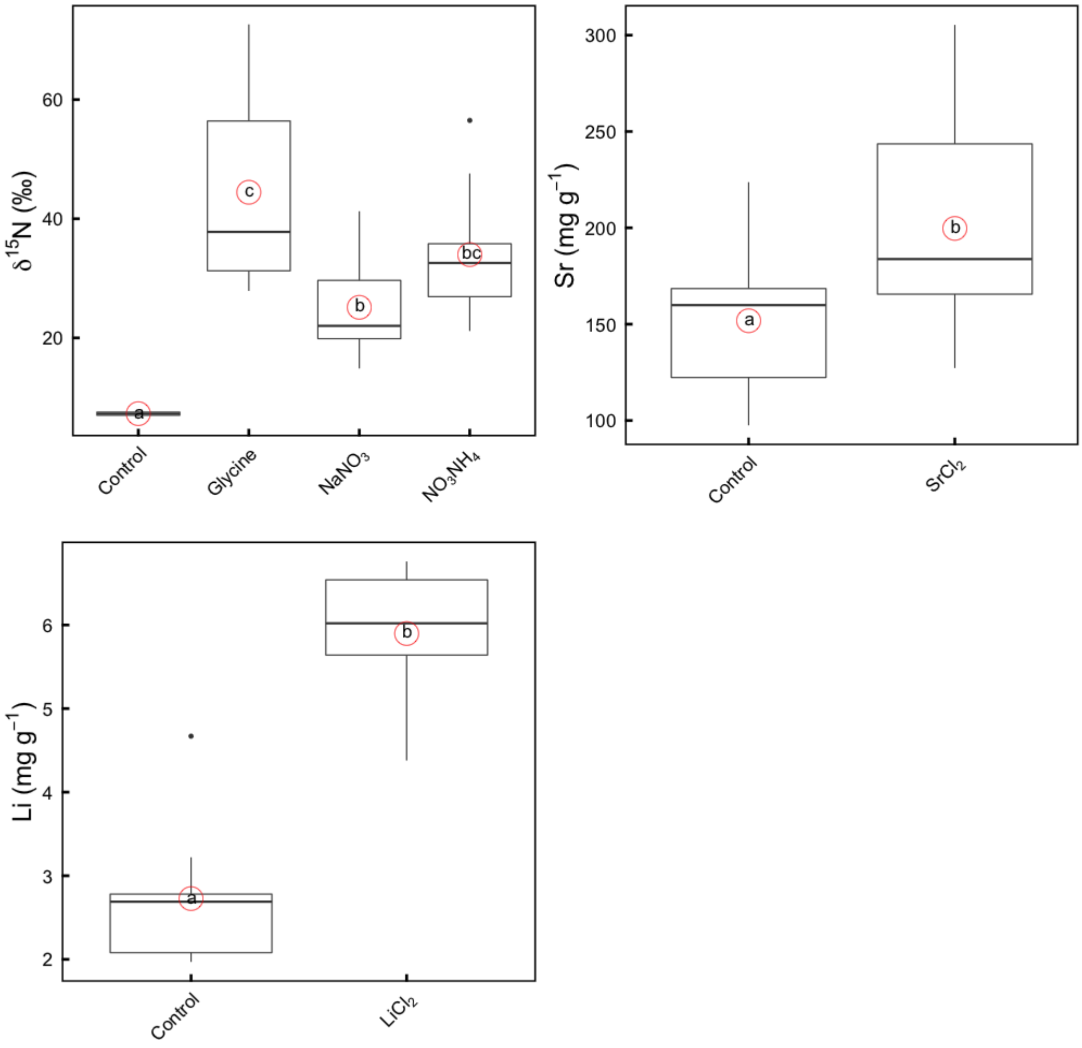


Figure 3.7: The uptake of ^{15}N containing compounds, Sr and Li (as a tracer for K) supplied to stems of *A. leubnitziae*. Values are the mean ± SE (n = 10) stem N isotope enrichments and stem concentrations of Sr and Li after the supply of ^{15}N-glycine $^{15}NaNO_3^-$, $^{15}NO_3NH_4^{+,}$ $SrCl_2$ and LiCl. The δ15N values are treated stems relative to the untreated stems. The different letters represent significant differences between species determined by Tukey post-hoc test following a one-way ANOVA.

3.3.4. Soil and plant nutrient concentrations

The total elemental concentrations suggest that nutrient compositions varied across the sites (Fig. 3.8). Concentrations of Ca were the highest, while Cu, Zn and N were lowest at all the sites. However, several nutrients had very low percentages and variations amongst the sites. Trends were only observed in the soil nutrients where there was a decrease in the percentage P and K , and increase in K across the transect of sites inland from the coast. Statistical differences among the sites were only recorded for N (SH and MK) and Mn (CM, SH and VF).

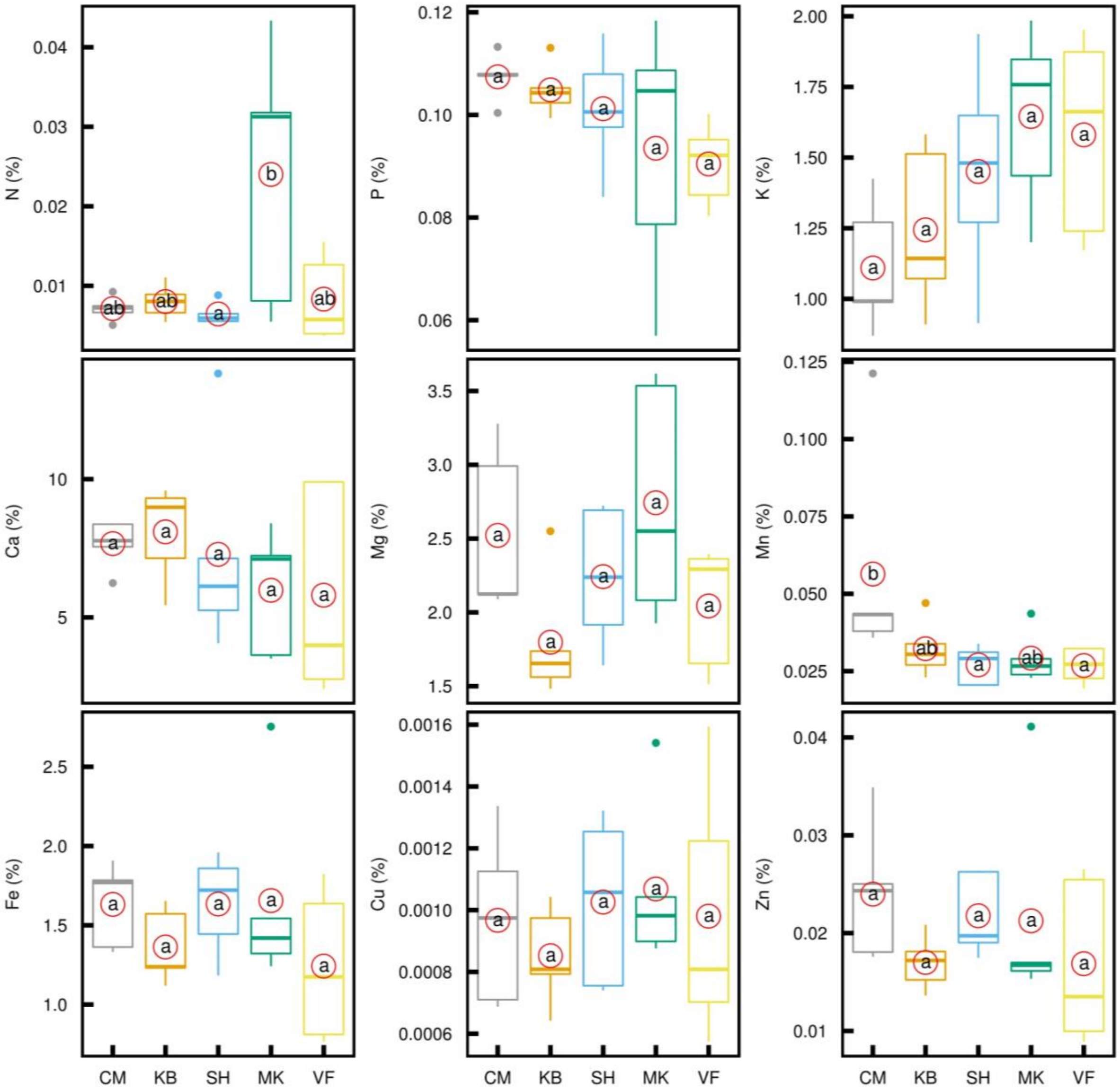


Figure 3.8: Soil element concentration and variation of 9 plant essential elements (N, P, K, Ca, Mg, Mn, Fe, Cu and Zn) averaged across sites. The different letters represent significant differences between species determined by Tukey post-hoc test following a one-way ANOVA.

As expected, there was wide variation in the percentage of nutrient concentrations in plants samples between the five sites (Fig. 3.9). The highest percentage of elemental concentration at all sites was recorded was of K and the lowest concentration was of Cu. Unlike the soils, more statistical differences were observed among the sites. Five (P, K, Mg, Fe and Zn) of the nutrients were statistically different amongst some of the stations. CM had the most statistical differences in all the sites (P, K, Mg and Fe). Zn was only statistically different at KB and SH. No statistical differences in plant nutrients were recorded for N, Ca, Mn and Cu.

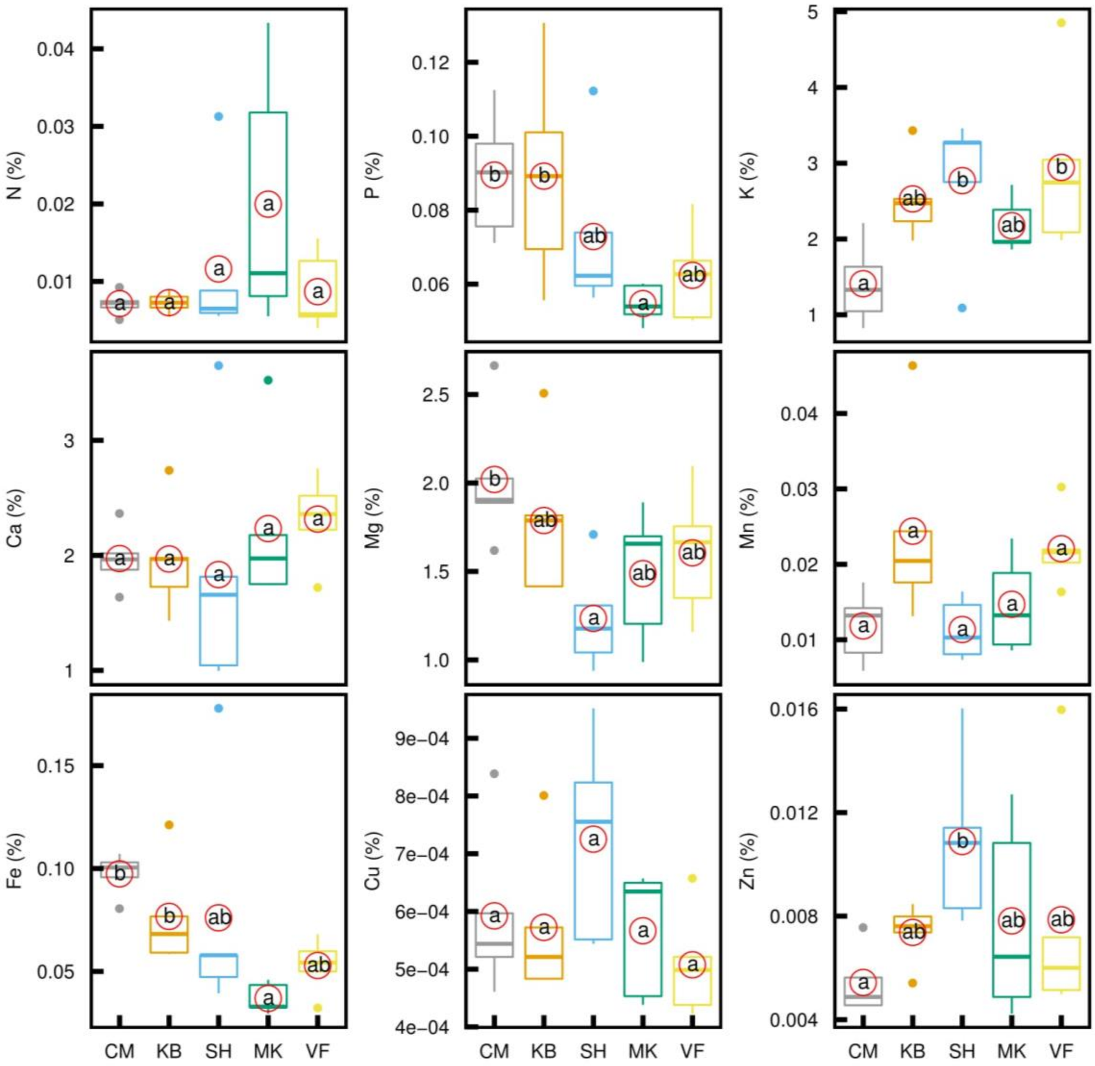


Figure 3.9: Plant element concentration and variation for 9 plant essential elements (N, P, K, Ca, Mg, Mn, Fe, Cu and Zn) averaged across the five study sites. The different letters indicate significant ($p<0.05$) differences as determined by ANOVA followed by post-hoc Tukey tests.

The correlation of the PC1 of the plant (*A. leubnitziae*) and soil nutrients to that of the PC1 of the fog nutrients revealed that there are similarities in the plant nutrients and the fog PC1 nutrients fog nutrients (Fig. 3.10). This suggests a significant contribution to plant nutrition from fog that was not evident in for the soil nutrients.

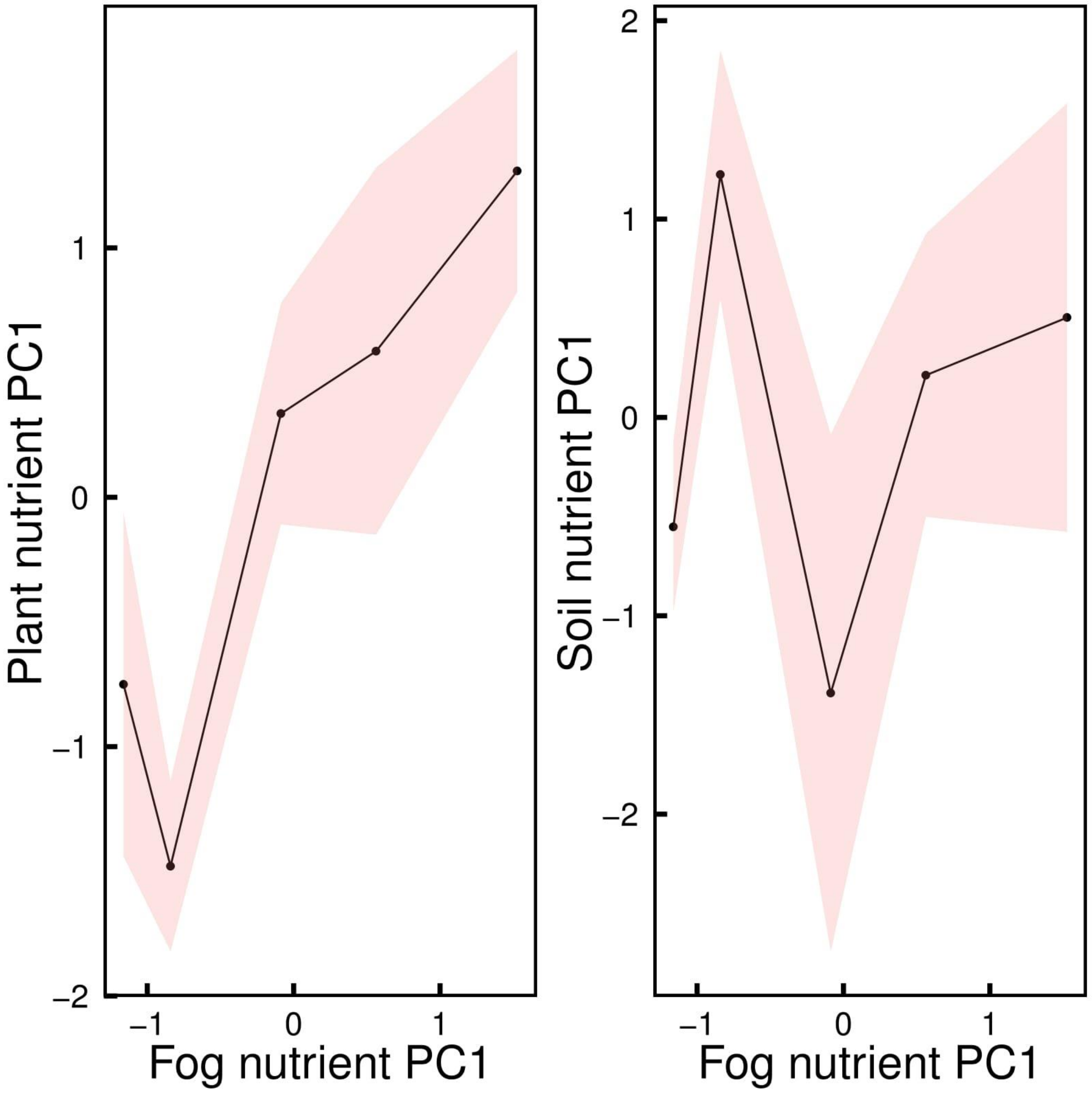


Figure 3.10: The PC1 patterns in soil and plant nutrients in relation to the PC1 of fog nutrients. A PCA was done on 9 plant essential element concentrations in the plant, soil samples and the fog. The PC1 explained 44.3% of the variance in the soil, 26.1 % of the variance in the plant and 82.5% of the variance in the fog. The PC1 of the soil and plant were then used to determine whether there was a relationship between the fog PC1 and the soil and plant PC1. Bands represent the 95% confidence limits.

The soil and plant δ^{15}N, and plant δ^{13}C followed a similar trend were of low variability across the study sites across all the sites. Soil δ^{15}N values ranged from 2.78‰ to 6.56‰, while plant δ^{15}N ranged from 2.36‰ to 7.10‰ (Fig. 3.11). Plant δ^{13}C values ranged from -22.4‰ to -23.9‰. MK returning the highest values for both the plant (7.1‰) and soil (6.5‰) δ^{15}N. KB returned the highest values for plant δ^{13}C (-22.4‰), while MK returned the lowest values (-23.9‰). There were no significant differences in N isotope discrimination (Δ^{15}N) values across the five study sites, suggesting that plant and soil δ^{15}N follow a pattern that might suggest an input from fog.

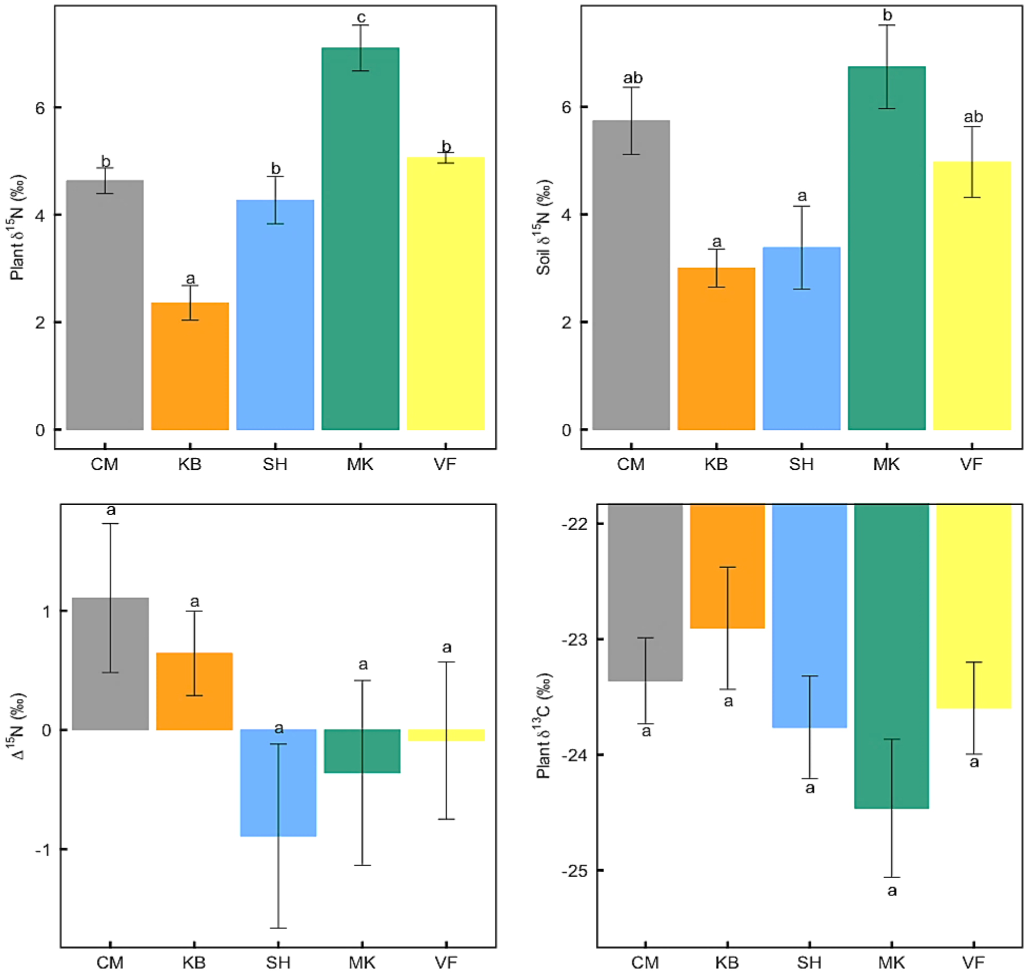


Figure 3.11: δ^{15}N in plant *A. leubnitziae* and soil samples and δ^{13}C in the plant samples averaged across the five used in the study. Values of δ^{15} N in plant *A. leubnitziae* and soil samples and δ^{13}C in the plant samples are the averages of five replicates from each study site. Δ^{15}N was calculated as the difference between in the soil δ^{15}N and the plant δ^{15}N. The different letters indicate significant ($p<0.05$) differences as determined by ANOVA followed by post-hoc Tukey tests.

The linear model relating Δ^{15}N to plant δ^{13}C and the PC1 from the PCA conducted on fog elements showed a significant correlation of observed Δ^{15}N to predicted Δ^{15}N (Table. 3.1). This model suggests that the offset between plant and soil δ^{15}N (e.g. Δ^{15}N) is associated with δ^{13}C and fog elemental concentrations in this region.

Table 3.1: Multivariate regression (R^2 = 0.99, p = 0.0245) analysis of the association between Δ^{15}N to plant δ^{13}C and the PC1 from the PCA**.**

Coefficients	Estimation	SE	t value	p
Intercept	-69.45759	2.7834	-24.95	0.0255
Plant □^{13}C	2.9325	0.11795	-24.86	0.0256
PC1 of fog PCA	-2.18173	0.0616	-35.42	0.0180
(PC1 of fog PCA)^2	0.29748	0.01819	16.35	0.0389

3.4. Discussion

Fog contributed significant amounts of moisture at the five study sites, confirming the importance of fog in the Namib Desert (Lancaster et al., 1984; Olivier, 1995). Fog occurs throughout the year, but is most common during the first half of the year at the coast and the second half of the year at the sites inland from the coast (Lancaster et al., 1984) supplying 92% of the yearly water input across the five study sites between Sep 2015 and Aug 2016. (Chapter 2). Fog is formed over the cold waters of the Benguela upwelling where aerosols entrain nutrients from nutrient-rich deep water and is transported more than a 100 km inland. *A. leubnitziae* absorbed and held water in their canopies, but no variation was found in the amount of water held between the sites (Supp Fig. 3.1). From water isotope data, *A. leubnitziae* does directly absorb fog water (Juergens et al., 2013; Loris, 2004; Soderberg, 2010) and transports the water for storage in the roots (Seely and Henschel, 2001). Using water isotopes Soderberg (2010), reported that fog water contributed

18% to the stem water of *A. leubnitziae,* thereby, and attributed fog the role of restoring the plant water status.

The fog was not only found to be an important source of moisture in this ecosystem, but relatively high concentrations of nutrients were measured in the collected water. The nutrients in the fog water likely included those directly transported with the fog from the Atlantic Ocean and those deposited by dust and accumulated on the fog collectors. The distinction between nutrients contributed by wet and dry deposition is not particularly relevant here as all these nutrients should be available to vegetation via direct absorption from above-ground plant components or indirectly from the soil. The elemental concentrations in the deposition I measured were generally high in comparison to literature data (Eckardt and Schemenauer, 1998; Schemenauer and Cereceda, 1992; Schemenauer and Cereceda, 1992; Supp Table. 3.1). This was attributable to the collection protocol, in which samples were collected over an entire month at a time (rather than being event-based) and because no attempt was made to exclude dry deposition between wet fog events. Although this study found high levels of elemental concentrations in deposition solutions, event-based fog collections in the Namib Desert have relatively low ion concentrations and were similar to those found in other coastal deserts (Oman and Chile; Eckardt and Schemenauer, 1998; Supp Table. 3.1). This suggests an important contribution of nutrients from dust, whether deposited directly to the collectors or entrained in the fog. Dust is often a rich source of nutrients (e.g. PO_4^-; Aciego et al., 2017; Gonzalez et al., 2011). There are, however, no other data on the ionic composition of fog measured on a monthly basis in the Namib Desert.

The highest concentration Ca, K, Mg, Na and Cl, in deposition were recorded at the site closest to the coast and the lowest concentration of the same nutrients at the most inland site. The fog is associated with northwesterly winds that advect the fog eastwards and southwards towards the inland part of the Namib Desert, crossing a large tract of terrestrial surface from which other particulates could potentially be entrained. For example, aerosols from the Kuiseb Delta, the dustiest geomorphological unit in the Namib Desert, contribute 54% of the dust to dust plumes in the Namib Desert (von Holdt and Eckardt, 2017). The high concentrations of these elements close to the coast may also indicate that these elements are, however, related to coastal aerosol from the Atlantic ocean. Using enrichment ratios, all the nutrients except Ca were found to be of marine origin. In comparison to other coastal deserts of Chile and Oman (Eckardt and Schemenauer, 1998; Schemenauer and Cereceda, 1992; Schemenauer and Cereceda, 1992; Supp Table. 3.2), enrichment factors (relative to seawater) of the fog water in the Namib Desert were low, indicating a strong dependence on marine sources. Ca was highly enriched in this study relative to marine sources, indicating the substantial contribution of terrestrial aerosols. In contrast, in the Strandveld, 91%, 97% and 56% of the average annual quantity of Mg, K and Ca in horizontal precipitation was attributed to seawater (Nyaga, 2013). Thus the high levels of Ca in deposition in the Namib are possibly from dust or calcareous exposures in the Namib Desert (Eckardt and Schemenauer, 1998).

The five study sites were relatively close geographically and had similar soil particle size indicating similar pedogenic histories. However, soil and plant nutrient concentrations were low and varied across the five sites. The variation in the elemental concentration in the soils and plants could be associated with the variation in the fog nutrient supply and associated dissolved particles across the five sites, as observed in other studies across plant species (Elser et al., 2010; Schlesinger and Marks, 1977; Sterner et al., 2002; Troxler, 2007). Soil and plant nutrients across sites did not yield consistent patterns. This is not surprising since the relationship between soil nutrient and plant nutrient concentrations is complex, with indirect influences of many soil nutrients on the concentration of foliar nutrients (Cramer and Verboom, 2017). Results from the correlation between the PC1 from the PCAs of the fog and plant nutrients, however, provide correlative evidence of a link between fog and plant nutrients. In addition to the contribution of fog to the soil nutrients, the elemental composition of deposition is potentially important in understanding the formation of gypsum ($CaSO_4 \cdot 2H_2O$) in the Namib Desert. The gravel plains are covered in extensive layers of gypsum (Drake et al., 2004; Eckardt and Schemenauer, 1998; Eckardt and Spiro, 1999; Heine and Walter, 1996; Heine and Walter, 1996) that extends up to 60-80 km from the coast (Heine and Walter, 1996; Scholz, 1972) These crusts developed from marine-derived S from the Atlantic ocean carried inland by fog and deposited onto soils that contain Ca-carbonate from aeolian deposition (Heine and Walter, 1996; Martin, 1963). Near the coast and where fog precipitation is highest, gypsum crusts are up to 4 m thick (Martin, 1963). Soils with gypsum are commonly N and P poor (FAO, 1990) because P in gypsum soils binds with Ca to form insoluble and poorly available calcium phosphate (Muhammad and Jones, 1992) resulting in low available P. Gypsum soils also contain low clay contents (Watson, 1982) which are particularly important for the higher nutrient and water holding capacity (Crouse, 2017). Thus the gypsum is related to the sustained deposition during pedogenesis, but currently likely provides a terrestrial dust source that could contribute to the high Ca concentrations in deposition found across the five study sites.

Fog is usually more concentrated with nutrients than rain (Collett et al., 2002; Dasch, 1988; Nyaga, 2013; Schemenauer et al., 1995; Weathers et al., 2000, 1986) and delivers substantial amounts of nutrients even in ecosystems where fog is not a major source of moisture. This suggests that fog is an important vector of nutrients and pollutants, especially to nutrient poor ecosystems. In the Namib Desert where soil nutrients are low (Jacobson, 1997) and nutrients usually higher around individual plants (Abanda et al., 2011; Garcia-Moya and McKell, 1970; Noy-Meir., 1985), fog may play a significant role in the nutrient cycles (Soderberg, 2010). Results on the concentration of nutrients in the fog water and contribution of fog nutrients to the plant nutrients emphasise how important fog and dust are in the supply of nutrients for *A. leubnitziae*.

Soil and plant δ^{15}N values followed similar patterns across the five sites, and there was no significant difference between Δ^{15}N across the study sites. A negative correlation between plant δ^{15}N and precipitation is common (Amundson et al., 2003; Hartman and Danin, 2010; Ma et al., 2007; Swap et al., 2004). For example, in the Kalahari, plant δ^{15}N values declined with an increase in precipitation (0.47‰/100 mm increase in precipitation; Aranibar et al., 2004). Consequently, variation in plant δ^{15}N across the five sites may be related to water availability. Plant δ^{13}C values did not vary significantly across the study sites. *Plant* δ^{13}C is mostly influenced by the availability of water in arid areas (Ma et al., 2007) with higher $\delta^{13}C$ indicating greater water deficit (Hartman and Danin, 2010; Liu et al., 2005). *A. leubnitziae* is known a C_3 photosynthetic plant (Soderberg, 2010) and the negative correlation between plant $\delta^{13}C$ and water availability (Anderson et al., 1996; Korol et al., 1999; Liu et al., 2005; Ma et al., 2007; Stewart et al., 1995; Van de Water et al., 2002) suggests that water availability is rather limited for *A. leubnitziae* at the five study sites because the $\delta^{13}C$ values are rather high relative to norms (-27‰) for C_3 plants (Kohn, 2010). Similar values of plant $\delta^{15}N$ and $\delta^{13}C$ were reported for *A. leubnitziae* by Soderberg (2010). These values suggest water stress in *A. leubnitziae* despite th*e frequent occurrence of fog in the region.* This may suggest that the nutrients in the fog water are more important for the plants than the actual moisture (Cramer et al., 2009).

Plants can absorb water and nutrients either directly through their leaves and stems (Dawson, 1998; Yates and Hutley, 1995), or indirectly from indirectly from the soil as fog drip (Azevedo and Morgan, 1974; Dawson, 1998). Plants both provide a surface roughness element that traps nutrients both on the foliage and by deposition around vegetation clumps (Abanda et al., 2011). Nutrients in fog water are directly deposited to leaf and stem surfaces, therefore, bypassing the loss of nutrients from the soils (e.g. through leaching). *A. leubnitziae* took up several nutrients directly from their stems, including the amino acid glycine. Glycine was used as a tracer for organic N and its uptake is important considering that plant and soil $\delta^{15}N$ follow a pattern that might suggest an input from fog. Foliar uptake is common in plants and has been demonstrated in about 70 species globally (Berry and Smith, 2013; Boucher et al., 1995; Burns et al., 2016; Goldsmith et al., 2013; Gouvra and Grammatikopoulos, 2003; Martin and Von Willert, 2000). For example, foliar N uptake by crop species is through stomata (Okana et al., 1990) and base cations are taken up by several species (*Acer saccharum, Acer platanoides, Citrus aurantium*; Tyree et al., 1990)*. A. leubnitziae* uptake of N, Li and Sr (as tracers for K and Ca) provides evidence that *A. leubnitziae* can utilise these nutrients directly from their stems. The uptake of nutrients of via the stems of these plants is likely dependent on the form of the nutrient properties(Peuke et al., 1998), the amount of nutrients deposited (Peuke et al., 1998) and particularly on the duration of moisture (Azevedo and Morgan, 1974). Considering that a significant amount of nutrients were found in the deposition and the frequency of fog events, the likelihood of *A. leubnitziae* participating in both the direct interception of the nutrients and deposition in the canopy and increasing deposition of nutrients to the soil is high.

3.5. Conclusion

Fog is a significant source of moisture and contributed more moisture than rain in the Namib Desert. Apart from the importance of fog as a moisture source, it is also associated with a significant wet and dry deposition nutrients in the study region, that contribute to the nutrient supply of *A. leubnitziae.* The growth of plant species in nutrient-poor gypsum soils is linked to the availability of moisture and nutrients, explaining why the distribution of this species is restricted to the fog zone of the Namib Desert.

3.6. References

Abanda, P.., Compton, J.., Hannigan, R., 2011. Soil nutrient content, above-ground biomass and litter in a semi-arid shrubland, South Africa. Geoderma 128–137. https://doi.org/10.1016/j.geoderma.2011.05.015

Abrams, M.M., Jacobson, P.J., Jacobson, K.M., Seely, M.K., 1997. Survey of soil chemical properties across a landscape in the Namib Desert. J. Arid Environ. 35, 29–38. https://doi.org/10.1006/jare.1995.0139

Aciego, S.M., Riebe, C.S., Hart, S.C., Blakowski, M.A., Carey, C.J., Aarons, S.M., Dove, N.C., Botthoff, J.K., Sims, K.W.W., Aronson, E.L., 2017. Dust outpaces bedrock in nutrient supply to montane forest ecosystems. Nat. Commun. 8, 14800. https://doi.org/10.1038/ncomms14800

Ahmed, A.F.M., Singh, R.P., Elmubarak, A.H., 1990. Chemistry of atmospheric precipitation at the Western Arabian Gulf Coast. Atmos. Environ. Part A. Gen. Top. 24, 2927–2934. https://doi.org/https://doi.org/10.1016/0960-1686(90)90473-Z

Amundson, R., Austin, A.T., Schuur, E.A.G., Yoo, K., Matzek, V., Kendall, C., Uebersax, A., Brenner, D., Baisden, W.T., 2003. Global patterns of the isotopic composition of soil and plant nitrogen. Global Biogeochem. Cycles 17, 1–10. https://doi.org/10.1029/2002GB001903

Anderson, J.E., Williams, J., Kriedemann, P.E., Austin, M.P., Farquhar, G.D., 1996. Correlations between carbon isotope discrimination and climate of native habitats for diverse eucalypt taxa growing in a common garden. Funct. Plant Biol. 23, 311–320.

Aranibar, J.N., Otter, L., Macko, S.A., Feral, C.J.., Epstein, H.E., Dowty, P.R., Frank, E., Shugart, H.H., Swap, R.J., 2004. Nutrient cycling in the soil-plant system along a precipitation gradient in the Kalahari sands. Glob. Chang. Biol. 10, 360–373.

Azevedo, J., Morgan, D.L., 1974. Fog precipitation in coastal California forests. Ecology 55, 1135–1141.

Berry, Z.C., Smith, W.K., 2013. Ecophysiological importance of cloud immersion in a relic spruce-fir forest at elevational limits, southern Appalachian Mountains, USA. Oecologia 173, 637–648. https://doi.org/10.1007/s00442-013-2653-4

Boucher, J.F., Munson, a D., Bernier, P.Y., 1995. Foliar absorption of dew influences shoot water potential and root growth in Pinus strobus seedlings. Tree Physiol. 15, 819–823. https://doi.org/10.1093/treephys/15.12.819

Burns, E., Simonin, K.A., Bothman, A.G., Dawson, T.E., Burns, E., Kevin, L., Bothman, A.G., Dawson, T.E., 2016. Foliar water uptake : A common water acquisition strategy for plants of the Redwood. Oecologia 161, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Cape, J.N., Sheppard, L.J., Crossley, A., Van Dijk, N., Tang, Y.S., 2010. Experimental field estimation of organic nitrogen formation in tree canopies. Environ. Pollut. 158, 2926–2933. https://doi.org/10.1016/j.envpol.2010.06.002

Chadwick, O.A., Derry, L.A., Vitousek, P.M., Huebert, B.J., Hedin, L.O., 1999. Changing sources of nutrients during four million years of ecosystem development. Nature 397, 491–497.

Charley, J.., Cowling, S.., 1968. Changes in soil nutrient status resulting from overgrazing and their consequences in plant communities of semi-arid areas, in: Proc. Ecol. Soc. Aust. pp. 28–37.

Collett, J.L., Bator, A., Sherman, D., Moore, K.F., Hoag, K.J., Demoz, B.B., Rao, X., Reilly, J.E., 2002. The chemical composition of fogs and intercepted clouds in the United States. Atmos. Res. 64, 29–40. https://doi.org/10.1016/S0169-8095(02)00077-7

Cramer, M.D., Hawkins, H.-J., Verboom, G.A., 2009. The importance of nutritional regulation of plant water flux. Oecologia 161, 15–24. https://doi.org/10.1007/s00442-009-1364-3

Cramer, M.D., Hoffman, M.T., 2015. The Consequences of Precipitation Seasonality for Mediterranean-Ecosystem Vegetation of South Africa. PLoS One 10, 1–21.

https://doi.org/10.1371/journal.pone.0144512

Cramer, M.D., Verboom, G.A., 2017. Measures of biologically relevant environmental heterogeneity improve prediction of regional plant species richness. J. Biogeogr. 44, 579–591. https://doi.org/10.1111/jbi.12911

Crawley, M.J., 2006. Statistics: An Introduction Using R, Second edi. ed, Technometrics. John Wiley & Sons LTD, Chichester: United Kingdom. https://doi.org/10.1198/tech.2006.s388

Crouse, D., 2017. Soils and plant Nutrients, in: Moore, K.A., Bradley, L.K. (Eds.), Extension Gardener Handbook. NC State Extension, Raleigh, North Carolina.

Culkin, F., Cox, R.A., 1966. Sodium, potassium, magnesium, calcium and strontium in sea water. Deep Sea Res. Oceanogr. Abstr. 13, 789–804. https://doi.org/https://doi.org/10.1016/0011-7471(76)90905-0

Dasch, J.., 1988. Hydrological and chemical input to fir trees from rain and clouds during a 1-month study at Clingmans Peak, NC. Atmos. Environ. 22, 2255–2262.

Dawson, T.E., 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117, 476–485.

Derry, L., Chadwick, O., 2007. Contributions from earth`s atmosphere to soil. Elements 3, 333–338.

Drake, N.A., Eckardt, F.D., White, K.H., 2004. Sources of sulphur in gypsiferous sediments and crusts and pathways of gypsum redistribution in southern Tunisia. Earth Surf. Process. Landforms 29, 1459–1471. https://doi.org/10.1002/esp.1133

Ebner, M., Miranda, T., Roth-Nebelsick, A., 2011. Efficient fog harvesting by Stipagrostis sabulicola (Namib dune bushman grass). J. Arid Environ. 75, 524–531. https://doi.org/10.1016/j.jaridenv.2011.01.004

Eckardt, F.D., 1996. The distribution and origin of gypsum in the central Namib Desert, Namibia:

A study of the sulphur cycle in a coastal hyper-arid desert. Hertford Coll. University of Oxford.

Eckardt, F.D., Livingstone, I., Seely, M., Von Holdt, J., 2013. The surface geology and geomorphology around Gobabeb, Namib desert, Namibia. Geogr. Ann. Ser. A Phys. Geogr. 95, 271–284. https://doi.org/10.1111/geoa.12028

Eckardt, F.D., Schemenauer, R.S., 1998. Fog water chemistry in the Namib Desert, Namibia. Atmos. Environ. 22, 2595–2599. https://doi.org/10.1016/S1352-2310(97)00498-6

Eckardt, F.D., Spiro, B., 1999. The origin of sulphur in gypsum and dissolved sulphate in the Central Namib Desert, Namibia. Sediment. Geol. 123, 255–273. https://doi.org/10.1016/S0037-0738(98)00137-7

Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Swenson, N.G., Enquist, B.J., 2010. Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change. New Phytol. 186, 593–608. https://doi.org/10.1111/j.1469-8137.2010.03214.x

Eltayeb, M.A.., Annegarn, H.., Maenhaut, W., Annegarn, H.., 1993. Aerosol-soil fractionation for Namib Desert samples. Atmos. Environ. Part A. Gen. Top. 27, 669–678.

Ewing, H.A., Weathers, K.C., Lindsey, A.M., Templer, P.H., Dawson, T.E., Bradbury, D.C., Firestone, M.K., Boukili, V.K.S., 2012. Fog and soil weathering as sources of nutrients in a California Redwood Forest, in: Proceedings of Coast Redwood Forests in a Changing California: A Symposium for Scientists and Managers. U.S. Department of Agriculture, Albany, pp. 265–272.

Ewing, H.A., Weathers, K.C., Templer, P.H., Dawson, T.E., Firestone, M.K., Elliott, A.M., Boukili, V.K.S., 2009. Fog water and ecosystem function: Heterogeneity in a California Redwood Forest. Ecosystems 12, 417–433. https://doi.org/10.1007/s10021-009-9232-x

FAO, 1990. Management of Gypsiferous Soils. Rome; Italy.

Frumau, A., Tobón, C., Bruijnzeel, S., 2006. Hydrological measurement protocol for montane cloud forest.

Garcia-Moya, E., McKell, C.M., 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology 51, 81–88.

Goldsmith, G.R., Matzke, N.J., Dawson, T.E., 2013. The incidence and implications of clouds for cloud forest plant water relations. Ecol. Lett. 16, 307–314. https://doi.org/10.1111/ele.12039

Gonzalez, A.L., Farina, J.M., Pinto, R., Perez, C., Weathers, K.C., Armesto, J.J., Marquet, P.A., 2011. Bromeliad growth and stoichiometry: Responses to atmospheric nutrient supply in fog-dependent ecosystems of the hyper-arid Atacama Desert, Chile. Oecologia 167, 835–845. https://doi.org/10.1007/s00442-011-2032-y

Goudie, A., Viles, H., 2015. The Namib Plains: Gypsum Crusts and Stone Pavements, in: World Geomorphological Landscapes. pp. 103–106. https://doi.org/10.1007/978-94-017-8020-9

Gouvra, E., Grammatikopoulos, G., 2003. Beneficial effects of direct foliar water uptake on shoot water potential of five chasmophytes. Can. J. Bot. 81, 1278–1284. https://doi.org/10.1139/b03-108

Hadley, N.F., Szarek, S.R., 1981. Productivity of Desert Ecosystems. Bioscience 31, 747–753.

Hartman, G., Danin, A., 2010. Isotopic values of plants in relation to water availability in the Eastern Mediterranean region. Oecologia 162, 837–852. https://doi.org/10.1007/s00442-009-1514-7

Heine, K., Walter, R., 1996. Gypcretes of the central Namib Desert, Namibia. Regensburg: Germany.

Heine, K., Walter, R., 1996. Gypcrete soils of the central Namib desert (Namibia) and their palaeoclimatological significance, Petermanns Geographische Mitteilungen.

Hesse, R., 2012. Spatial distribution of and topographic controls on Tillandsia fog vegetation in coastal southern Peru: Remote sensing and modelling. J. Arid Environ. 78, 33–40. https://doi.org/10.1016/j.jaridenv.2011.11.006

Holwerda, F., Bruijnzeel, L.A., Scatena, F.N., 2011. Comparison of passive fog gauges for determining fog duration and fog interception by a Puerto Rican elfin cloud forest. Hydrol. Process. 25, 367–373. https://doi.org/10.1002/hyp.7641

Ingraham, N.L., Matthews, R.A., 1995. The importance of fog-drip water to vegetation: Point Reyes Peninsula, California. J. Hydrol. 164, 269–285. https://doi.org/10.1016/0022-1694(94)02538-M

Jacobson, K.M., 1997. Moisture and substrate stability determine VA-mycorrhizal fungal community distribution and structure in an arid grassland. J. Arid Environ. 35, 59–75. https://doi.org/10.1006/jare.1995.0140

Juergens, N., Oldeland, J., Hachfeld, B., Erb, E., Schultz, C., 2013. Ecology and spatial patterns of large-scale vegetation units within the central Namib Desert. J. Arid Environ. 93, 59–79. https://doi.org/10.1016/j.jaridenv.2012.09.009

Juvik, J.O., Ekern, P.C., 1978. A climatology of Mountain Fog on Mauna Loa, Hawai'i Island, Fog Precipitation Along Topo-C1imatic Gradients on the Island of Hawaii. Hawaii: USA.

Kaseke, K.F., Wang, L., Seely, M.K., 2017. Nonrainfall water origins and formation mechanisms. Sci. Adv. 3, 1–8. https://doi.org/10.1126/sciadv.1603131

Kennedy, M.J., Chadwick, O.A., Vitousek, P.M., Derry, L.A., Hendricks, D.M., 1998. Changing sources of base cations during ecosystem development, Hawaiian Islands. Geology 26, 1015–1018. https://doi.org/10.1130/0091-7613(1998)026<1015:CSOBCD>2.3.CO

Kennish, M.J., 1989. Chemical oceanography, in: Practical Handbook of Marine Science. CRC Press, p. 544. https://doi.org/10.1017/CBO9781107415324.004

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proc. Natl. Acad. Sci. U. S. A. 107, 19691–5. https://doi.org/10.1073/pnas.1004933107

Korol, R.L., Kirschbaum, M.U.F., Farquhar, G.D., Jeffreys, M., 1999. Effects of water status and soil fertility on the C-isotope signature in Pinus radiata. Tree Physiol. 19, 551–562.

Lajtha, K., Schlesinger, W.H., 1988. The biogeochemistry of phosphorus cycling and phosphorus availability along a desert soil chronosequence. Ecology 69, 24–39. https://doi.org/10.2307/1943157

Lancaster, J., Lancaster, N., Seely, M.K., 1984. Climate of the central Namib Desert. Madoqua 16, 5–61.

Likens, G.E., Driscoll, C.T., Buso, D.C., 1996. Long-Term Effects of Acid Rain: Response and Recovery of a Forest Ecosystem. Science (80-.). https://doi.org/10.1126/science.272.5259.244

Liu, W., Feng, X., Ning, Y., Zhang, Q., Cao, Y., An, Z., 2005. d13C variation of C3 and C4 plants across an Asian monsoon rainfall gradient in arid northwestern China. Glob. Chang. Biol. 11, 1094–1100. https://doi.org/10.1111/j.1365-2486.2005.00969.x

Loris, K., 2004. Nebel als wasserressource für den strauch Arthraerua leubnitziae, in: Walter, H., Breckle, S.. (Eds.), Ökologie Der Erde: Spezielle Ökologie Der Tropischen Und Subtropischen Zonen. pp. 485–489.

Ma, J.Y., Chen, K., Xia, D.S., Wang, G., Chen, F.H., 2007. Variation in foliar stable carbon isotope among populations of a desert plant, Reaumuria soongorica (Pall.) Maxim. in different environments. J. Arid Environ. 69, 365–374. https://doi.org/10.1016/j.jaridenv.2006.11.002

Martin, C.E., Von Willert, D.J., 2000. Leaf epidermal hydathodes and the ecophysiological consequences of foliar water uptake in species of Crassula from the Namib Desert in southern Africa. Plant Biol. 2, 229–242. https://doi.org/10.1055/s-2000-9163

Martin, H., 1963. A suggested theory for the origin and a brief description of some gypsum deposits of South West Africa. Trans. Geol. Soc. South Africa 345–351.

Mcknight, J.H., Juvik, J.O., 1975. Fog precipitation along topo-climatic gradients on the island of Hawaii: Methodological approaches in Hawaiian fog research. Hawaii: USA.

Moisel, A., Moll, E.., 1981. A Braun-Blanquet survey of the vegetation of the Welwitschia plain. Dinteria 15, 3–11.

Morris, A.W., Riley, J.P., 1966. The bromide/chlorinity and sulphate/chlorinity ratio in sea water. Deep Sea Res. Oceanogr. Abstr. 13, 699–705. https://doi.org/https://doi.org/10.1016/0011-7471(66)90601-2

Muhammad, H.J., Jones, K.C., 1992. Phosphorus in gypsiferous soils: the influence of soil properties on P fractionation. Geoderma 53, 97–104. https://doi.org/https://doi.org/10.1016/0016-7061(92)90023-Z

Muller, C.H., 1953. The association of desert annuals with shrubs. Am. J. Bot. 40, 53–60.

Noy-Meir, I., 1985. Desert ecosystem structure and function, in: Evenari, M., Noy-Meir, I., Goodall, D.. (Eds.), Hot Deserts and Arid Shrublands. Elsevier Science, Amsterdam, pp. 93–103.

Nyaga, J.M., 2013. Nutrional contribution of atmospheric deposition to the Strandveld vegetation of West Coast South Africa. University of Cape Town.

Nyaga, J.M., Neff, J.C., Cramer, M.D., 2015. The contribution of occult precipitation to nutrient deposition on the West Coast of South Africa. PLoS One 10, 1–21. https://doi.org/10.1371/journal.pone.0126225

O’Dowd, C.D., de Leeuw, G., 2007. Marine aerosol production: a review of the current knowledge. Philos. Trans. R. Soc. A 365, 1753–1744. https://doi.org/10.1098/rsta.2007.2043

Okana, K., Tobe, K., Furukawa, A., 1990. Foliar uptake of peroxyacetyl nitrate (PAN) by herbaceous species varying in susceptibility to this pollutant. New Phytol. 114, 139–145. https://doi.org/10.1111/j.1469-8137.1990.tb00384.x

Olivier, J., 1995. Spatial distribution of fog in the Namib. J. Arid Environ. 29, 129–138. https://doi.org/10.1016/S0140-1963(05)80084-9

Peuke, A.D., Jeschke, W.D., Hartung, W., 1998. Foliar application of nitrate or ammonium as sole nitrogen supply in Ricinus communis. II. The flows of cations, chloride and abscisic acid. New Phytol. 140, 625–636. https://doi.org/10.1046/j.1469-8137.1998.00304.x

Pietruszka, R.., Seely, M.., 1985. Predictability of two moisture sources in the Namib Desert. S. Afr. J. Sci. 81, 682–685.

R Core Team, 2017. R: A language and environment for statistical computing [WWW Document]. R Found. Stat. Comput.

Schemenauer, R., Banic, C., Urquizo, N., 1995. High elevation fog and precipitation chemistry in southern Quebec, Canada. Atmos. Environ. 29, 2235–2252.

Schemenauer, R., Cereceda, P., 1992. Monsoon cloudwater chemistry on the Arabian Peninsula. Atmos. Environ. 9, 1583–1587.

Schemenauer, R.S., Cereceda, P., 1992. The quality of fog water collected for domestic and agricultural use in Chile. Am. Meteorol. Soc. 31, 275–290.

Schlesinger, W.H., Marks, P.L., 1977. Mineral cycling and the niche of Spanish Moss, Tillandsia usneoides L. Am. J. Bot. 64, 1254–1262.

Scholz, H., 1972. The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. Mad 16, 33–51.

Seely, M.., de Vos, M.., Louw, G.., 1977. Fog imbition, satellite fauna and unusual leaf structure in a Namib Desert dune plant. S. Afr. J. Sci. 73, 169–172.

Seely, M., Henschel, J., 2001. Developing fog harvesting in Namibia, in: Developing Fog Harvesting in Namibia. Desert Research Foundation of Namibia, Windhoek: Namibia, p. 9.

Soderberg, K., 2010. The role of fog in the ecohydrology and biogeochemistry of the Namib Desert. University of Cape Town.

Sterner, R.W., Elser, J.J., Vitousek, P.M., 2002. Ecological stoichiometry: The biology of elements from molecules to the biosphere. Princeton University Press.

Stewart, G.R., Turnbull, M.H., Schmidt, S., Erskine, P.D., 1995. 13C Natural abundance in plant communities along a rainfall gradient: A biological integrator of water availability. Aust. J. Plant Physiol. 22, 51–55. https://doi.org/10.1071/PP9950051

Swap, R.., Aranibar, J.., Dowty, P.., Gilhooly, W.., Macko, S.., 2004. Natural abundance of 13C and 15N in C3 and C4 vegetation of southern Africa: patterns and implications. Glob. Chang. Biol. 10, 350–358. https://doi.org/10.1046/j.1529-8817.2003.00702.x

Thalmann, E., Burkard, R., Wrzesinsky, T., Eugster, W., Klemm, O., 2002. Ion fluxes from fog and rain to an agricultural and a forest ecosystem in Europe. Atmos. Res. 64, 147–158. https://doi.org/10.1016/S0169-8095(02)00087-X

Troxler, T.G., 2007. Patterns of phosphorus, nitrogen and δ15N along a peat development gradient in a coastal mire, Panama. J. Trop. Ecol. 23, 683–691. https://doi.org/10.1017/S0266467407004464

Tyree, M.T., Scherbatskoy, T.D., Tabor, C.A., 1990. Leaf cuticles behave as asymmetric membranes : Evidence from the measurement of diffusion potentials. Plant Physiol. 92, 103–109.

Van de Water, P.K., Leavitt, S.W., Betancourt, J.L., 2002. Leaf δ13C variability with elevation, slope aspect, and precipitation in the southwest United States. Oecologia 132, 332–343. https://doi.org/10.1007/s00442-002-0973-x

Vogelmann, H.., 1973. Fog Precipitation in the Cloud Forests of Eastern Mexico. Bioscience 23, 96–100.

Vogelmann, H.., Siccama, T., Leedy, D., Ovitt, D., 1968. Precipitation from Fog Moisture in the Green Mountains of Vermont. Ecology 49, 1205–1207.

von Holdt, J., Eckardt, F., 2017. Dust activity and surface sediment characteristics of the dustiest river in southern Africa: the Kuiseb River, Central Namib, South African Geographical

Journal. https://doi.org/10.1080/03736245.2017.1339627

Ward, D., 2016. The Biology of Deserts, second edi. ed. Oxford University Press, New York.

Watson, A., 1982. The origin, nature, and distribution of gypsum crusts. Unpubl. D.Phil Diss. University of Oxford.

Watson, I., Lemon, R. &r, 1985. Geomorphology of a Coastal Desert: The Namib, South West Africa/Namibia. J. Coast. Res. 1, 329–342.

Weathers, K.C., 1999. The importance of cloud and fog in the maintenance of ecosystems. Trends Ecol. Evol. 14, 214–215. https://doi.org/10.1016/S0169-5347(99)01635-3

Weathers, K.C., Likens, G., Herbert, B., Eaton, J.S., Bowden, B.W., Andersen, J.L., Cass, D., Galloway, J.N., Keene, W.C., Kimball, K.D., Huth, P., Smiley, D., 1986. A regional acidic cloud/fog water event in the Eastern United States. Nature 319, 657–658. https://doi.org/10.1038/319657a0

Weathers, K.C., Lovett, G.M., Likens, G.E., Caraco, N.F.M., 2000. Cloudwater inputs of nitrogen to forest ecosystem in southern Chile: Forms, fluxes, and sources. Ecosystems 5, 590–595. https://doi.org/10.1007/s100210000051

Williams, S.., Arsenault, M.., Buczkowski, B.., Reid, J.., Flocks, J.., Kulp, M.., Penland, S., Jenkins, C.., 2006. Surficial sediment character of the Louisiana offshore Continental Shelf region: a GIS Compilation, U.S. Geological Survey Open-File Report [WWW Document]. U.S. Geol. Surv. Open-File Rep. 2006-1195. URL http://pubs.usgs.gov/of/2006/1195/index.htm (accessed 8.1.17).

Yates, D.J., Hutley, L.B., 1995. Foliar uptake of water by wet leaves of Sloanea woollsii, an Australian subtropical rainforest tree. Aust. J. Bot. 43, 157–167. https://doi.org/10.1071/BT9950157

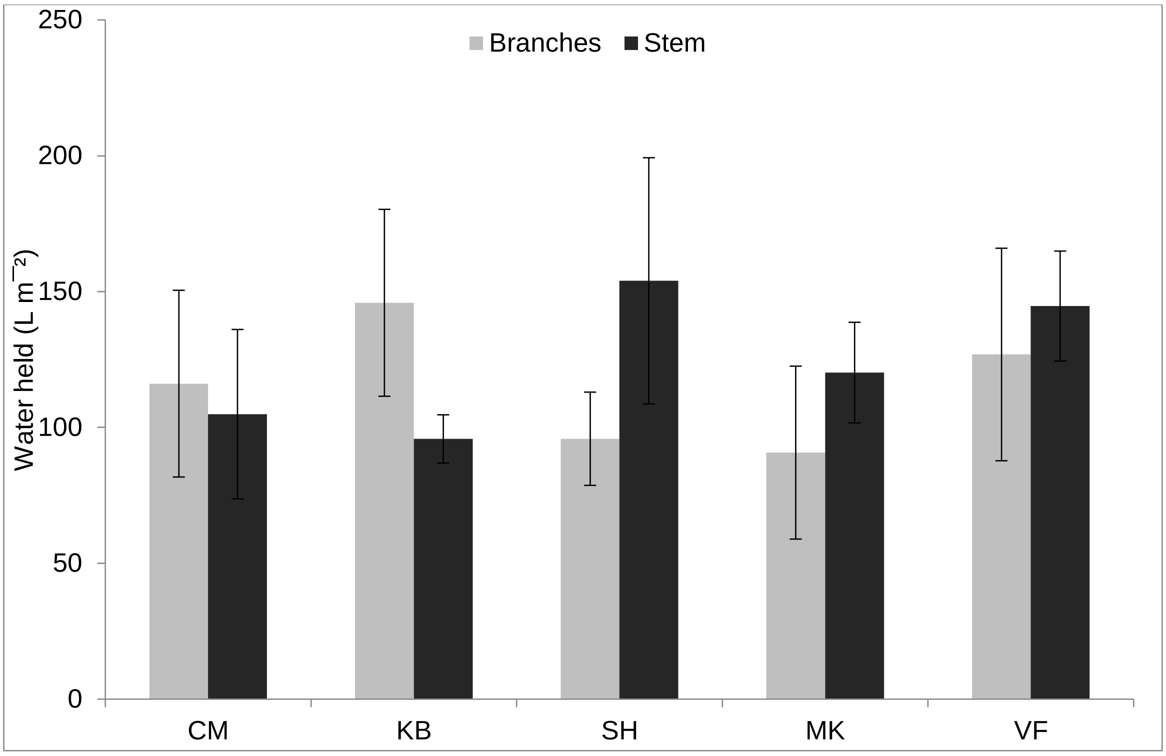
3.7. Supplementary:

Supp Table 3.1: A comparison of major ions (ppm) in fog water from Chile, Oman and Namibia. The results for this study are from monthly fog water samples and are a measure of ionic concentration form both fog water and dry deposition onto the fog collectors. Results of Chile and Oman adapted from Schemenauer and Cereceda, (1992) and Schemenauer and Cereceda, (1992).

Location	Type (ppm)	*n*	Ca	K	Mg	Na	Cl	NO_3	SO_4
Gravel plains (this study)	Fog (wet and dry)	60	86.0	14.1	29.3	462.6	930.9	54.3	215.1
Chile[a]	Fog	7	1.0	0.5	0.7	5.4	8.7	1.6	12.3
Chile[a]	Dry	1	2.8	1.3	2.8	27.4	42.9	5.9	17.5
Oman[b]	Fog	7	15.1	1.1	2.9	24.1	44.1	4.7	3.4
Namibia	Fog	7	1.2	0.2	0.4	2.9	4.8	3.4	3.2
Namibia	Dry	3	12.9	1.8	4.9	41.3	67.3	3.01	18.7

Supp Table 3.2: Mean enrichment factors relative to chlorine in monthly fog water samples from this study, and enrichment values from Chile, Oman and another study done in Namibia. Results of Chile and Oman adapted from Schemenauer and Cereceda, (1992) and Schemenauer and Cereceda, (1992).

Location	Type	Ca	K	Mg	Na	SO_4
Gravel plains (this study)	Fog (wet and dry)	6.44	0.83	0.59	0.97	0.54
Chile[a]	Fog	5.3	2.6	1.3	1.1	10.1
Chile[a]	Dry	3.1	1.5	1.0	1.2	2.9
Oman[b]	Fog	16.3	1.2	1.0	1.0	0.5
Namibia	Fog	17.3	2.3	1.1	1.2	5.8
Namibia	Dry	9.1	1.2	0.9	1.1	2.0



Supp Figure 3.1: The variation in the amount of water (L m^{-2}) held on individual branches and stems of *A. leubnitziae* at the five stations in a transect inland from the coast. Branches and individual stems were wetted by spraying them with water until saturation. Points represent mean ± SE.

4. Synthesis

This study confirms that fog plays a significant role in the distribution of *A. leubnitziae* in the Namib Desert, which is common where fog occurrence is high. Fog contributed 36% to model prediction of the occurrence and distribution range of *A. leubnitziae* (Chapter 2). Based on the distribution of *A. leubnitziae*, its confinement to the central Namib Desert and its easternmost distribution coinciding with the end of the major fog zone, there appears to be a link and dependency of *A. leubnitziae* on fog. The use of fog water by plant species has been demonstrated in other plant species in other fog ecosystems (Baguskas et al., 2016; Borthagaray et al., 2010; Ebner et al., 2011; Gabriel and Jauze, 2008; Hiatt et al., 2012), and this has also been shown *for A. leubnitziae* (Loris, 2004). Apart from occurring in an arid region, *A. leubnitziae* also occurs in an ecosystem with low soil nutrients, especially N and P. Atmospheric deposition of fog and dust is a significant source of nutrients. In the case of nutrients that deposited out of the atmosphere onto plant and soil surfaces, fog is additionally important for making these nutrients available to plants for absorption. It is however not clear whether fog is significant to *A. leubnitziae* for the provision of moisture, nutrients or both.

In addition to the Namib Desert, there are multiple other fog ecosystems around the world, such as Chile (Cereceda et al., 2008), California (Burgess and Dawson, 2004; Dawson, 1998) and the Strandveld of South Africa (Nyaga, 2013). In these Mediterranean coastal ecosystems, fog is the main source of moisture during the dry summer months (Azevedo and Morgan, 1974; Dawson, 1998; Del-Val et al., 2006; Nyaga, 2013; Olivier, 2002). While several studies report fog deposition to ecosystems around the world, most of these studies were specifically focused on the moisture aspect of the fog and the extent to which fog may provide nutrients or facilitate nutrient access in these ecosystems is not clear. Here I discuss the diverse roles of fog in providing moisture, reduction of environmental stress, providing nutrients and facilitating nutrient access within a global context, but informed by my study of *A. leubnitziae*.

4.1. *Contribution of fog to moisture*

Fog is frequent, extends several kilometres inland and is an important source of moisture in the Namib Desert (Fig. 2.2). Fog is also important in other ecosystems and unlike in the Namib Desert where fog is common throughout the year, fog is only common and the key source of moisture during the dry summer months in the Mediterranean fog ecosystems (Azevedo & Morgan, 1974; Dawson, 1998; Nyaga, Neff, & Cramer, 2015; Olivier, 2002). Fog moisture is important in the delivery of moisture to ecosystems, where it is intercepted by the canopies of vegetation and then taken up through the leaves, making this an efficient way to obtain water (Peuke et al., 1998; Yates and Hutley, 1995). For example, fog contributed 92% of the moisture at the five study sites between Sep 2015 and Aug 2016 and contributed 90% of the moisture to the Cape Columbine, along the West Coast of South Africa (Olivier, 2002). The uptake of fog water by vegetation, as a source of moisture has been studied in a number of these ecosystems (Azevedo and Morgan, 1974; Berry, 2014; Carter Berry and Smith, 2014; Dawson and Vidiella, 1998; Eller et al., 2013; Martorell and Ezcurra, 2007; Menges, 1994; Nyaga, 2013; Soderberg, 2010; Westbeld et al., 2009). In the coastal California redwood forest, 25-50% of the total water input each year is contributed by fog (Burgess and Dawson, 2004; Dawson and Vidiella, 1998). In addition, in the Tropical Montane Forests (TMFs) in Chile, up to 42% of the foliar water was contributed by fog water (Eller et al., 2013). Here the uptake of fog by the leaves of water-stressed conifer, *Araucaria angustifolia* showed the greatest impact on their water relations when compared to root moisture uptake (Cassana and Dillenburg, 2013).

Additionally, fog can increase soil water and the direct uptake of water by vegetation (Goldsmith, 2013), thereby improving the water status of plants (Burgess and Dawson, 2004; Gotsch et al., 2014; Reinhardt and Smith, 2008). In other studies on *A. leubnitziae,* fog contributed 18% to the plant stem water of *A. leubnitziae* (Soderberg, 2010). This and other evidence has led to the central Namib Desert, where *A. leubnitziae* occurs, being considered one of the global fog-linked ecosystems. Despite this, the present study found high values of plant $\delta^{13}C$ at the five sites that were similar to those reported by (Soderberg, 2010). Higher $\delta^{13}C$ abundance is expected in plants that are adapted to arid environments (Farquhar, 1991; Farquhar et al., 1989). *A. leubnitziae* is a C_3 photosynthetic plant (Soderberg, 2010) and the high $\delta^{13}C$ values (Liu et al., 2005) suggest *A. leubnitziae* was relatively water stressed. Therefore, despite the large amount of moisture from fog (Fig. 2.1), the plants are still relatively water stressed and it is, therefore, possible that the nutrients in the fog water are of importance in addition to the moisture provided by the fog. Nutrients contained in this moisture may enhance plants growth and could influence biochemistry of the ecosystem (Dawson, 1998).

4.2. Fog ameliorates environmental stresses

In addition to the moisture, the occurrence of fog can have physiological benefits for vegetation. As a result of the cooler conditions associated with fog, harsh climatic conditions can be ameliorated. Fog can reduce temperature, increase moisture availability for plants and minimize water loss (Berry and Smith, 2012). For example, in the presence of fog at the study sites, the average temperature is in the range of 16-17°C during fog events, and in the absence of fog, the range is 17-21°C. Relative humidity is higher (range of 70-80%) during fog and is lower when there is no fog (range of 49-70%), thus showing that fog can make conditions cooler and wetter for *A. leubnitziae* in the Namib Desert. In addition, fog provides shading, therefore, reducing daily water stress, (Burgess and Dawson, 2004) and possibly improving photosynthetic rates (Carbone et al., 2013) due to diffuse rather than direct-beam radiation. As a result of the occurrence of fog in the tropics, cloud forests temperatures are 4°C cooler (Berry, 2014). The alteration of the climate in fog ecosystems can influence the hydraulic functioning and photosynthetic gas exchange of plants and the moisture in the air can reduce transpiration rates by reducing the vapour gradient from the leaf or stem to the air (Berry, 2014). The reduced transpiration rates may improve the plant water status.

4.3. Wet and dry deposition contributes to the nutrients of vegetation

The current study confirmed that wet (fog and rain) and dry deposition contribute significantly to the nutrient availability to *A. leubnitziae* in the central Namib Desert. A substantial input of nutrients (e.g. Ca, Mg, and K) from marine aerosols and dust (Chapter 3) are contributed to the Namib Desert ecosystem by this deposition. While little is known about the contribution of nutrients and pollutants by dry and wet deposition in the Namib Desert, this deposition appears to be a major source of nutrients in this nutrient poor ecosystem, increasing the nutrients available to plants. Nutrients are generally more concentrated in fog than in rain (Collett et al., 2002; Ewing et al., 2012; Weathers et al., 2000, 1986), and fog is, therefore, an important vector of nutrients (Ewing et al., 2012), even in ecosystem where it contributes a small percentage of the water input (Azevedo and Morgan, 1974; Ewing et al., 2009; Weathers et al., 2000). The dry deposition at *A. leubnitziae* sites may be due to dust particles suspended in the air, particles deposited directly onto vegetation or those that were transported from other areas. These particles are then partially dissolved in fog and then taken up by plants. Dust particles trapped by plants on leaves or stems may be washed off by the fog and either increase nutrient availability in the soil (Ochoa-Hueso et al., 2011) or be directly absorbed by the plants once the fog has moistened them. Like fog, dust is common in the Namib Desert (Eckardt et al., 2001) and particles from dust were found in the chemical composition of fog (Soderberg, 2010). Dust inputs from the interior continental regions of Africa may also influence nutrient cycling in the Fynbos biome of South Africa (Soderberg and Compton, 2007) and thereby, improving the nutrient budgets of this ecosystem.

4.4. Fog enables nutrient capture by vegetation

Frequent fog events can increase the leaf-to-water contact surface, thereby allowing water absorption by leaves (Limm et al., 2009) and opportunistic uptake of nutrients, thereby improving nutrient acquisition (FAO, 1990; Heine and Walter, 1996). In addition to the nutrients that form part of fog, dry nutrients (e.g. from dust) are deposited onto plant and soil surfaces (Chen et al., 1985; Kaya and Tuncel, 1997; Ochoa-Hueso et al., 2011). The nutrients in the fog are either taken up directly through the leaves/stems by vegetation or through the soils when plants have been fully saturated and the fog water (enriched with nutrients) drips onto the soil (Azevedo and Morgan, 1974; Vogelmann, 1973). Accumulation of dust particles have been observed at the study sites and this study provided evidence of the uptake of nutrients through the stems of *A. leubnitziae* (Chapter 3). Similarly, Nyaga et al. (2013) showed that nutrients in wet and dry deposition could be taken up from leaf surfaces of Strandveld species in South Africa. The uptake of the nutrients is, however, influenced by the form and amount nutrients (Azevedo and Morgan, 1974), and particularly on the duration of moisture on the leaves and stems (Matimati, 2013). In other fog ecosystems, foliar N uptake by crop species is through stomata (Okana et al., 1990) and base cations were taken up by several species (e.g. *Acer saccharum, Acer platanoides, Citrus aurantium* (Tyree et al., 1990). Thus the depositional nutrient inputs to *A. leubnitziae* are likely both through direct uptake from plant surfaces (e.g. Azevedo and Morgan, 1974; Dawson, 1998) and indirectly from the soil (e.g. Peuke et al., 1998).

Fog is therefore important in making nutrients available to plants by 1) delivering nutrients into ecosystems (for direct absorption and fog drip), 2) moistening nutrients deposited onto plants for direct absorption by the leaves or stems and 3) washing the nutrients off into the soil and increasing soil nutrients (Ochoa-Hueso et al., 2011).

4.5. *Consequences of climate change*

Climate change models suggested that the Benguela current and the adjacent Namib Desert will become warmer as a result of the southward displacement of the Atlantic Ocean High (Engelbrecht et al., 2009). The increase in temperature may cause a decrease in fog in the region. Meanwhile, research over the past century has implicated fog as a key component of the desert ecosystem (Ebner et al., 2011; Louw and Seely, 1980; Louw, 1972; Roth-Nebelsick et al., 2012; Seely et al., 2005; Vogel and Müller-Doblies, 2011). Other studies from similar ecosystems such as the Namib Desert found that due the rise in temperature caused by climate change, the base height of fog clouds will increase and will essentially make this source of water unavailable to plants at lower elevation (Foster, 2001; Still et al., 1999).

A. leubnitziae and other plants in the Namib Desert have been found to directly use fog in various ways and appear to be strongly dependent on this source of water and nutrients for growth and reproduction (Ebner et al., 2011; Roth-Nebelsick et al., 2012; Seely et al., 1977; Soderberg, 2010; Chapter 3). In the California redwood forest, the change in climate has already affected the distribution and frequency of fog (Baldocchi and Waller, 2014; Johnstone and Dawson, 2010). Since the early 20th century, the frequency of fog has decreased by 33% and vegetation may be increasingly drought-stressed (Johnstone and Dawson, 2010). Some of the vegetation in some of the fog ecosystems are closely associated with the occurrence of fog and their distribution and survival rely on the presence of fog (e.g. *A. leubnitziae,* Chapter 1). Further warming is projected for the 21st century (4-6 °C increase relative to present day climate) over the subtropics (Engelbrecht et al., 2015). The increase in temperatures and decrease in the fog could by the end of this century, therefore, have negative impacts on *A. leubnitziae* that relies on fog for moisture and nutrients.

4.6. Conclusion

Foliar uptake of water has been studied in over 70 species globally and has been found to contribute to the water status of these species that includes two species in the Namib Desert. However, work is still required to better understand the importance of fog water uptake. While other studies have focused on the importance of fog water for moisture for other plant species (e.g. *Trianthema hereroensis* and *Stipagrostis sabulicola*) in the Namib Desert, they have neglected consideration of the possible nutritional supply from fog to these species. This work has demonstrated that fog provides and/or enables access to nutrients for *A. leubnitziae* and the same is possibly true for other species in this region, and elsewhere globally. While many studies have considered the importance of fog for nutrient provision globally, there has been a greater focus on moisture provision. The importance of water, nutrients and environmental stress alleviation should not be considered separately in studying the role of fog in determining plant distributions.

4.7. References

Azevedo, J., Morgan, D.L., 1974. Fog precipitation in coastal California forests. Ecology 55, 1135–1141.

Baguskas, S.A., Still, C.J., Fischer, D.T., D'Antonio, C.M., King, J.Y., 2016. Coastal fog during summer drought improves the water status of sapling trees more than adult trees in a California pine forest. Oecologia 181, 137–148. https://doi.org/10.1007/s00442-016-3556-y

Baldocchi, D., Waller, E., 2014. Winter fog is decreasing in the fruit growing region of the central valley of California. Geophys. Res. Lett. 41, 2786–2793. https://doi.org/10.1002/2014GL059712.Received

Berry, Z.C., 2014. The importance of fog for carbon gain, water balance and foliar uptake in southern Appalachian cloud forests. Wake Forest University graduate school of arts and science.

Berry, Z.C., Smith, W.K., 2012. Cloud pattern and water relations in Picea rubens and Abies fraseri, southern Appalachian Mountains, USA. Agric. For. Meteorol. 162–163, 27–34. https://doi.org/10.1016/j.agrformet.2012.04.005

Borthagaray, A.I., Fuentes, M.A., Marquet, P.A., 2010. Vegetation pattern formation in a fog-dependent ecosystem. J. Theor. Biol. 265, 18–26. https://doi.org/10.1016/j.jtbi.2010.04.020

Burgess, S.S.., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): Foliar uptake and prevention of dehydration. Plant, Cell Environ. 27, 1023–1034. https://doi.org/10.1111/j.1365-3040.2004.01207.x

Burns, E., Simonin, K.A., Bothman, A.G., Dawson, T.E., Burns, E., Kevin, L., Bothman, A.G., Dawson, T.E., 2016. Foliar water uptake : A common water acquisition strategy for plants of the Redwood. Oecologia 161, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Carbone, M.S., Park Williams, A., Ambrose, A.R., Boot, C.M., Bradley, E.S., Dawson, T.E., Schaeffer, S.M., Schimel, J.P., Still, C.J., 2013. Cloud shading and fog drip influence the metabolism of a coastal pine ecosystem. Glob. Chang. Biol. 19, 484–497. https://doi.org/10.1111/gcb.12054

Carter Berry, Z., Smith, W.K., 2014. Experimental cloud immersion and foliar water uptake in saplings of Abies fraseri and Picea rubens. Trees - Struct. Funct. 28, 115–123. https://doi.org/10.1007/s00468-013-0934-5

Cassana, F.F., Dillenburg, L.R., 2013. The periodic wetting of leaves enhances water relations and growth of the long-lived conifer Araucaria angustifolia. Plant Biol. 15, 75–83. https://doi.org/10.1111/j.1438-8677.2012.00600.x

Cereceda, P., Larrain, H., Osses, P., Farías, M., Egaña, I., 2008. The spatial and temporal variability of fog and its relation to fog oases in the Atacama Desert, Chile. Atmos. Res. 87, 312–323. https://doi.org/10.1016/j.atmosres.2007.11.012

Chen, L., Arimoto, R., Duce, R.A., 1985. The sources and forms of phosphorus in marine aerosol particles and rain from Northern New Zealand. Atmos. Environ. 19, 779–787. https://doi.org/10.1016/0004-6981(85)90066-6

Collett, J.L., Bator, A., Sherman, D., Moore, K.F., Hoag, K.J., Demoz, B.B., Rao, X., Reilly, J.E., 2002. The chemical composition of fogs and intercepted clouds in the United States. Atmos. Res. 64, 29–40. https://doi.org/10.1016/S0169-8095(02)00077-7

Dawson, T., Vidiella, P.E., 1998. Plant-fog interactions in California and Chile, in: Conference on Fog and Fog Water Collection. Vancouver: Canada, pp. 225–228.

Dawson, T.E., 1998. Fog in the California redwood forest: ecosystem inputs and use by plants.

Oecologia 117, 476–485.

Del-Val, E., Armesto, J.J., Barbosa, O., Christie, D.A., Gutiérrez, A.G., Jones, C.G., Marquet, P.A., Weathers, K.C., 2006. Rain Forest Islands in the Chilean Semiarid Region: Fog-dependency, Ecosystem Persistence and Tree Regeneration. Ecosystems 9, 598–608. https://doi.org/10.1007/s10021-006-0065-6

Ebner, M., Miranda, T., Roth-Nebelsick, A., 2011. Efficient fog harvesting by Stipagrostis sabulicola (Namib dune bushman grass). J. Arid Environ. 75, 524–531. https://doi.org/10.1016/j.jaridenv.2011.01.004

Eckardt, F.D., Drake, N., Goudie, A.S., White, K., Viles, H., 2001. The role of playas in pedogenic gypsum crust formation in the Central Namib Desert: A theoretical model. Earth Surf. Process. Landforms 26, 1177–1193. https://doi.org/10.1002/esp.264

Eller, C.B., Lima, A.L., Oliveira, R.S., 2013. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, Drimys brasiliensis (Winteraceae). New Phytol. 199, 151–162. https://doi.org/10.1111/nph.12248

Engelbrecht, F.., McGregor, J.., Engelbrecht, C.., 2009. Dynamics of the conformal-cubic atmospheric model projected climate-change signal over southern africa. Int. J. Climatol. 29, 1013–1033. https://doi.org/10.1002/joc

Engelbrecht, F., Adegoke, J., Bopape, M.-J., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., Werner, M., Ichoku, C., Gatebe, C., 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. Environ. Res. Lett. 10, 17. https://doi.org/10.1088/1748-9326/10/8/085004

Ewing, H.A., Weathers, K.C., Lindsey, A.M., Templer, P.H., Dawson, T.E., Bradbury, D.C., Firestone, M.K., Boukili, V.K.S., 2012. Fog and soil weathering as sources of nutrients in a California Redwood Forest, in: Proceedings of Coast Redwood Forests in a Changing

California: A Symposium for Scientists and Managers. U.S. Department of Agriculture, Albany, pp. 265–272.

Ewing, H.A., Weathers, K.C., Templer, P.H., Dawson, T.E., Firestone, M.K., Elliott, A.M., Boukili, V.K.S., 2009. Fog water and ecosystem function: Heterogeneity in a California Redwood Forest. Ecosystems 12, 417–433. https://doi.org/10.1007/s10021-009-9232-x

FAO, 1990. Fertility of gypsiferous soils [WWW Document]. FAO SOILS Bull. 62.

Farquhar, G.., 1991. Use of stable isotopes in evaluating plant water use efficiency., in: Proceedings of an International Symposium on the Use of Stable Isotopes in Plant Nutrition, Soil Fertility and Environmental Studies Atomic Energy Agency, FAO Vienna, Austria. pp. 475–488.

Farquhar, G.D., Hubick, K.T., Condon, A.G., Richards, R.A., 1989. Carbon Isotope Fractionation and Plant Water-Use Efficiency, in: Rundel, P.., Ehleringer, J.., Nagy, K.. (Eds.), Stable Isotopes in Ecological Research. Springer, New York: USA, pp. 21–40. https://doi.org/10.1007/978-1-4612-3498-2_2

Foster, P., 2001. The potential impacts of global climate change on tropical montane cloud forests. Earth-Science Rev. 55, 73–106. https://doi.org/10.1016/S0012-8252(01)00056-3

Gabriel, G., Jauze, L., 2008. Fog water interception by Sophora denudata trees in a Reunion upper-montane forest, Indian Ocean. Atmos. Res. 87, 338–351. https://doi.org/10.1016/j.atmosres.2007.11.014

Goldsmith, G.R., 2013. Changing directions: The atmosphere-plant-soil continuum. New Phytol. 199, 4–6. https://doi.org/10.1111/nph.12332

Gotsch, S.G., Asbjornsen, H., Holwerda, F., Goldsmith, G.R., Weintraub, A.E., Dawson, T.E., 2014. Foggy days and dry nights determine crown-level water balance in a seasonal tropical montane cloud forest. Plant, Cell Environ. 37, 261–272.

https://doi.org/10.1111/pce.12151

Heine, K., Walter, R., 1996. Gypcretes of the central Namib Desert, Namibia. Regensburg: Germany.

Hiatt, C., Fernandez, D., Potter, C., 2012. Measurements of fog water interception by shrubs on the California central coast. J. Coast. Conserv. 2, 525–531. https://doi.org/10.1007/s11852-016-0443-y

Johnstone, J.A., Dawson, T.E., 2010. Climatic context and ecological implications of summer fog decline in the coast redwood region. Proc. Natl. Acad. Sci. 107, 4533–4538. https://doi.org/10.1073/pnas.0915062107

Kaya, G., Tuncel, G., 1997. Trace element and major ion composition of wet and dry deposition in Ankara, Turkey. Atmos. Environ. 31, 3985–3998.

Liu, W., Feng, X., Ning, Y., Zhang, Q., Cao, Y., An, Z., 2005. d13C variation of C3 and C4 plants across an Asian monsoon rainfall gradient in arid northwestern China. Glob. Chang. Biol. 11, 1094–1100. https://doi.org/10.1111/j.1365-2486.2005.00969.x

Loris, K., 2004. Nebel als wasserressource für den strauch Arthraerua leubnitziae, in: Walter, H., Breckle, S.. (Eds.), Ökologie Der Erde: Spezielle Ökologie Der Tropischen Und Subtropischen Zonen. pp. 485–489.

Louw, G., Seely, M., 1980. Exploitation of fog water by a perennial Namib Dune grass, Stipagrotis sabulicola. S. Afr. J. Sci. 76, 38–39.

Louw, G.N., 1972. The role of advective fog in the water economy of certain Namib Desert animals. Symp.zool.soc.Lond 31, 297–314.

Martorell, C., Ezcurra, E., 2007. The narrow-leaf syndrome: a functional and evolutionary approach to the form of fog-harvesting rosette plants. Oecologia 151, 561–573. https://doi.org/10.1007/s00442-006-0614-x

Matimati, I., 2013. Functional role of plant water fluxes in nutrient acquisition. University of Cape Town.

Menges, E.S., 1994. fog temporarily increases water potential in Florida scrub oaks. Florida Sci. 57, 65–74.

Nyaga, J.M., 2013. Nutrional contribution of atmospheric deposition to the Strandveld vegetation of West Coast South Africa. University of Cape Town.

Nyaga, J.M., Neff, J.C., Cramer, M.D., 2015. The contribution of occult precipitation to nutrient deposition on the West Coast of South Africa. PLoS One 10, 1–21. https://doi.org/10.1371/journal.pone.0126225

Ochoa-Hueso, R., Allen, E.B., Branquinho, C., Cruz, C., Dias, T., Fenn, M.E., Manrique, E., Pérez-Corona, M.E., Sheppard, L.J., Stock, W.D., 2011. Nitrogen deposition effects on Mediterranean-type ecosystems: An ecological assessment. Environ. Pollut. 159, 2265–2279. https://doi.org/10.1016/j.envpol.2010.12.019

Okana, K., Tobe, K., Furukawa, A., 1990. Foliar uptake of peroxyacetyl nitrate (PAN) by herbaceous species varying in susceptibility to this pollutant. New Phytol. 114, 139–145. https://doi.org/10.1111/j.1469-8137.1990.tb00384.x

Olivier, J., 2002. Fog-water harvesting along the West Coast of South Africa: A feasibility study. Water SA 28, 349–360.

Peuke, A.D., Jeschke, W.D., Dietz, K., Schreiber, L., Hartung, W., 1998. Foliar application of nitrate or ammonium as sole nitrogen supply in Rzcznus communis I. Carbon and nitrogen uptake and inflows. New Phytol. 138, 675–687.

Peuke, A.D., Jeschke, W.D., Hartung, W., 1998. Foliar application of nitrate or ammonium as sole nitrogen supply in Ricinus communis. II. The flows of cations, chloride and abscisic acid. New Phytol. 140, 625–636. https://doi.org/10.1046/j.1469-8137.1998.00304.x

Reinhardt, K., Smith, W.K., 2008. Impacts of cloud immersion on microclimate, photosynthesis and water relations of Abies fraseri (Pursh.) Poiret in a temperate mountain cloud forest. Oecologia 158, 229–238. https://doi.org/10.1007/s00442-008-1128-5

Roth-Nebelsick, A., Ebner, M., Miranda, T., Gottschalk, V., Voigt, D., Gorb, S., Stegmaier, T., Sarsour, J., Linke, M., Konrad, W., 2012. Leaf surface structures enable the endemic Namib desert grass Stipagrostis sabulicola to irrigate itself with fog water. J. R. Soc. Interface. https://doi.org/10.1098/rsif.2011.0847

Seely, M.., de Vos, M.., Louw, G.., 1977. Fog imbition, satellite fauna and unusual leaf structure in a Namib Desert dune plant. S. Afr. J. Sci. 73, 169–172.

Seely, M., Henschel, J.R., Hamilton, W.J., 2005. Long-term data show behavioural fog collection adaptations determine Namib Desert beetle abundance. S. Afr. J. Sci. 101, 570–572.

Soderberg, K., 2010. The role of fog in the ecohydrology and biogeochemistry of the Namib Desert. University of Cape Town.

Soderberg, K., Compton, J.S., 2007. Dust as a Nutrient Source for Fynbos Ecosystems , South Africa. Ecosystems 10, 550–561. https://doi.org/10.1007/S10021-007-9032-0

Still, C.J., Foster, P.N., Schneider, S.H., 1999. Simulating the effects of climate change on tropical montane cloud forests. Nature 398, 608–610. https://doi.org/10.1038/19293

Tyree, M.T., Scherbatskoy, T.D., Tabor, C.A., 1990. Leaf cuticles behave as asymmetric membranes : Evidence from the measurement of diffusion potentials. Plant Physiol. 92, 103–109.

Vogel, S., Müller-Doblies, U., 2011. Desert geophytes under dew and fog: The “curly-whirlies” of Namaqualand (South Africa). Flora Morphol. Distrib. Funct. Ecol. Plants 206, 3–31. https://doi.org/10.1016/j.flora.2010.01.006

Vogelmann, H.., 1973. Fog Precipitation in the Cloud Forests of Eastern Mexico. Bioscience 23, 96–100.

Weathers, K.C., Likens, G., Herbert, B., Eaton, J.S., Bowden, B.W., Andersen, J.L., Cass, D., Galloway, J.N., Keene, W.C., Kimball, K.D., Huth, P., Smiley, D., 1986. A regional acidic cloud/fog water event in the Eastern United States. Nature 319, 657–658. https://doi.org/10.1038/319657a0

Weathers, K.C., Lovett, G.M., Likens, G.E., Caraco, N.F.M., 2000. Cloudwater inputs of nitrogen to forest ecosystem in southern Chile: Forms, fluxes, and sources. Ecosystems 5, 590–595. https://doi.org/10.1007/s100210000051

Westbeld, A., Klemm, O., Grießbaum, F., Sträter, E., Larrain, H., Osses, P., Cereceda, P., 2009. Fog deposition to a Tillandsia carpet in the Atacama Desert. Ann. Geophys. 27, 3571–3576. https://doi.org/10.5194/angeo-27-3571-2009

Yates, D.J., Hutley, L.B., 1995. Foliar uptake of water by wet leaves of Sloanea woollsii, an Australian subtropical rainforest tree. Aust. J. Bot. 43, 157–167. https://doi.org/10.1071/BT9950157