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Efficient fog harvesting by Stipagrostis sabulicola (Namib dune bushman grass)

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ABSTRACT

Stipagrostis sabulicola, an endemic grass species of the central Namib Desert, grows on dune fields under conditions of very low annual precipitation punctuated by regular nocturnal fog events. The objective of this study is to determine to what extent *S. sabulicola* relies on water supply by fog harvesting. The following parameters were monitored: 1) climate, 2) stem runoff, 3) leaf water potential (LWP) and 4) soil water content (SWC). Collected fog water was 5.0 L (liter) per m^{-2} leaf surface and therefore a total harvest of 4-5 L per fog event for a medium-sized mound of *S. sabulicola*. SWC close to a mound increased substantially during a fog event, with SWC at about 2.2% within a mound. LWP of *S. sabulicola* ranged between -1.7 MPa and -3.5 MPa. On days without fog, LWP was highest during the morning and decreased during the afternoon. No significant decrease of LWP occurred during days following a fog event. The increase of *S. sabulicola* a fog event indicates that fog harvest of *S. sabulicola* occurs mainly via stem flow with subsequent absorption by the root system and that fog catchment therefore represents a substantial water source for this species.

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1. Introduction

Fog is recognized as an important plant water source in many habitats and can improve the water status of plants in various ways (Corbin et al., 2005; Dawson, 1998; Fischer et al., 2008; Martorell and Ezcurra, 2002; Ritter et al., 2008; Schemenauer and Cereceda, 1991). The presence of fog can decrease water loss indirectly, mostly via high relative humidity which reduces the water vapor diffusion gradient between atmosphere and leaf interior (Ritter et al., 2009; Simonin et al., 2009). Fog and other sources of foliarly intercepted water can be directly absorbed by leaves (or stems) of many cryptogams and higher plants (Breshears et al., 2008; Gouvra and Grammatikopoulos, 2003; Limm et al., 2009; Munné-Bosch, 2010; Slatyer, 1960). Atmospheric bromeliads, mostly of the genus Tillandsia, provide a classic example, but the ability of water absorption can be found in various other taxa as well (Boucher et al., 1995; Burgess and Dawson, 2004; Yates and Hutley, 1995). Another way how fog can contribute to the water supply of higher plants is via fog drip (occult precipitation) (Dawson and Pate, 1996; Fischer et al., 2008; Schemenauer et al., 1988) which functions in that fog is intercepted by surfaces, the droplets coalesce and finally water trickles down to the ground. Water input by fog can represent

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a substantial amount of the annual precipitation rate at certain sites (Kämmer, 1974; Ritter et al., 2008).

The relative importance of fog as a source of water supply for vegetation increases with decreasing annual amounts of rain (Kämmer, 1974). It is therefore to be expected that fog precipitation is of particularly high significance for arid environments in which fog events regularly occur. A hyperarid system with a regular and reliable fog season is represented by the Namib Desert of the southwestern African coast. Its dune fields are an extremely challenging environment for life. Annual rainfall amounts to about 19 mm on average (Lancaster et al., 1984; Southgate, 1996). Due to the upwelling Benguela Current of the southwestern African coast, the Namib receives quite regular fog events. The fog is transported into the Namib by inland winds and subsequent input of water by fog can be higher than precipitation by rain (Pietruszka and Seely, 1985). Fog represents the only predictable source of water in the western area of the hyperarid Namib Desert. For example, between 1966 and 2000, fog events occurred in 88% of 324 months (Seely et al., 2005). Fog therefore represents a significant source of water for the Namib biota (Pietruszka and Seely, 1985).

Since the Namib is a very old desert — arid conditions have been nearly continuous for the last 20 million years (Ségalen et al., 2006) its flora and fauna have been exposed to selection pressure of drought over a very long time span. The Benguela Current, that leads to the development of fog in this region intensified during the Upper Miocene onwards (Ségalen et al., 2006) and fog water input therefore very probably represents a condition that has prevailed





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over several million years. It is thus to be expected that many organisms developed strategies to utilize fog water via selective pressure. Various studies confirm the ability of different Namib organisms to exploit fog water. Several tenebrionid beetles, for example, use different strategies of fog harvesting, such as direct fog basking or the construction of fog catching sites in the dune sand (Hamilton and Seely, 1976; <u>Naidu, 2008; Seely and Hamilton, 1976</u>). The ability of fog harvesting is therefore to be expected for plants of the Namib as well.

Various species of the genus Stipagrostis (Poaceae) are important elements of the Namib vegetation. The genus Stipagrostis occurs only in the Old World, mostly Africa, Middle East and Asia, where it is limited to the drier areas (Clayton et al., 2006; de Winter, 1965; GrassBase - The Online World Grass Flora.http://www.kew.org/ data/grasses-db.html[accessed 08 November 2006; 15:30 GMT]*). Despite the preferentially arid habitat, most species of *Stipagrostis* are perennials. This is also valid for Stipagrostis sabulicola (Pilg.) De Winter (Poaceae) which occurs exclusively in the Namib-Erg (or Namib Sand Sea). Together with Trianthema hereroensis (Aizoaceae), it represents one of the few successful and persistent inhabitants of the dunes (Robinson and Seely, 1980). Particularly S. sabulicola is able to add biomass to the dune system while nothing else can grow (Southgate, 1996). Frequently, T. hereroensis and S. sabulicola occur together and both are able to survive under annual rain precipitation rates less than 20 mm (Louw and Seely, 1980; Seely et al., 1977; Veste and Mohr, 2005). An ecological study of a transect reaching 100 km inlands after a period with subaverage annual rainfall of several years (Veste and Mohr, 2005) showed that in the western region of the Central Namib, only S. sabulicola and T. hereroensis were able to persist on many sites.

Direct fog absorption was demonstrated for *T. hereroensis* (Aizoaceae), which absorbs titrated water via its leaves and transports it to the root system (Seely et al., 1977). The strong ability to persist on dunes during dry years indicates that *S. sabulicola* is also able to utilize high amounts of fog. In the present study, the ability of *S. sabulicola* for fog harvesting by stem flow during fog events ("fog combing") was explored. For this purpose, several parameters were determined during a fog season: 1) the amount of stem flow during fog events, 2) soil water content (SWC) at different distances from a plant, 3) leaf water potential (LWP) and 4) climate parameters during the entire study. Particularly, this study focuses on the quantification of stem flow rates and the influence of stem flow on SWC close and within tussocks of *S. sabulicola*.

2. Material and methods

2.1. Site description

The study site is located close to the Gobabeb research station (23°34′S, 15°03É, elevation 408 m) on a dune, termed Station dune which is 1 km off the station. Numerous individuals of *S. sabulicola* settle at this dune (Supplementary Information, Figure S1). *S. sabulicola* represents the dominant plant species (see also Yeaton, 1990). At the base of the dune where soil conditions change due to the transition from dune sand into gravel, some individuals of *S. sabulicola* coexist with the grass species *S. lutescens, S. ciliata, Centropodium glaucum* and isolated patches of *Acanthosicyos horridus*, the Nara melon (Cucurbitaceae). *S. sabulicola* is the only higher plant that can be found on the upper section of the transect and in pure dune sands.

The position of all plants at the study site was mapped by a GARMIN 60 Csx GPS, plotted out by the MAPESOURCE software and related to the topography of the dune. Five tussocks of *S. sabulicola* were selected settling at a transect along the western slip of the Station dune (Supplementary Information, Figure S1). All measurements were performed on these 5 individuals from 6 September 2008 to 26 November 2008. During this time interval, 10 fog events occurred.

2.2. Monitoring of environmental parameters

2.2.1. Climate

The climatic parameters at the study site were recorded by using the mobile weather station WD-2700 (Watchdog, PCE group, PCE Germany, D-59872 Meschede, Germany). The weather station was placed in the vicinity of individuals 1 and 2 (Supplementary Information, Figure S1). The recordings were read with the software WD-SPEC. Air temperature, soil temperature, leaf temperature, relative humidity (RH), photosynthetic active radiation (PAR) and solar radiation, precipitation, wind speed and wind direction were logged at intervals of 5 min during the entire observation period (6 Sep 2008–25 Nov 2008). Fog occurred during periods with an RH of 100% and was additionally verified by observation.

2.2.2. Soil water content

Soil water dynamics adjacent to the study plants were determined by using the ML2x Theta Probe Soil Moisture Sensor (Delta-T Devices, Burwell, Cambridge, U.K.). The Theta Probe was connected to an HH2 read-out device (Delta-T Devices, Burwell, Cambridge, U.K.). The Theta Probe determines soil moisture content by measuring the apparent dielectric constant of the soil (Delta-T devices 1999). The measurement procedure applies to a sample volume of about 75 cm³ around the central signal rod. The signal rod had a length of 6 cm. Since the Theta Probe may overestimate SWC slightly (Robinson et al., 1999), the original substrate (dune sam) was used for a laboratory calibration. For this, SWC of several samples of moistened substrate was measured with the Theta Probe and subsequently determined gravimetrically. The difference in SWC between both methods amounted to 0.1%.

In the field, SWC was measured during days with and without fog and at different times of the day. Measurements were carried out on 7 days with fog and on 20 days without fog events. During the measurement, soil water was determined at defined locations with respect to culms and mounds of S. sabulicola. Within a mound, measurements were located directly at a stalk in such a way, that the (theoretical) connection line between two of the three probe rods is a tangent to the stalk. The measurements were then performed subsequently at a distance of about 0.05 m from the stalk bases (for the entire measurement set up, see Fig. 1). After performing the in-mound measurements, additional measurements were carried out outside the mounds, at distances of 0.5 m and 1.5 m from the boundary of the mound (see Fig. 1). Measurements were performed at least two times per measurement day and at different times of the day: in the early morning (4 AM), morning (8 AM), forenoon (11 AM) and afternoon (5 PM).

Three measurements of soil water content (SWC) were carried out at each of the 26 positions (Fig. 1). The three measurement results per position were subsequently averaged. This measuring procedure was performed at each study plant.

2.2.3. Leaf runoff

Water runoff at leaves of *S. sabulicola* represents the fog harvesting performance of the plant. To determine runoff, clamp-on collectors were constructed according to the following requirements: 1) high absorptive capacity, 2) fog absorption by the collector itself as small as possible, 3) minimized evaporative loss of runoff water already collected, 4) no influence on position or shape of leaves, and 5) non-invasive. The resulting collectors consisted of a hinged block of a super absorbent cellulose material (sponge cloth, Vileda GmbH, Weinheim, Germany).



Fig. 1. Locations of measurements of SWC with respect to mound and culms of *S. sabulicola*. Dotted circle: mound of *S. sabulicola*. Thin black circular and elliptic outlines: Bases of culms and culm groups within a mound. Thick black circles: arrangement of in-mound measurements. Black rectangles: measurements directly at a stalk base (Position X = 0). Gray rectangles: measurements at a distance of about 0.05 m from a stalk base (Position X = 1). White rectangles: measurements outside mounds at defined distances from the mound border (X = 2) (0.5 and 1.5 m). The distance between the mound and the measurement points outside of the mound in the figure has been interrupted at various positions for depiction purposes.

The collectors were coated by a plastic tape, which served as an isolation device preventing evaporation or fog interception to a large degree. Between leaf surface and collector, a small gap allowed for the entrance of fog water running down the leaf (see Figure S2). The dimensions of the collectors were $3 \times 2 \times 0.5$ cm, with a dry weight of around 1 g. The collectors were clamped around the leaves, at a distance of about 30 cm from the leaf tip (Figure S3). This ensured that the collecting area was almost identical for each measurement and this allowed for calculating the fog harvesting rate per leaf area. The collectors could be easily clamped to and removed from the leaves without substantially changing their natural position. The collectors were extensively tested under natural conditions, at the Federsee Lake in Baden-Württemberg, Germany. Here, the collectors were clamped to various grasses, in particular to *Phragmites australis*.

During each measurement cycle, collectors were attached to 3-5 leaves of the 5 test plants of S. sabulicola, respectively, which were (randomly) selected from the individuals that populate the dune slope (Figures S1, S2). Per measurement cycle, 20 leaves were thus monitored on average. Since several plants of S. lutescens grew in the vicinity of the S. sabulicola tussocks, three leaves of these individuals were included in the runoff monitoring to obtain information on the magnitude of fog harvesting in this species, compared to S. sabulicola. Furthermore, a control collector was placed on a pad adjacent to the study plants to obtain control data with respect to fog absorption by the collector material. During a measurement cycle, collectors were sampled at 4:00 AM (only during fog events), 8:00 AM (each day), 10:30 AM (only during fog events), and at 4:00 PM (each day). After sampling, the collectors were exchanged with dry collectors. The amount of absorbed water in the sampled collectors was gravimetrically determined by the precision balance KERN EW 620 (Kern and Sohn, Balingen, Germany). For this purpose, sampled collectors were sealed in a plastic bag and immediately brought to the station for weighing. The control collectors were treated identically. The weight gain of the control collectors (which was always very low) was subtracted from the data of the leaf collectors.

Leaf runoff (= water that trickled down the leaves and was finally absorbed by the collectors during a measurement cycle) was calculated as follows. Geometric features (diameter and height) of the plants were determined with a tape measure and calipers. This served as a basis for approximating the aboveground biomass and surface area. The upper part of the leaf segment above the collectors is coneshaped (upper 4/5 of segment length) whereas the remaining lower part (lower 1/5 of the segment length) is cylindrical. From these measurements, the following equation for the total surface area of the leaf segment was derived (A_{total} = total surface area, A_{cone}^{approx} = approximated area of cone part, $A_{cylinder}$ = surface area of cylinder part, D = diameter, h = height = segment length):

$$A_{total} = A_{cone}^{approx} + A_{cylinder} = \frac{D^*h^*\pi}{5} + D^*h^*\pi^*\frac{1}{2}*\frac{4}{5} = D^*h^*\pi^*\frac{3}{5}$$
(1)

2.2.4. Measurement of leaf water potential

The water potential of *S. sabulicola* leaves was determined for two study plants which were also used for the runoff measurements. Water potential was measured by using a portable PSY-PRO[™] water potential system (Wescor, Inc., Logan, Utah, USA). As water potential sensor, a C-52 sample chamber (Wescor, Inc., Logan, Utah, USA) was connected to the PSYPRO. Leaf sap was obtained by using the Markhart leaf press (Wescor, Inc., Logan, Utah, USA) which allows for extraction of the liquid sample directly onto a filter paper disc. After soaking of the filter paper disc, it was swiftly transferred to the C-52 sample chamber.

For determination of leaf water potential (LWP), leaves were harvested in the field, sealed in a plastic bag and immediately brought to the station. In order to facilitate the extraction of leaf sap, the leaf samples were frozen at -20 °C while still sealed in the bag, and liquid samples were obtained after thawing. Previous control measurements of frozen versus unfrozen samples revealed no significant differences in water potential. The measurement and calibration routines of the PSYPROTM water potential system was carried out according to standard routines with a commercial calibration solution (Wescor, Inc, Logan, USA). Calibration was performed before each measurement cycle and one to two times during a measurement cycle. From the 17th until the 25th of September 2008, water potential was measured during 8 days with and without fog at different daytimes. Fog events occurred during this time on the 18th, the 22nd and the 25th of September. The water potential of leaves of (at least) a young and an old study plant was determined, with separate measurement of leaf blade and leaf sheath. Younger leaves could be identified by color and texture. At least three measurements were performed on each sample.

2.2.5. Statistical analysis

For the statistical analysis, SPSS 16.01 was used. For soil water content, a non-parametric test for dependent samples was applied, because the data showed no clear trend for normal distribution (Q–Q diagram in SPSS 16.01) and the data were collected from the same individuals during the measurement period. Differences between all soil locations under conditions of either fog and no fog were therefore tested with the Friedman-test for K dependent samples (SPSS 16.01). Furthermore, the differences in SWC at the single locations for the two conditions fog and no fog were tested

pairwise with the Wilcoxon test for dependent samples (SPSS 16.01).

Leaf water potential data also showed no normal distribution. The non-parametric Wilcoxon test (SPSS 16.01) for dependent samples was used to test the differences between the average water potential values on days following a fog event and on days without previous fog event.

3. Results

3.1. Climate parameters

Usually, fog occurred between 12 AM and 4 AM during the night and early morning. The occurrence of fog has no large impact on most parameters of daily average climate (Fig. 2). Besides saturation



Fig. 2. Daily average climate for each month of the measurement period for days with and without fog, based on daily and continuous climate monitoring. (A), (B) and (C): Daily average climate on days with fog for the months September, October and November, respectively. (D), (E) and (F): Daily average climate on days without fog for the months September, October and November, respectively. Wind speed: [km/h]. SVPD_{air}: Saturation vapor pressure deficit [kPa]. Solar radiation: [Watt/m²]. Leaf temperature: [°C]. Soil temperature: [°C]. Air temperature [°C].

vapor pressure deficit of air (SVPDair), which is substantially higher during fog nights compared to nights without fog, wind speed is often somewhat higher during fog nights. Typically, high wind speeds occurred during the afternoon to early evening, and reached lowest levels during the night. Nocturnal wind speed was by about 5 km/h slightly higher during nocturnal fog events. Temperature fluctuated between about 10 °C minimum during the night and 30 °C maximum during the day. During nocturnal fog events, air temperature decreased faster toward the minimum. Air temperature during fog events amounted typically to about 10 °C, some degrees lower than during nights without fog. Also, air temperature can be some degrees lower on days with preceding nocturnal fog event. Leaf temperature usually exceeded air temperature about several degrees during the day, with the highest leaf temperatures during September (more than 5° higher than air temperature). Soil temperature increased during the morning, approaching almost 50 °C during noon.

3.1.1. Fog precipitation and leaf runoff

Soon after onset of fog, drop formation and coalescence could be observed on the leaves of *S. sabulicola* (Figure S4(a)). Dripping occurred from the tips of sagging leaves. In many cases, however, the plant axes were straight and upright. In these cases, the drops increased in size, fused by coalescence and then a trickle formed periodically toward the plant base (Figure S4(a)). Moist patches developed at the plant bases which frequently showed significant extension after a fog event (Figure S4(b)).

In corroboration to these qualitative observations, the collectors attached to S. sabulicola leaves showed regularly significant input of fog water (Fig. 3). The fog collection rate showed a high temporal variability. It was on average highest in the collectors sampled at 4:00 AM, usually some few hours after onset of fog. No substantial amount of fog absorption could be detected in collectors sampled later than 8:00 AM. The total average amount of fog harvesting per leaf area and fog event amounted to about 5.5 L m^{-2} (amount of collected water per leaf surface area) for S. sabulicola (Fig. 3). For a medium-sized individual of S. sabulicola, with around 70 culms and a height of 1.5 m, this means an average water acquisition amount of about 4-5 L per fog event. Fog harvesting was markedly lower for S. lutescens with about 0.91 Lm⁻². In fact, the development of moist patches around S. lutescens was much weaker or even absent during fog events. The data that were available for S. lutescens did not allow for a further systematic statistical comparison with the results for S. sabulicola. The results for S. lutescens, however, do not indicate a substantial fog harvesting rate for this species as well.

3.2. Soil water dynamics

SWC showed a high spatial and temporal variability. No statistically significant differences could be detected for 1) SWC at a defined location at the days before and at least 24 h after fog events (= days with fog absence) and 2) SWC at different locations outside the mounds on days with fog or on days without fog. The data were therefore analyzed by using the following grouping variables: 1) Location X "Stalk" (X = 0), "Mid-canopy" (X = 1) and "Intercanopy" (X = 2, bare soil), and 2) days "with fog" and "without fog" (Fig. 1).

During days with fog, SWC at *S. sabulicola* was particularly higher inside the mounds with highest values at the culm bases (X = 0) (Fig. 4). Here, values of about 2.2% were attained. Further away from the culm bases (X = 1), but within the mound, the average SWC amounted to about 1.28%. Bare soil outside the mound (X = 2) showed generally much lower water content with about 0.8% also during fog events (Fig. 4). SWC therefore decreased with 1) distance from culm bases, and 2) fog absence.



Differences between all locations under conditions of either fog and no fog were tested with the Friedman-test for K dependent samples and found to be highly significant under fog as well as no fog (P < 0.001). Furthermore, the differences in SWC at the single locations for the two conditions fog and no fog were tested pairwise with the Wilcoxon test for dependent samples. The differences for the position "Stalk" between days with and without fog as well as the position "Mid-canopy" are highly significant (P > 0.001) whereas the differences for the position "Intercanopy" are insignificant (P = 0.4).



Fig. 4. Soil water content (SWC) at mounds of *S. sabulicola* on days following a fog event (gray boxes) and on days without previous nocturnal fog (white boxes). The measurements were performed on five plants (see Supplementary Information, Figure S1). The number of measurements is indicated in the figure. SWC was determined at different locations with respect to mound and culms: X = 0: "Stalk", close to culm base. X = 1: "Mid-canopy", at a distance of 0.05 m from culm base but within mound. X = 3: "Intercanopy", outside the mound. The vertical lines mark the highest and lowest value, and the boxes span the 50% interquartile. The median is indicated by the horizontal line within the boxes. Single outliers are drawn as circles. Extreme values are represented by asterisks.

3.3. Leaf water potential

Leaf water potential values of *S. sabulicola* ranged between -1.7 MPa and -3.5 MPa and reached highest negative values on days without fog toward the afternoon (Fig. 5). After nights with fog, the leaf water potential was particularly high in the morning and decreased only slightly during morning and noon (Fig. 5). The differences between the average water potential values on days following a fog event and on days without previous fog event were statistically significant *P* < 0.001 (non-parametric Wilcoxon test for dependent samples).

4. Discussion

According to the data presented in this study, S. sabulicola is able to harvest substantial amounts of water from nocturnal fog events. For a plant with 70 culms forming a total leaf area of 1 m² and which occupies a mound area of about 1 m², an average amount of 4-5 L is harvested per fog night which corresponds to a local precipitation event of 4-5 mm for the mound. As fog occurs on 60-200 days per year in the hyperarid Namib desert (Lancaster et al., 1984) annual fog precipitation can thus range between 240 and 1000 mm for a single mound. This mound precipitation inside S. sabulicola plants equals the precipitation in vegetated savannas (Walter and Breckle, 2004) and is substantially higher than the average amount of 20 mm that this region receives per year. This is probably the principle reason why S. sabulicola is able to support a high amount of vital, assimilating aboveground biomass throughout the year. Nutrient availability, however, may limit the productivity of S. sabulicola (Southgate, 1996).

As a result of fog water input, SWC within the mound increases significantly, particularly close to the culm bases. Since culms of *S. sabulicola* are often stiff with an upright habitus, fog harvesting occurs via stem flow that conducts water directly toward the root

-1.8 -2.0 -2.2 -2.4 -2.2 -2.4 -2.5 -2.6 -3.0 -3.2 -4:00 8:30 11:00 16:00 Time of day

Fig. 5. Leaf water potential of *S. sabulicola*, measured at different daytimes for days with (circles) and without (rectangles) previous nocturnal fog event. The data points represent the statistical mean, with the error bars representing the 95% Confidence Interval. The measurements were performed on different leaves of two plants. Number of measurements: for days without fog: 4:00, n = 42, 8:30, n = 67, 11:00, n = 33, 16:00, n = 77; for days with fog: 4:00, n = 44, 8:30, n = 61, 11:00, n = 64, 16:00, n = 23. For details see text.



zone of a plant and water is collected within the area of the mound. Due to the uneven distribution of water by stem flow and by fog drip due to sagging leaves, SWC within a mound shows high spatial heterogeneity after a fog event. Outside a mound, the water content is not substantially increased and the values for bare soil agree with results obtained for dry sand by Yeaton (1988) who measured SWC values of 0.4%–0.9%. According to Yeaton (1988), SWC of Namib dunes were 1.5%–2.6% 10 days after rain. The measured in-mound SWC after fog events is therefore close to SWC during rainy periods.

Leaf water potentials of S. sabulicola were similar to results obtained for several other grass species of arid zones (Grigg et al., 2008; Liu et al., 2004; Pavlik, 1980). There are, however, reports about much lower water potentials in tussock grasses elsewhere. The differences in water potential and its diurnal course between days with and without fog suggest that the water status of the plants is improved by fog. The fact that grasses can benefit from fog was also demonstrated for other sites. Uptake of fog water was shown for tussock grass in New Zealand and for coastal prairie grasses in California (Corbin et al., 2005; Ingraham and Mark, 2000). In the study of Corbin et al. (2005), it was found that the different species exploit fog water to a different degree. Calamagrostis nutkaensis benefited particularly from fog input. For this species, 66% of its water originated from fog (Corbin et al., 2005). Whereas it could not be excluded that some water entered the plants via the leaves, the main portion of water was absorbed by the roots which concentrated in shallow soil lavers despite the fact that SWC was higher in larger soil depths (Corbin et al., 2005).

For S. sabulicola, the increase in SWC within a mound and the improved afternoon water status of culms indicate that also in this species the harvested fog water is preferentially absorbed by the root system. Another possibility would be imbibition of fog water by the leaves, as was demonstrated for T. hereroensis (Seely et al., 1977) and for leaves of Sequoia sempervirens (Burgess and Dawson, 2004). There are no specialized sites for water absorption detectable in S. sabulicola, contrary to T. hereroensis where petiolar wings being fused at their basis are considered as absorptive sites (Seely et al., 1977). In S. sempervirens, however, older stomata were suggested as sites of entrance of fog water (Burgess and Dawson, 2004). It therefore cannot be excluded that in S. sabulicola fog water may also be absorbed to a certain degree directly be the leaves. It should be noted that leaf wetting alone can be beneficial for plant water relations since it can prevent water loss due to nocturnal transpiration, facilitates nighttime re-equilibration with soil water and therefore increases pre-dawn leaf water potential (Caird et al., 2007; Donovan et al., 2003; Limm et al., 2009).

That stem flow and subsequent absorption by the root system is an important mechanism for fog exploitation in *S. sabulicola* is also supported by the results of the irrigation experiments of Yeaton (1990). In these experiments the water was exclusively supplied to the soil around the plants. Leaf water potential of *S. sabulicola* increased rapidly, within 1.5 h after irrigation (Yeaton, 1990). Other species needed much longer time for water uptake. *S. sabulicola* is therefore in fact able to take up water very rapidly, probably due to the preferentially shallow root system of this species (Louw and <u>Seely, 1980;</u> Yeaton, 1990) which represents a good device for absorbing surface moisture. In our own observations, roots of *S. sabulicola* were found to be not deeper than about 0.2 m. It should be noted, however, that rooting depth is quite dynamic due to sand movements (Yeaton, 1990).

S. sabulicola also possesses a rhizosheath, a layer of soil particles which are cemented to root hairs by root mucopolysaccharides (<u>Price, 1911</u>). Besides other functional benefits, a rhizosheath may also prevent water loss from root to soil by forming soil-air gaps during soil drying (Nobel and North, 1992). Additionally,

a rhizosheath is able to store a limited amount of water and thus to improve water supply up to 25% (<u>Bristow et al., 1985</u>). The rhizosheath of *S. sabulicola* may therefore contribute to the efficient exploitation of collected fog water.

Louw and Seely (1980) moistened the top 1 cm of the soil with tritiated water close to some individuals of S. sabulicola. Since the main portion of tritiated water was present in horizontal roots 24 h after irrigation. Louw and Seely (1980) inferred that S. sabulicola would exploit fog water by absorbing condensed fog water by shallow roots. During a fog event, however, only the topmost layer up to a depth of about 2 mm is wetted in most cases as reported by Veste and Mohr (2005) and as was also observed by the authors (pers. obs.). Whereas it is possible that during intense fog events some substantial amount of fog moistens the sand surface, this is probably seldom the case for the majority of fog events. Values of SWC of the sand outside a mound were still in the range of values characteristic for dry sand (Yeaton, 1988), contrary to the area within mounds where SWC showed values of available water. That S. sabulicola benefits from fog by uptake via the roots, as suggested by Louw and Seely (1980) is therefore corroborated by the results of this study. The presented data, however, do not support water supply by fog condensation on the sand but by efficient fog harvesting and subsequent stem flow and fog drip.

How does S. sabulicola attain the high runoff rates? The total amount of water that is combed out during a fog event and reaches the ground depends on various factors originating from climate, terrain and vegetation characteristics (Ritter et al., 2008 and references therein). Climate factors that particularly contribute to fog drip are fog properties (such as droplet size and density) and wind speed. Vegetation characteristics include factors such as canopy height and size and arrangement and size of leaves. Narrow leaves with a high length-to-width ratio are usually expected to represent efficient fog-catchers (Martorell and Ezcurra, 2007; Merriam, 1973; Ritter et al., 2008; Went, 1955 and references therein). The first step of fog catchment is the contact between fog droplet and an obstacle and the subsequent absorption and coalescence of fog droplets. The most important mechanism for fog collection is represented by impaction and interception (Goodman, 1982; Monteith and Unsworth, 2008; Rubenstein and Koehl, 1977; Walmsley et al., 1996). Collection efficiency by these mechanisms increases with decreasing obstacle diameter, increasing obstacle density, increasing droplet size and density, increasing wind velocity and decreasing boundary layer thickness (which decreases with decreasing obstacle diameter and increasing wind velocity).

Like in many other species of Stipagrostis, the leaves of S. sabulicola are stiff and pungent and often rolled into a horse-shoe like shape, with a diameter of about 3 mm. The culm surface as well as the lower surface of the leaf blade (which represents the surface if the leaf blade is convolute) is glabrous. Water droplets, which are transported horizontally in a wind-driven airstream impact on the surface of S. sabulicola, coalesce and are subsequently channeled down along the leaves and stalks to the base of the plant. In other species of Stipagrostis growing in the same region, such as S. lutescens, the leaves are not upright but usually more perpendicular to the culm and the plants are substantially shorter than S. sabulicola which attains heights of 2 m and builds mounds of considerable size (see Figure S2). Furthermore, the inflorescences of S. sabulicola appear to be not very persistent, contrary to other species, such as S. lutescens and S. ciliata. All plants of S. stipagrostis that were visited during this study showed shed inflorescences (flowering time December-January). It is possible that the presence of inflorescences during the fog season would impair fog harvesting capacity, because inflorescences may prevent fog water from running straight down the leaf and culm. The combination of numerous tall, upright and narrow linear culm/leaf elements, together with a quite high density of these elements appears to be rather suitable for fog harvesting. The overall architecture of *S. sabulicola* is probably one important factor that leads to a high capability for fog harvesting.

It is very likely that the fog harvesting ability of S. sabulicola represents the most important factor that enables this species to persist successfully in the Namib dune area even in very dry years and to contribute vital biomass to this hyperarid environment. Since mounds of S. sabulicola provide shelter and food for many animals, such as termites, ants, beetles and lizards, the nocturnal fog catchment is of high significance for the ecosystem of the Namib dunes as a whole.

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Appendix. Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.jaridenv.2011.01.004.

References

- 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 Physiology 15, 819-823.
- Breshears, D., McDowell, N.G., Goddard, K.L., Dayem, K.E., Martens, S.N., Meyer, C.W., Brown, K.M., 2008. Foliar absorption of intercepted rainfall improves woody plant water status most during drought. Ecology 89, 41-47.
- Bristow, C.E., Campbell, G.S., Wullstein, L.H., Neilson, R., 1985. Water uptake and storage by rhizosheaths of Oryzopsis hymenoides. A numerical simulation. Physiologia Plantarum 65, 228–232. Burgess, S.S.O., 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 and Environment 27, 1023–1034.
- Caird, M.A., Richards, J.H., Donovan, L.A., 2007. Nighttime stomatal conductance and transpiration in C₃ and C₄ plants. Plant Physiology 143, 4–10. Clayton, W.D., Harman, K.T., Williamson, H., 2006. In: Trustees, T.B.O. (Ed.), Grass-
- Base The Online World Grass Flora. Royal Botanic Gardens, Kew.
- 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.
- Dawson, T.E., 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117, 476-485.
- Dawson, T.E., Pate, J.S., 1996. Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia 107, 13-20.
- de Winter, B., 1965. The South African Stipeae and Aristideae (Gramineae). Bothalia 8 201-404
- Donovan, L.A., Richards, J.H., Linton, M.J., 2003. Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. Ecology 84, 463-470.
- Fischer, D.T., Still, J.C., Williams, A.P., 2008. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. Journal of Biogeography 36 (4), 783-799.
- Goodman, J., 1982. Water Potential from Advection Fog. Department of Meteorology Progress Report. San Jose State University.
- Gouvra, E., Grammatikopoulos, G., 2003. Beneficial effects of direct foliar water uptake on shoot water potential of five chasmophytes. Canadian Journal of Botany 81, 1278–1284.
- Grigg, A.M., Veneklaas, E.J., Lambers, H., 2008. Water relations and mineral nutrition of Triodia grasses on desert dunes and interdunes. Australian Journal of Botany 56, 408-421
- Hamilton III, W.J., Seely, M.K., 1976. Fog basking by the Namib desert beetle, Onymacris unguicularis. Nature 262, 284-285.

- Ingraham, N.L., Mark, A.F., 2000. Isotopic assessment of the hydrologic importance of fog deposition on tall snow tussock grass on southern New Zealand uplands. Austral Ecology 25, 402-408.
- Kämmer, F., 1974. Klima und Vegetation auf Tenerife, besonders im Hinblick auf den Nebelniederschlag. Lehrstuhl für Geobotanik der Universität Göttingen, Göttingen.
- Lancaster, J., Lancaster, N., Seely, M.K., 1984. Climate of the central Namib desert. Madoqua 14 (1), 5-61.
- Limm, E.B., Simonin, K.A., Bothman, A.G., Dawson, T.E., 2009. Foliar water uptake: a common water acquisiton strategy for plants of the redwood forest. Oecologia 161, 449-459.
- Liu, W., Meng, F.-R., Zhang, Y., Liu, Y., Li, H., 2004. Water input from fog drip in the tropical seasonal rain forest of Xishuangbann, South-West China. Journal of Tropical Ecology 20, 517–524.
- Louw, G.N., Seely, M.K., 1980. Exploitation of fog water by a Perennial Namib dune grass, Stipagrotis sabulicola. South Africa Journal of Science 76, 38-39.
- Martorell, C., Ezcurra, E., 2002. Rosette scrub occurrence and fog availability in arid mountains of Mexico. Journal of Vegetation Science 13, 651-662.
- 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
- Merriam, R.A., 1973. Fog drip from artificial leaves in a fog wind tunnel. Water Resources Research 9, 1591-1598
- Monteith, J.L., Unsworth, M.H., 2008. Principles of environmental physics. 3rd Ed. Elsevier, Academic Press, Amsterdam.
- Munné-Bosch, S., 2010. Direct foliar absorption of rainfall water and its biological significance in dryland ecosystems. Journal of Arid Environments 74, 417-418.
- Naidu, S.G., 2008. Why does the Namib desert tenebrionid Onymacris unguicularis (Coleoptera:Tenebrionidae) fog-bask? European Journal of Entomology 105, 829-838
- Nobel, P.S., North, G.B., 1992. Drought-induced changes in hydraulic conductivity and structure in roots of Ferocactus acanthodes and Opuntia ficus-indica. New Phytologist 120, 9–19.
- Pavlik, B.M., 1980. Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. Oecologia 46, 147-154.
- Pietruszka, R.D., Seely, M.K., 1985. Predictability of two moisture sources in the Namib desert. South Africa Journal of Science 81, 682-685.
- Price, R.S., 1911. The roots of some North African desert grasses. New Phytologist 10, 328-339.
- Ritter, A., Regalado, C.M., Aschan, G., 2008. Fog water collection in a subtropical elfin laurel forest of the Garajonay National Park (Canary Islands): a combined approach using artificial fog catchers and a physically based impaction model. Journal of Hydrometeorology 9, 920–935.
- Ritter, A., Regalado, C.M., Aschan, G., 2009. Fog reduces transpiration in tree species of the Canarian relict heath-laurel cloud forest (Garajonay National Park, Spain). Tree Physiology 29, 517–528
- Robinson, M.D., Seely, M.K., 1980. Physical and biotic environments of the southern Namib dune ecosystem. Journal of Arid Environments 3, 183-203.
- Robinson, D.A., Gardner, C.M.K., Cooper, J.D., 1999. Measurement of relative permittivity in sandy soils using TDR, capacitance and theta probes: comparison, including the effects of bulk soil electrical conductivity. Journal of Hydrology 223, 198–211.
- Rubenstein, D.I., Koehl, M.A.R., 1977. The mechanisms of filter feeding. American Naturalist 111, 981-994.
- Schemenauer, R., Cereceda, P., 1991. Fog water collection in arid coastal locations. Ambio 20 (7), 303–308. Schemenauer, R.S., Fuenzalida, H., Cereceda, P., 1988. A neglected water resource:
- the camanchaca of South America. Bulletin of the American Meteorological Society 69, 138-147
- Seely, M.K., de Vos, M.P., Louw, G.N., 1977. Fog imbibition, satellite fauna and unusual leaf structure in a Namib desert dune plant Trianthema hereroensis. South Africa Journal of Science 73, 169–172.
- Seely, M.K., Hamilton III, W.J., 1976. Fog catchment sand trenches constructed by tenebrionid beetles, Lepidochora, from the Namib desert. Science 193, 484-486.
- Seely, M.K., Henschel, J.R., Hamilton III, W.J., 2005. Long-term data show behavioural fog collection adaptations determine Namib desert beetle abundance. South Africa Journal of Science 101, 570–572
- Ségalen, L., Renard, M., Lee-Thorp, J.A., Emmanuel, L., Le Callonnec, L., de Rafélis, M., Senut, B., Pickford, M., Melice, J.-L., 2006. Neogene climate and emergence of C_4 grasses in the Namib, Southwestern Africa, as reflected in ratite ¹³C and ¹⁸O. Earth and Planetary Science Letters 244, 725-734.
- Simonin, K.A., Santiago, L.S., Dawson, T.E., 2009. Fog interception by Sequoia sempervirens (D. Don) crowns decouples physiology from soil water deficit. Plant, Cell and Environment 32, 882-892.
- Slatyer, R.O., 1960. Absorption of water by plants. Botanical Reviews 26, 331–392. Southgate, R.I., 1996. Precipitation and biomass changes in the Namib desert dune ecosystem. Journal of Arid Environments 33, 267-280.
- Veste, M., Mohr, M., 2005. Vegetation der Lineardünen der zentralen Namib und deren Ionenhaushalt. In: Ökologische Forschung im globalen Kontext. Cuvilier Verlag, Göttingen., 93-107.
- Walmsley, J.L., Schemenauer, R.S., Bridgman, H.A., 1996. A method for estimating the hydrologic input from fog in mountainous terrain. Journal of Applied Meteorology 35, 2237-2249.
- Walter, H., Breckle, S., 2004. Ökologie der Erde. Band 2: Spezielle Ökologie der tropischen und subtropischen Zone, 3.Auflage. Elsevier, Spektrum akademischer Verlag.

- Went, F.W., 1955. Fog, Mist, Dew, and Other Sources of Water. USDA Yearbook of Agriculture, Washington, DC, pp. 103–109.
 Yates, D.J., Hutley, L.B., 1995. Foliar uptake of water by wet leaves of Sloanea woolsii, an Australian subtropical rainforest tree. Australian Journal of Botany 43, 157–167.
- Yeaton, R.I., 1988. Structure and function of the Namib dune grasslands: charac-teristics of the environmental gradients and species distributions. Journal of Ecology 76, 744–758. Yeaton, R.I., 1990. The structure and function of the Namib dune grasslands: species
- interactions. Journal of Arid Environments 18, 343–349.