Tree water potentials supporting an explanation for the occurrence of Vachellia erioloba in the Namib Desert (Namibia)

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Georg-August-Universität Göttingen
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Tree water potentials supporting an explanation for the occurrence of *Vachellia erioloba* in the Namib Desert (Namibia)

Joachim H. A. Krug

Abstract

Background: Site-vegetation relations of *Vachellia erioloba*, *Faidherbia albida*, *Euclea pseudebenus* and *Tamarix usneoides* in two contrasting locations in the Namib Desert (Namibia) were evaluated with the goal to relate soil water availability to the occurrence of trees under hyper-arid conditions.

Methods: Plant water potentials were measured using a pressure chamber in the field. Pre-dawn water potentials were assessed to reflect the soil water potential of the rhizosphere. Midday water potentials were measured to assess the strongest negative water potential applied by the sample trees.

Results: Pre-dawn water potentials and midday water potentials indicated access to soil water in the rhizosphere and by this, provide an explanation for an occurrence of *V. erioloba* within the extreme environmental conditions of sand dunes in the Namib Desert. Diurnal ranges seem to reflect more and less suitable stands, in terms of soil water availability, within the sampling sites. While the impact of the ephemeral Kuiseb river on soil water availability was assessed through the four species' plant-internal water relations, comparable pre-dawn water potentials of *V. erioloba* at both sites indicate soil water availability also in the dunes of Namibrand. The extreme midday water potentials of the dune plants possibly show the upper limit of tolerance for *V. erioloba*.

Conclusions: The preliminary data provide an explanation of the occurrence and distribution of the investigated species in beds of ephemeral rivers and on dunes under the hyper-arid climatic conditions of the Namib Desert and qualify suitability within the assessed sites. Understanding the plant-physiological processes and assessing the plant-internal water potential provides a valuable tool to evaluate soil water availability within the rhizosphere and to describe an adaptation potential of investigated species. The comparability of pre-dawn water potentials at both sites indicates unexpected soil water availability within lower parts of the dunes of Namibrand. Further research needs are derived concerning the origin and distribution of such soil water. These species in these specific tree-environments are understudied and little published, thus the results support an improved understanding of the ecology in arid environments.

Keywords: Water potential, Arid land, Soil water availability, Namibia, *V. erioloba*

Background

The objective of this study is to develop a testable explanation of the occurrence and distribution of *V. erioloba* by site-vegetation relations, in terms of soil water availability in the rhizosphere, under extreme conditions of two example sites in the Namib Desert.

The Namib Desert is defined as a hyper-arid area, where rainfall is so low that water controls most biological processes (Seely 1987). This water-controlled ecosystem with infrequent, discrete and largely unpredictable water inputs (Berry 2000) and far higher rates of potential evaporation than precipitation (Mendelsohn et al. 2002) allows only a few plant and animal species inhabitation. In this context, availability of soil water is considered as being a limiting factor for plants (Hobbs 1984; Mitlöhner 1998; Serrano et al. 1998; Reynolds et al. 2004; Otieno et al. 2005a; Nobel 2017). Access to available soil water and the ability to endure water stress varies from species to species and can determine growth

Correspondence: jokrug@fastmail.de
Institute for Silviculture and Forest Ecology, Georg-August-University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

success if not solely enabling any growth or survival. Here, water stress is determined in terms of the plant water relation parameter 'water potential' (compare Vertovic et al. 2001 and Nobel 2017). In this understanding, the term 'site-vegetation relation' reflects the interaction between specific sites and specific plant species. It encompasses manifold factors and functions like soil conditions, climatic parameters, as well as genetic pre-conditions which, on the other hand, determine certain characteristics of plant-reaction and adaptation. The more difficult the site conditions are for plant growth, the higher is the level of species adaptation requirement and the fewer the number of species that are able to adapt and solely survive under these conditions (NATH 2000). It is remarkable to discover the comparably rich growth of higher plants or even trees at certain sites within the hyper-arid Namib Desert.

Tree species investigated are *V. erioloba* E. Mey (Mimosoideae), the 'Camelthorn Tree' (basionym: *Acacia erioloba* E. Mey), *Faidherbia albida* A. CHEV. (Mimosoideae, 'Ana-tree'), *Euclea pseudebenus* E. MEY ex A. DC. (Ebenaceae, 'African Ebony'), and *Tamarix usneoides* E. MEY ex BUNGE (Tamaricaceae, 'Wild Tamarisk').

Throughout *V. erioloba*'s extensive range within central and western Southern Africa, it varies from a small, spiny shrub, of barely two metres in height, to a tree of up to 16 m tall. Occurring in dry woodlands in stony or sandy arid areas, this is one of the major tree species of the desert regions of Southern Africa (Palgrave 2002). The outstanding adaptation of *V. erioloba* to desert sites is reflected in its root-system. In addition to surface roots growing in a radius of up to 20 m around the tree, a strong tap root reaches deep into the ground (Palgrave 2002; Burke 2006).

Faidherbia albida is a large tree reaching up to 30 m in height with wide-spreading branches and a rounded crown. It is a lower elevation species which is widely distributed throughout Africa and usually found on alluvial floodplains, along dry watercourses, in riverine fringe forests and around pans and swamps (Palgrave 2002).

Euclea pseudebenus forms a shrub to medium-sized slender tree of 3 to 10 m in height, with slender drooping branches. It occurs in stony and sandy desert areas where few tree species can survive, but usually in depressions and along watercourses (Palgrave 2002).

Tamarix usneoides is an evergreen, gregarious, many-branched shrub or small tree of up to 5 m in height, occurring in desert areas and their fringes, along shore lines and brackish rivers, and frequently in dry riverbeds.
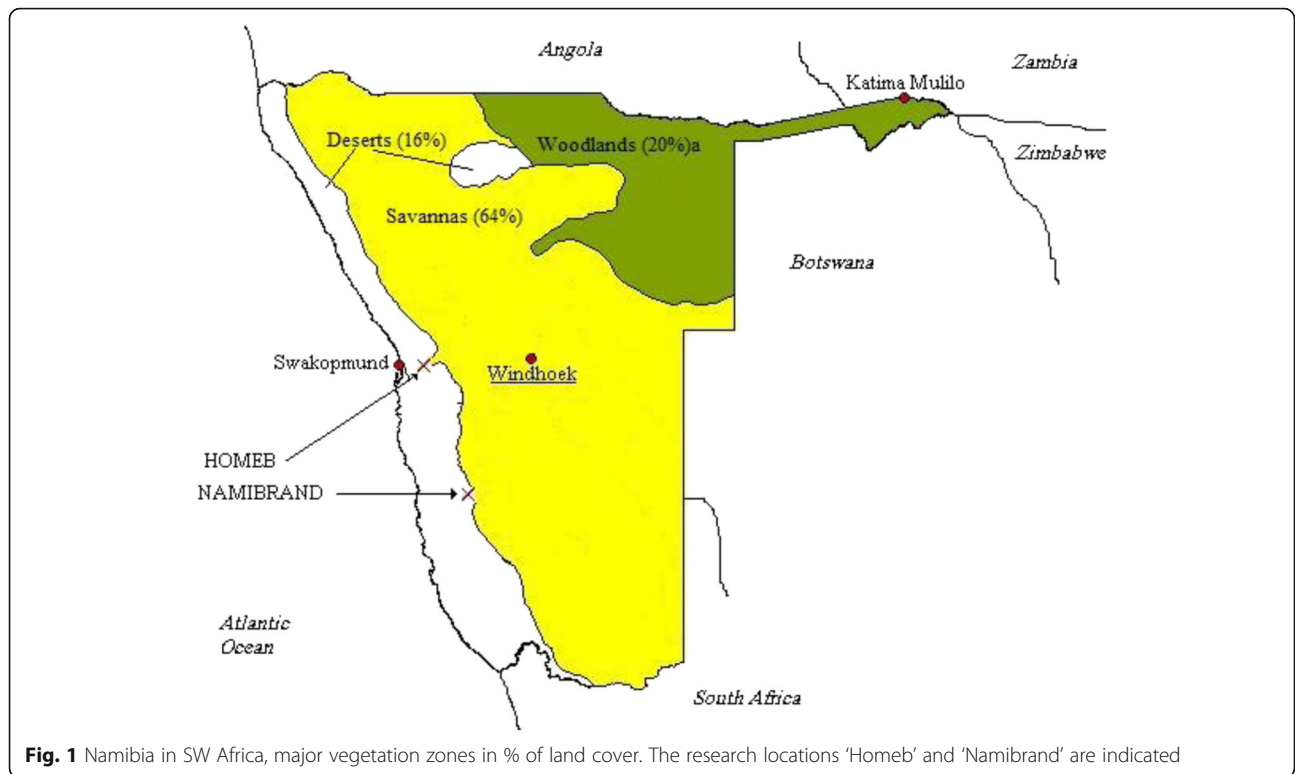
Methods
Study sites
Two research locations with contrasting site characteristics were selected in the hyper-arid Namib Desert of Western Namibia: The location 'Namibrand' within the 'Sand Sea' of the South Namib, and the location 'Homeb' at the Kuiseb River, the border between the 'Sand Sea' and the gravel plains of the Namib Desert (Barnard 1998). Figure 1 indicates the location in Namibia.

The Namibrand location (25°13′S–16°02′E) is situated ca. 122 km east of the Atlantic Ocean in the South Namib at an elevation of ca. 1070 m a.s.l. The site is characterised by an almost 200 m high dune ridge, which is situated on top of permanent sand plains originating from Tertiary deposits (Seely 1987). Annual precipitation is around 40 mm (usually occurring between November and February), annual potential evaporation is around 3400 mm (Mendelsohn et al. 2002). The climatic conditions are described as hyper-arid (Seely 1987) with a mean minimum temperature of 4 °C to 6 °C and a mean maximum temperature of 34 °C to 36 °C (Mendelsohn et al. 2002). Two to three nights with frost can occur annually. A few days of fog may prevail annually, predominantly originating from the cool Benguela current at the coast (Shanyengana et al. 2002; Eckhardt et al. 2012). The sand dunes move about one metre per year in the prevailing south-westerly wind direction (NATH 2000). The continuously homogenous, coarse dune sand of the Namib is a combination of silica-oxide and mica/feldspar in a relation of 9:1 from eroded quartz (NATH 2000). Human impacts on the vegetation are not noted. The woody vegetation of Namibrand is limited to a dispersed stock of *V. erioloba*. However, even long tap roots of *V. erioloba* are not expected to be long enough to reach a ground-water Table. A nearest borehole, located ca. 4 km S of the Namibrand research location, reveals its ground-water table to be at ca. 1010 m a.s.l., which is 50 to 160 m below the dune's surface. Figure 2 illustrates the location after rare precipitation.

In addition to *V. erioloba*, the endemic, perennial *Stipagrostis sabulicola* (Poaceae, 'Namib Dune Bushman Grass'), and *Cladoraphis spinosa* (Poaceae, 'Spiny Love Grass') grass species occur. Both species show an intensive system of surface roots (Ganssen 1968). According to NATH (2000), the extensive shallow root system of *S. sabulicola* may extend up to 20 m² laterally close to the sandy soil surface. Powrie (2017) describes the perennial grass *S. sabulicola* as occurring sporadically on large dunes which contain substantial water storage. Roth-Nebelsick et al. (2012), on the other hand, describe *S. sabulicola*'s outstanding self-irrigating ability: The endemic grass species seems to rely on its 'highly efficient natural fog-collecting system' by specific leaf surface structures. *C. spinosa* is portrayed by Dallwitz et al. (1999) as a species of open habitats on desert dunes and in sandy beds of dry watercourses.

A transect of 3200 m by 60 m was recorded in a straight line of 154° from north to cover, as best possible,

Fig. 1 Namibia in SW Africa, major vegetation zones in % of land cover. The research locations 'Homeb' and 'Namibrand' are indicated

the gradient of the dune's profile. The starting point was located at 1086 m a.s.l. At the end, the dune surface touches the Tertiary sand layer at 1062 m a.s.l. The transect crosses two ridges (highest elevation: 1108 m a.s.l.). All trees (total number of 77) on 19.2 ha, with a total basal area of 0.32 $m^2 \cdot ha^{-1}$ were assessed. The mean diameter at breast height is 31.2 cm (±14.6 cm SD). Following the age determination approach for *V. erioloba* by Steenkamp et al. (2008), the median age is presumed at 79 years.

The Homeb location (23°38′S–15°10′E) is situated ca. 68 km east of the Atlantic Ocean in the Namib Desert, at 440 m a.s.l. along the ephemeral Kuiseb River. The Kuiseb is the largest ephemeral river in Namibia and carries surface water almost every year for several days. At the Gobabeb Research and Training Centre, ca. 25 km upstream of the research site, Henschel (pers. com.) recorded between 1963 to 2000 an average of 17.6 days of annual flooding. Homeb receives a mean annual precipitation of about 20 mm (Mendelsohn 2002). The

Fig. 2 The location 'Namibrand' in Namibia after September rain (9.5 mm in about 30 min)

mean minimum and maximum temperatures vary between 8 °C to 10 °C and 30 °C to 32 °C respectively, the annual potential evaporation is ca. 3200 mm.

Homeb itself represents an open dale within the gorge of the Kuiseb river. Because the Kuiseb has regular surface flows and a perennial aquifer, it supports a closed forest stand of almost 5 ha of *V. erioloba*, *F. albida*, *E. pseudebenus* and *T. usneoides*. The latter dominates the stand on the southern part of the riverbed and forms an almost impenetrable bush (diameter at breast height: 3 to 7 cm, height: 2 to 3 m).

A section crossing the riverbed of 250 m by 10 m (0.25 ha) was demarcated as research site. Within that section elevation does not vary. Only the riverbed itself forms a depression of ca. 2 m in depth. All 51 trees with a minimum of 10 cm DBH were recorded in terms of position, height, diameter, and crown dimension. The water potentials of twelve individuals with sufficient sample material (leaves) at both pre-dawn and midday were recorded.

Plant water potential

Plant water potential was measured using a pressure chamber (Scholander et al. 1965), which is a method widely used (Sellin 1996; Mitlöhner 1998; Rodriguez et al. 2003; Gebrehiwot et al. 2005; Gebrekirstos et al. 2006). Extensive reviews on pressure chamber measurements are available, e.g. in Tyree and Hammel 1972; Ritchie and Hinckley 1975; Boyer 1995 and Richter 1997. In line with Horton et al. (2001a, 2001b), Mitlöhner (1995, 1998), Teskey and Hinckley (1986), and Hennessey and Dougherty (1984), the pre-dawn water potential is understood to reflect the soil water potential of the rhizosphere, which affects the assessed trees. The water potential assessed at midday describes the strongest negative water potential applied by the sample species to access soil water at the given measuring time.

The field measurements were carried out in the late dry season in September, just before the fall of leaves. Within designated transects (3200 m × 60 m at 'Namibrand' and 250 m × 10 m at 'Homeb'), all trees providing sufficient sample material were measured by two samples at pre-dawn (4:00 to 6:00), the time of presumed highest water potential, and by two samples at midday (12:30 to 14:30) when the water potential is expected to be at its daily minimum. The samples were taken from the same part of a branch and the same insertion height and exposure: The height of two to three metres at the western exposure of trees was chosen and only fully developed leaves of about the same age status were selected. The pressure chamber measurements were carried out in the field, at each tree as the leaf was picked.

Soil samples

Soil samples were taken at three different places within the transect of Namibrand (after the first, second and third quarter of the transect), while one was taken in the Tertiary sand layer. At Homeb, two samples were taken at river centre, two samples 50 m to the north and another two samples 50 m to the south. All samples have been taken at 30 cm depth. The general soil classification was based on literature, soil samples taken were analysed by a standard soil analysis (Soil Analysis by the Soil Laboratory, Ministry of Agriculture, Water and Rural Development, Windhoek).

Statistical analysis

The statistic evaluation of recorded data was carried out using QED and SPSS: After verifying the data's normal distribution and the homogeneity of variance, the means were evaluated with a one-way ANOVA test. Additionally, the Tukey test (Tukey's Honestly Significant Difference, LSD test) was carried out to obtain more sensitive statements for distinguishing significantly mean differences (vide Fowler et al. 1998). According to these procedures, all results presented are statistically significant (at $P < 0.05$), unless indicated otherwise.
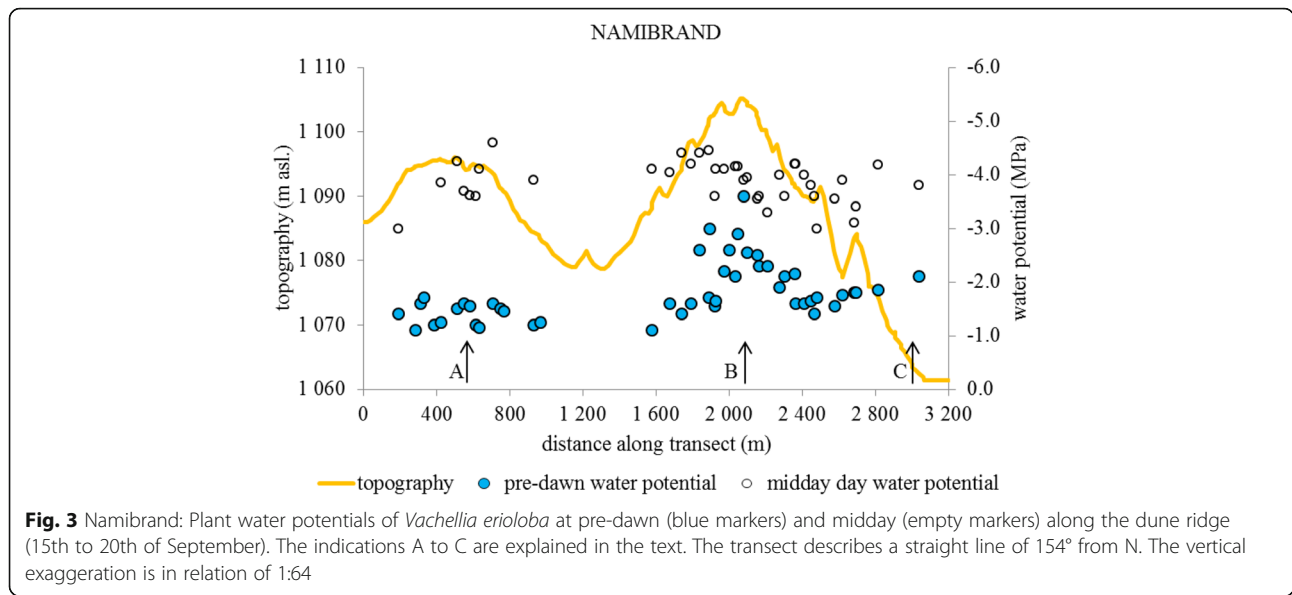
Results

Plant water potentials at Namibrand

The Namibrand location is illustrated from a vertical view combined with recorded pre-dawn and midday plant water potentials in Fig. 3. The marks are situated according to the sample trees' positions within the investigated transect. Since the samples are collected at the end of the dry season, not all sample trees offered a suitable number or condition of leaves: Out of a total of 77 trees, 45 could be assessed according to their pre-dawn water potential and 37 according to their midday water potential. During sampling, pre-dawn temperatures were recorded at 6.8 ± 2.9 °C, midday temperatures at 26.3 ± 0.9 °C.

The soil texture describes 99.9% sand within the dune, and 93.8% sand complemented by 2.9% silt and 3.3% clay at the Tertiary layer that forms the base of the sand dunes. The electric conductivity (EC_{H_2O}), as a proxy for salinity, was assessed at 0.21 ± 0.05 mS·cm^{-1} in the dune's samples and at 0.62 mS·cm^{-1} in the sample of the Tertiary layer.

Assuming that the upper limit of the Tertiary does not vary in elevation, the dune's elevation a.s.l. provides a proxy for the dune's volume. Thus the statistical evaluation indicates a significant correlation between the dune's volume and pre-dawn water potential of the sample trees (Pearson Correlation Test, $r = 0.37$, $t = 2.63$, DF = 43, $P \leq 0.05$). However, since the distribution of the pre-dawn water potentials of all sample trees deviate from a normal distribution (Shapiro-Wilk test, $W = 0.90$,
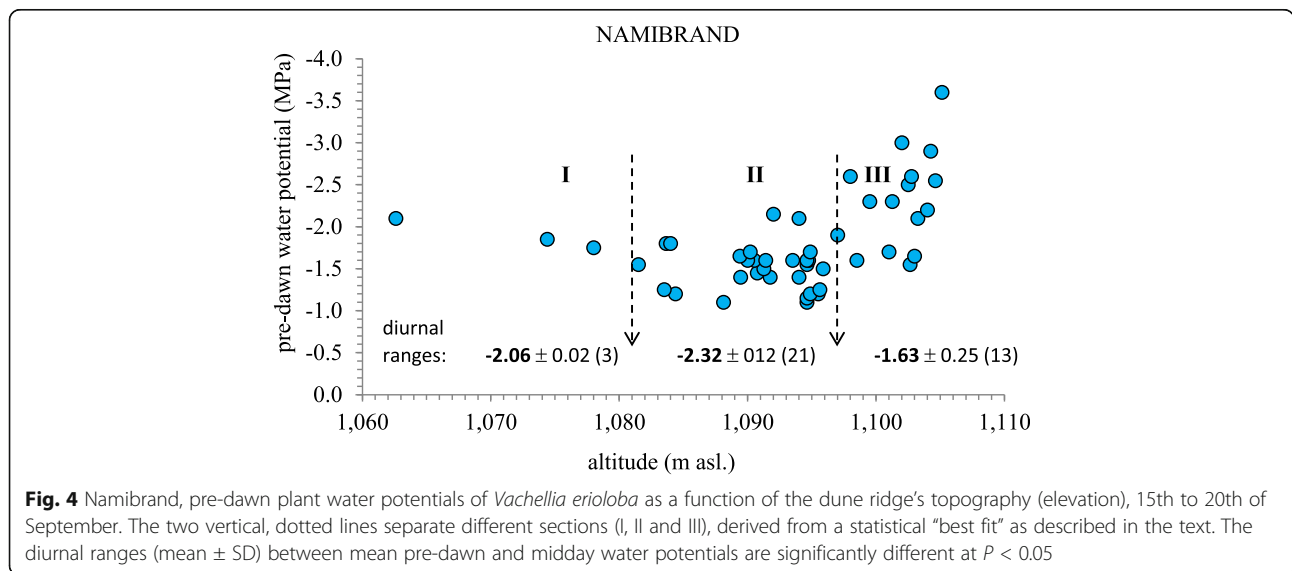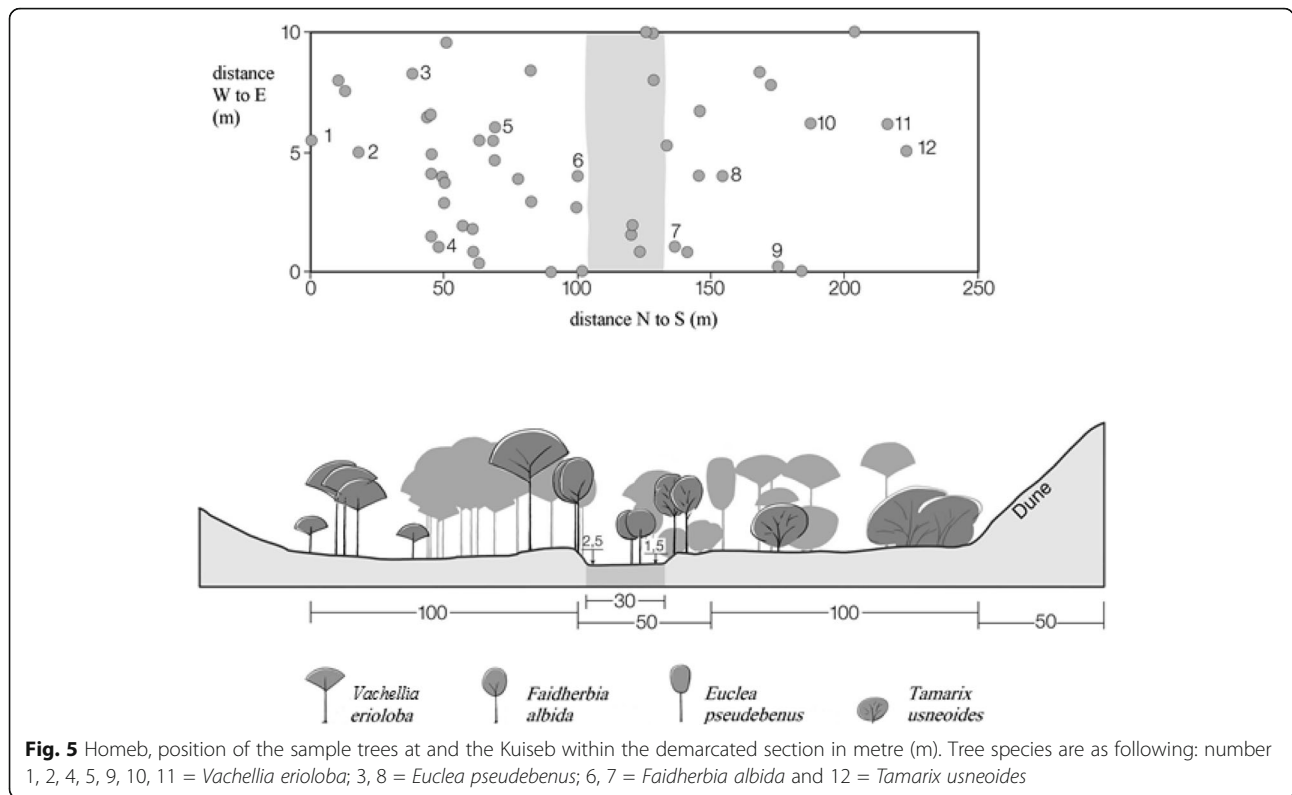
Fig. 3 Namibrand: Plant water potentials of *Vachellia erioloba* at pre-dawn (blue markers) and midday (empty markers) along the dune ridge (15th to 20th of September). The indications A to C are explained in the text. The transect describes a straight line of 154° from N. The vertical exaggeration is in relation of 1:64

$n = 45$, $P \leq 0.05$), it was tested whether a separation into subsamples allows more significant results: The separation of the whole sample into three sections (within elevation steps of 17 m, indicated by the dotted vertical line in Fig. 4) provides subsamples which do not deviate significantly from a normal distribution at $P > 0.05$ (Shapiro-Wilk test, $W = 0.94$ for the first section (1062–1080 m a.s.l.), $W = 0.95$ for the second section and $W = 0.95$ for the third section of 1098 to 1115 m). The three sections' variables are distributed normally; the limits of each section, the attribution of single samples to the upper or lower section, respectively, were tested by the single-sample t-test. Furthermore, there is a statistically significant association between the three sections and the variable pre-dawn water potential (Chi-

squared test = 20.93, DF = 2, $P \leq 0.05$). Thus the results are indicating that a comparison of the means within the sections can be allowed. Moreover, it is notable that the pre-dawn plant water potentials vary highly significantly ($P < 0.001$ Kolmogorov – Smirnov Test of Normality) whereas the midday water potentials hardly vary at all ($P < 0.05$ Kolmogorov – Smirnov Test of Normality).

Plant water potentials at Homeb

At Homeb, the impact of perennial water access is expected. These conditions, different tree species and the dissimilar soil composition, show basic differences in comparison to Namibrand. The research section is illustrated in Fig. 5. Table 1 describes the soil conditions of the location and illustrates different starting conditions

Fig. 4 Namibrand, pre-dawn plant water potentials of *Vachellia erioloba* as a function of the dune ridge's topography (elevation), 15th to 20th of September. The two vertical, dotted lines separate different sections (I, II and III), derived from a statistical "best fit" as described in the text. The diurnal ranges (mean ± SD) between mean pre-dawn and midday water potentials are significantly different at $P < 0.05$

Fig. 5 Homeb, position of the sample trees at and the Kuiseb within the demarcated section in metre (m). Tree species are as following: number 1, 2, 4, 5, 9, 10, 11 = *Vachellia erioloba*; 3, 8 = *Euclea pseudebenus*; 6, 7 = *Faidherbia albida* and 12 = *Tamarix usneoides*

compared to the first location. To characterise the site conditions in terms of plant-available water supply, the plant-water potential values at Homeb are compared with those of Namibrand as well as within the sample trees of the research site itself. Temperatures recorded during sampling were 8.4 ± 0.3 °C (pre-dawn), and 21.7 ± 1.8 °C (midday), the recorded water potentials are illustrated in Fig. 6.
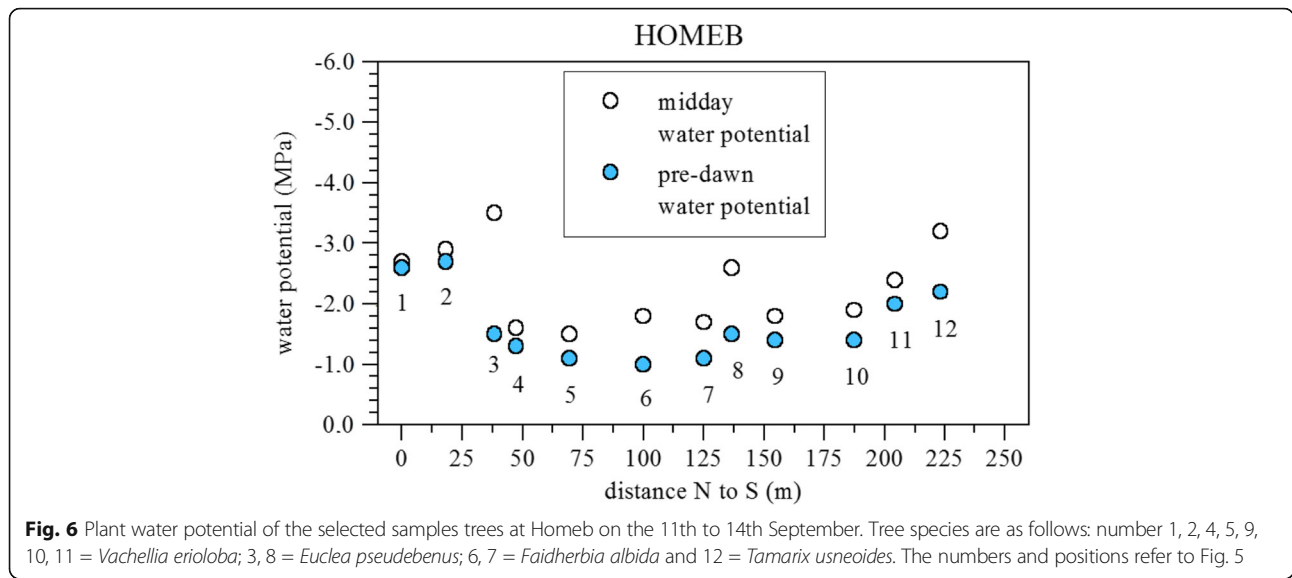
The indications of the water potentials represent a slightly concave distribution in Fig. 6. The centre of the illustration is positioned at the Kuiseb riverbed, between ca. 100 and 125 m from north to south and bordered by sample trees number 6 and 7 (both *F. albida*). *V. erioloba* indicates relatively low values: On average, this species indicates a mean pre-dawn water potential of around –1.78 ± 0.64 MPa (N = 7) and a mean midday water potential of –2.11 ± 0.55 MPa (N = 7). The diurnal range within the seven observations is only –0.34 ± 0.13 MPa. Whereas the pre-dawn values are comparable

to those at Namibrand, the indications of the midday water potential were much more moderate. At Namibrand, *V. erioloba* applies a much stronger water potential: the lowest value measured by a single observation at Namibrand was –2.90 MPa, the strongest at –4.60 MPa (compare Fig. 4 and Table 2). As a result the diurnal range at Homeb is quite low with only about 16% of that at Namibrand (Table 3).

The other species, especially *E. pseudebenus*, indicate a higher diurnal range than *V. erioloba*. This is illustrated by the broader distribution of the midday plant water potentials observed at Homeb (vide Fig. 6, Table 2). However, the small sample size limits this information value. It must also be considered that leaf characteristics differ between those mentioned species: *E. pseudebenus* and *T. usneoides* have narrow and leathery designed leaves, different to pinnately compound leaves of *V. erioloba* and *F. albida*. Since these characteristics coincide with potentials to limit water loss, a comparison within

Table 1 Soil characterisation of Homeb location. The numbers of observations are in brackets. (Soil Analysis by the Soil Laboratory, Ministry of Agriculture, Water and Rural Development, Windhoek)

Sample	Texture (vol%)			EC_{H_2O}
	Sand (> 0.063 mm)	Silt (0.063–0.002 mm)	Clay (< 0.002 mm)	(mS·cm^{-1})
Northern Riverbank (2)	83.4 ± 4.2	14.1 ± 2.3	2.5 ± 0.2	(no data)
Riverbed (2)	98.3 ± 0.2	0.9 ± 0.1	0.8 ± 0.1	0.26 ± 0.02
Southern Riverbank (2)	93.7 ± 0.5	5.4 ± 0.3	0.9 ± 0.2	0.29 ±0.09

Fig. 6 Plant water potential of the selected samples trees at Homeb on the 11th to 14th September. Tree species are as follows: number 1, 2, 4, 5, 9, 10, 11 = *Vachellia erioloba*; 3, 8 = *Euclea pseudebenus*; 6, 7 = *Faidherbia albida* and 12 = *Tamarix usneoides*. The numbers and positions refer to Fig. 5

all four species water potentials is of limited validity. A comparison of *V. erioloba* between Namibrand and Homeb also underlies the consideration of different site conditions.

Discussion

First, following limitations of the study must be considered: Conclusions on soil water availability are technically limited to locations where plants can be measured. Thus an absence of plants can not be explained by this approach and such sites can not be regarded as less suitable. Further, other potential determinants concerning the occurrence of trees are not assessed. Also possible differences of atmospheric site conditions are not investigated. In consequence, the results can only offer one explanation for the occurrence and distribution of trees: access to soil water in the rhizosphere.

At Namibrand, the plant-internal water potentials at midday remain fairly even (Fig. 3). The changing volume of the dune, recorded by topography, is the only gradient noted and it seems not to impact these values: They seem to describe the actual species' limit of 'suction force' within its environment at the given time and under high atmospheric water demand. The recorded

plant water potentials at pre-dawn, on the other hand, do show decreasing values (stronger plant potentials) with the dune's ascending topography. In the assumption that the soil substrate (the coarse dune sand) is fairly homogeneous within the whole transect, these results allow the suggestion that the pre-dawn plant water potentials are related to the position of the tree in relation to the volume of the dune ridge. Pre-dawn water potentials were plotted versus elevation to support this hypothesis in Fig. 4.

According to Gebrehiwot et al. (2005) and Gebrekirstos et al. (2006), the difference between the soil-induced pre-dawn value and the climate-induced midday value of the plant water potential reflects the range of plant water potential to overcome the soil water potential. Thus it is inferred that the results of the pre-dawn water potential (in relation to the changing topography) and the midday water potential reveal consequences for the plant-internal needs in balancing its internal water budget. At point A in Fig. 3, the noticeable difference between the pre-dawn values and the midday values indicates an actual situation without severe water stress: For the re-saturation at pre-dawn, the trees only need to apply about a third of the 'suction force' of midday. On the other hand, at point B, the situation indicates higher water stress: Some trees have to apply almost double the force than at point A to balance their internal water condition at pre-dawn. Since

Table 2 Mean plant water potential at Homeb for the different species. (Means for *Vachellia erioloba* are significant at $P < 0.05$)

Species	Plant water potentials (MPa)		
	Pre-dawn	Midday	Diurnal range
Vachellia erioloba (7)	−1.78 ± 0.64	−2.11 ± 0.55	−0.34 ± 0.13
Faidherbia albida (2)	−1.05 ± 0.07	−1.75 ± 0.07	−0.70 ± 0.14
Euclea pseudebenus (2)	−1.50 ± 0.00	−3.05 ± 0.45	−1.55 ± 0.64
Tamarix usneoides (1)	−2.20	−3.20	−1.00
all (12)	−1.65 ± 0.58	−2.30 ± 0.68	−0.65 ± 0.52

Table 3 Mean plant water potentials at Homeb in comparison to Namibrand for *Vachellia erioloba* ($P < 0.05$)

Location	Plant water potentials (MPa)		
	Pre-dawn	Midday	Diurnal range
Homeb	−1.78 ± 0.64 (7)	−2.11 ± 0.55 (7)	−0.34 ± 0.13 (7)
Namibrand	−1.80 ± 0.54 (48)	−3.89 ± 0.36 (39)	−2.07 ± 0.63 (39)

soil texture conditions do not change within the sand dune, it is assumed that the changing topography causes these indications - as supported by Fig. 4. The area within section II appears to be a more favourable location for *V. erioloba* in consideration of soil water availability (Fig. 4). The diurnal range indicates lowest values at around 1081 to 1097 m a.s.l. Only at a distance of about 2100 to 2600 m from the transect starting point, the pre-dawn water potential is revealed as increasing in relation to declining elevation (at the right side next to B in Fig. 3).

In contrast, however, at point C (Fig. 3), the pre-dawn water potential decreases again. At an elevation of ca. 20 m below point A and about 30 m lower than point B, the impact of the consolidated sand layer seems to come into account (point C). This observation is supported by Fig. 4: at elevation levels lower than 1079 m the pre-dawn water potentials decrease. Here the water potential is likely affected by the different soil conditions of the ground layer. The consolidated sand layer below the dunes contains higher proportions of silt and clay than the dune sand. An impact of salinity might come into account as well: The electric conductivity was tested as three times higher in that layer than within the dunes.

A gap between point A and B is characterised by the absence of sample trees and describes a valley between two major dune ridges. On this plain *S. sabulicola* densely covers the sand.

Nevertheless, the recorded range between the pre-dawn plant water potentials and the midday plant water potentials at Namibrand is still surprisingly low (indicated in Fig. 4). Stronger values had been expected for a site in the Namib Desert, which receives such little precipitation (compare to e.g. Mitlöhner 1998; Gebrehiwot et al. 2005; Gebrekirstos et al. 2006). Thus unexpected soil water access is reflected in relation to the dune's volume, but the source is unknown. Access to a deep ground-water table (known by a borehole ca. 4 km south) cannot be considered. Fog precipitation may also not come into account in sufficient extent for the growth of trees in that distance to the sea. Although a few days of fog occur annually and these may support growth of *S. sabulicola* (Roth-Nebelsick 2012), Schachtschneider and February (2010) state that also riparian trees in hyper-arid environments of the Namib Desert are rather relying on a 'seasonally fluctuating combination of ground water, shallow soil water and deep soil water' than on fog precipitation. Thus it might be presumed that the dunes store noteworthy amounts of soil water from precipitation. It may be caused by a water-storing effect of the coarse sand, which allows deep percolation and minimizes runoff and evaporation losses, and thus can be expected to provide storage of plant available water (compare Ganssen 1968; Weidelt

1989; Minnich 1995; Bodnar and Hulshof 2006). According to the author's own observations, even after a little rainfall of less than 10 mm, the surface dries fast (illustrated in Fig. 2), while water is stored within a few centimetres below the surface for many days and even weeks. The coarse pore system hardly allows any capillary water ascent (Mensching 1990). According to Weidelt (1989), such 'basic soil moisture' of sites without any noteworthy capillary ascent, can support a limited stock of perennial grass and potentially even trees, even in extremely arid areas over years. However, since such 'profile water' would not explain the observed, elevation-related changes of midday water potential unless situated in deeper layers of the dunes, it could alternatively be assumed that the observations are linked to another underground aquifer in the dune, possibly accumulated from episodic events and a while ago. Such episodic events were observed by Namibrand Nature Reserve authorities e.g. in 2001 and 2011 (seasonal precipitation of 130 and 420 mm, respectively, pers. com.), but may have supported water availability for *V. erioloba* also a decade ago – considering the age of present individuals. Following these observations, a reasonable water supply may be assumed to be available for deep-rooted trees.

The observations at Homeb reveal the underground water supply of the Kuiseb, considering that the pre-dawn water potential reflects the availability of soil water independently from the species which has been assessed: The trees located close to the riverbed seem to enjoy sufficient water supply. The maximum values of the plant water potential at midday close to the riverbed (e.g. sample trees 4, 5 and 9) are even higher (indicating a lower water potential) than the relaxation values reflecting soil water availability (pre-dawn plant water potential) of sample trees are ca. 75 m further away (e.g. sample trees numbers 1, 2 and 11). Figure 6 illustrates different values of water availability according to the sample trees' position in relation to the riverbed: The abundant ground-water supply, illustrated by all species as the pre-dawn plant water potential, reflects a site-specific value. As long as the assessed tree species root within the same depth and site, the different species reflect the same parameter of soil water condition. Summarising these findings, the availability of ground water is implied by the pre-dawn water potentials of the sample trees: The closer the sample trees are located to the riverbed, the greater the availability of plant-available soil water (Fig. 6). Salinity might be expected to increase with distance away from the riverbed; although the soil samples did not provide clear results for this assumption (Table 1). However, the soil sample depth is questionable and thus limits the information value. Horton et al. (2001b) describe similar experiences with native riparian tree species in Arizona, where the pre-dawn water

potential described the availability or the reduction of available soil water according to river-flow regulation. Comparable results are available from Otieno et al. (2005b), who recorded leaf water potentials to assess root access to soil water at varying soil depths and how this affects the expression of morphological and physiological traits developed during drought in the savannah region of Kenya.

The comparable re-saturation values of *V. erioloba* (the species' pre-dawn water potentials) observed at both sites support the assumption made for Namibrand - assumed existence of certain soil water access within the dunes. Only the values of the water potential at midday reflect the different site conditions. At Namibrand, *V. erioloba* applies a much stronger water potential than at Homeb. Furthermore, the fact that the diurnal range at Homeb is quite low (compared to that at Namibrand, vide Table 3) seems to reflect a more sufficient ground water supply at Homeb - the species does not need to apply a stronger water potential to cope with midday water-deficiency.

Whereas site conditions are reflected by the water potential at pre-dawn, the adaptation of the different species is illustrated by the plant water potential at midday (compare Table 2 and Fig. 6). Comparing *E. pseudebenus* (sample trees numbers 3 and 8) with neighbouring *V. erioloba*, it is observable that *E. pseudebenus* shows a more 'excessive character' regarding its water potential. By withstanding a similar or even higher pre-dawn water potential than the neighbouring trees, it applies a remarkably lower midday water potential. Gebrehiwot et al. (2005) reveal comparable characteristics of various species by using the same methods in the N-Ethiopian drylands. This difference in the species' water-usage-character could support an explanation for the different distribution and dominance of the tree species (Mitlöhner 1998). While *V. erioloba* is widely distributed in the Namib Desert, the species *E. pseudebenus*, illustrating a 'more excessive character', is usually found along dry watercourses and in riverine fringe forests (vide Van Wyk and Van Wyk 1997; Palgrave 2002).

Conclusion

A rather unexpected occurrence of *V. erioloba* on sand dunes of Namibrand is related to soil water availability in the rhizosphere. Water availability, determined as minimum factor to tree growth or even survival, was assessed by the plant-internal parameter 'water potential', and related to the distribution of trees on both extreme sites within the Namib Desert. A species' internal ability of adaptation towards the sites' soil water budget was reflected by the diurnal range of water potentials. The comparison between both sites, a bed of the ephemeral river Kuiseb and the sand dunes on Namibrand,

indicated a comparable access to soil water in the rhizosphere for *V. erioloba*.

The relation between a diurnal range of water potentials and the dune's volume at Namibrand suggests the hypothesis of water storage low down in the dune: Since the dunes are comprised of loose and coarse sand into which precipitation percolates easily, and from which little soil water is lost by evaporation, noticeable precipitation water might have been stored. This could create a situation where water is more difficult to be accessed by trees situated on the dune's top, but available for trees growing in the mid portion of the dune – as reflected by Fig. 4: That is where *V. erioloba* experiences lesser midday water potentials. For trees about 15–20 m higher, on the dune top, the water sources seem to be too far down to be reached with *V. erioloba*'s root system, extensive as it may be. Supporting that hypothesis, the proximity of the Tertiary layer seems to be less favourable in terms of water supply. Also that layer might provide further conditions more unsuitable for *V. erioloba*, possibly a combination of consolidation and higher EC.

A limitation in this concern is the fact that the origin of that soil water can not be determined. It is assumed, that 'episodic events' with unusual precipitation (as recorded in 2001 and 2011) contributed to water storage in the dunes. Considering the median age of the sampled trees, 79 years, such 'episodic events' might have occurred with some frequency. Unfortunately, a respective documentation is not available for this part of the Namib Desert.

However, the results encourage further investigations: While water availability was demonstrated, the origin of the source was not. Using stable isotopes of water (^{2}H, ^{18}O) for determining the sources of water transpired could allow deeper insight, as proposed by Brunel, Walker and Kennett-Smith (1995), or Verweij et al. (2011). More investigations are suggested concerning the soil water abundance in relation to rooting design and position of *V. erioloba* on the dunes. A distribution and age of *V. erioloba* within a wider proximity for a potential relation between age clusters could further support conclusions on presumed episodic precipitation events that facilitate the propagation of *V. erioloba* within the dunes.

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