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Roots point to water sources of *Welwitschia mirabilis* in a hyperarid desert

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Running head: Roots as ecohydrological pointers of welwitschia

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Abstract

Welwitschia mirabilis is a long-lived evergreen in the hyperarid Namib Desert; at our study site, rainfall is rare (MAP=31 mm), groundwater deep (57-75 m), and fog frequent (50-90 events y^{-1}). By examining root architecture in relation to soil moisture and analysing the isotopic composition of hydrogen and oxygen of plant and soil water, we established whether *welwitschia* sources water from a stable supply of deep groundwater, or from shallow moisture originating from fog and dew, or from rain water at infiltration depth. Isotopes suggested rainwater as principal water source. Most (55%) major roots and fine roots occurred in 10-66 cm deep layers of gypsum containing 10% moisture. A further 25% of both root types grew in moist sand in petrocalcitic horizons at 93-125 cm depths. A high density of fine roots (14% of total) grew upwards towards the ground surface in a 1.5 m radius around plants, an area occasionally wetted by runoff of fog and dew. We conclude that *welwitschia* mainly rely on rainwater obtained in perched horizons. Supplemental water is obtained from fog and dew from the surface and potentially from gypsum blocks. Multiple strategies enable this extremely long-lived evergreen to be resilient against dehydration in hyperarid conditions.

KEYWORDS

long-lived broad-leaved evergreen, resilience to drought stress, gypsum, petrocalcitic horizon, perched water, fog, root map

1. INTRODUCTION

The fundamental question of how plants source water is acute for long-lived woody species in extremely water-scarce conditions. An understanding of their adaptations to hyperaridity can help elucidate ecohydrological processes and strategies evolved by plants to avoid or survive dehydration. This should be especially true for the continuously-growing broadleaved evergreen welwitschia, *Welwitschia mirabilis* Hook. Fil. (Figure 1), a long-lived gymnosperm endemic to the Namib Desert.

Land use changes, mining, agriculture, and potentially also climate change, are increasing risks to biota, including welwitschia (Wassenaar *et al.*, 2013). A large population of this species on the Welwitschia Plains, adjacent to one of the largest uranium mines in the world, is potentially threatened by interference with its water supply. It has therefore become critical to resolve uncertainties about its ecohydrology, including the roles of different water sources and its physiological and anatomical strategies to cope with continuous drought.

The mean annual precipitation (MAP) across welwitschia's distribution range is ~20-100 mm. Yet this evergreen plant, which rarely employs the water-saving crassulacean acid metabolism (CAM) photosynthetic pathway (Schulze *et al.*, 1976; von Willert *et al.*, 2005), but primarily uses the C3 pathway (von Willert *et al.*, 2005), daily transpires 0.2-1.4 litres of water m⁻² of leaf (von Willert & Wagner-Douglas, 1994). The question how it manages to survive in hyperarid conditions has intrigued generations of biologists (Henschel *et al.*, 2000), and is, indeed, iconic (Henschel, 2012; van Jaarsveld & Pond, 2013). Its remarkable resilience to drought stress is partly based on ecophysiological mechanisms within leaf tissues, such as stomatal limitation, and ultimately biochemical limitation, which conserves water (Krüger *et al.*, 2017), but it still beckons questions concerning its water sources.

In the Namib Desert the ratio of MAP to mean annual potential evapotranspiration (PET) is very low (0.006-0.02; Lancaster *et al.*, 1984), and soil is generally dry (Li *et al.*, 2016). Plant available moisture is potentially derived from deep groundwater, regular fog and dew, or rare rainfall. Groundwater on the Namib gravel plains is recharged from cloud bursts in small catchments some 50 km to the east (Mills *et al.*, 2006). Fog occurs frequently (Henschel & Seely, 2008; Eckardt *et al.*, 2013) and atmospheric moisture penetrates the top few centimetres of soil during cool nights, but evaporates as it warms during daytime (Kaseke *et al.*, 2011). By night, evaporated moisture often condenses as dew or radiation fog (Kaseke *et al.*, 2017), and is potentially available for absorption by plants (Agam & Berliner,

2006; Hill *et al.*, 2015). Rainfall is rare and unpredictable over space and time (Henschel *et al.*, 2005; Eckardt *et al.*, 2013). The depth to which rainwater penetrates into the gravel plains is affected by the nature of soil (Mills *et al.*, 2006; Li *et al.*, 2016). Where the plains are underlain by a petrocalcic horizon, this can block rainwater infiltration at depths of one or more metres, forming a thin horizon of perched water, overlain by gypsum (Wilkinson, 1990; Heine & Walter, 1996). Duniway *et al.* (2010) recognised that petrocalcic horizons represent favourable conditions for retaining plant available moisture in arid regions, although the resulting shallow soil limits the storage capacity, as found with shallow bedrock (Schwinning, 2010).

Some forty percent of *welwitschia*'s range (Kers, 1967) falls in a region with relatively predictable fog (Cermak, 2012). It has been suggested that *welwitschia* could absorb fog water through the top of its stem and leaves and from run-off of fog down its leaves (Bornman *et al.*, 1973; Kutschera, 1997), as has, for example, been recorded for the dwarf shrub, *Arthroerua leubnitziae* (Loris *et al.*, 2001; Gottlieb, 2018). The idea that *welwitschia* is a phreatophyte with a taproot that sources water from deep underground (Van Jaarsveld & Pond, 2013) is not based on evidence, but probably on deduction from its geographical distribution and tendency to grow adjacent to drainage lines, supported by the fact that rooting depths of some desert species, such as *Vachellia erioloba* (Schachtschneider & February, 2010) and *Acanthosicyos horridus* (Müller, 2004), are second only to those of plants from the tropical savannas and grasslands (Canadell *et al.*, 1995), and that broadleaf evergreen trees tend to have deep roots (Fan *et al.*, 2017). However, the little evidence that is available points to the contrary: isotopic analyses confirmed that *welwitschia* did not tap into 25 m deep groundwater at Hope Mine in the central Namib (Soderberg *et al.*, 2014).

The spatial configuration of the root system (i.e. the explicit geometric deployment of root axes) and its associated rhizosphere is of functional importance for the efficient acquisition of resources from soil (Lynch, 1995; Laliberté, 2016), and may also provide evidence of the sources of water (von Willert *et al.*, 1992; Esler & Rundel, 1999). Root architecture is related to both MAP and PET in a complex manner (Warren *et al.*, 2015) and some species can reach extreme depths in their search for reliable water sources (Schenk & Jackson, 2002). In arid regions, roots structure tends to be either shallow and wide laterally, or very deep, provided that roots can grow through a more or less thick dry layer to get at groundwater (Fan *et al.*, 2017). There has been much research on *welwitschia* (see bibliography by Henschel *et al.*, 2000), but its roots have only been described in detail for

one plant before the current study (Kutschera, 1997) although its water source could not be identified.

In this paper, we test three hypotheses: 1) that *welwitschia* preferentially accesses a stable supply of deep groundwater; 2) that fog and dew are important sources of water; 3) that *welwitschia*'s water supply relies mainly on local rainfall. We test this by examining the root architecture and soil moisture of seven *welwitschia* plants on the Welwitschia Plains. We posit that a strong downward-trending taproot suggests dependence on groundwater and very shallow lateral roots suggest dependence on fog. All other root architectures will suggest a predominant dependence of vadose zone moisture on local rainfall. The locations of fine roots in relation to measured soil moisture, as well as the isotopic water composition of leaves, roots and soil, which can distinguish between rain, fog, dew and groundwater (Soderberg 2010; Kaseke *et al.*, 2017), provide further evidence concerning the source of water.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted on the Welwitschia Plains, located 50-km inland from the central Namib coast, south and east of the Husab Mine of Swakop Uranium (Figure 2). This area is close to the southern edge of *welwitschia*'s geographic range, which extends from latitude 14.9-23.6°S (Kers, 1967).

The 30-year MAP at Rössing Uranium mine located 10-30 km north of our study site (Figure 2) was 30.6 mm (range 1-98, median 24.5 mm; Rössing Uranium Ltd, 2013). Spatial and temporal variability of rainfall is high (Henschel *et al.*, 2005), and, given that the rainfall mainly occurs as convective summer storms (Lindesay & Tyson, 1990), the total annual rain may fall as one shower. Daily total evaporation rate from bare soil at a nearby site averaged 3.73 mm (Kaseke *et al.*, 2011). Warm summer climate is tempered by cool coastal winds and cool winter climate is interspersed by hot easterly bergwind events (Lindesay & Tyson, 1990; Eckardt *et al.*, 2013). The study area is close to the interior edge of the advective fog zone (Cermak, 2012), annually experiencing 50-90 fog events (Hachfeld & Jürgens, 2000).

Dominant geomorphologic features are large, gentle gravel plains with shallow ephemeral drainage lines, weathered marble ridges and deeply incised river valleys (Eckardt *et al.*, 2001). Geologically the area is characterised by granites, gneisses, meta-sediments,

marble ridges, and partially consolidated gravels and sands. Soils are shallow alluvium, and organic components are poorly developed (Abrams *et al.*, 1997). The soil in our study area mainly comprises sand and gravel often embedded in pedogenic gypsum typical for this part of the Namib Desert (Eckardt *et al.*, 2001). The gypsum forms an unconsolidated weakly structured, slightly porous gypsitic matrix containing meso- and microcrystalline gypsum cobbles. At some sites, a consolidated layer of calcrete underlies the gypsum.

Monitoring of boreholes (RS5 & RS6; Jolly & Smith, 2010) close to our excavation sites north of the Swakop River indicated that groundwater levels were 57-75 m deep, recharged from runoff generated in the catchment, extending about 60 km north-eastwards.

Vegetation cover is sparse, predominantly dwarf shrubs concentrated in washes and on rocky ridges. The Welwitschia Plains support a population of >52,200 welwitschia plants, most on broad gravel plains (Figure 2; Swakop Uranium, unpublished data). A smaller and the southernmost welwitschia field, where a previous study was conducted, occurs at Hope Mine about 100 km south of the study area.

2.2. Plant excavation

The need for the mine to remove seven welwitschias to make way for pipeline and road construction presented an opportunity to study their roots. Four plants were completely excavated (or nearly so), and most of what is reported here on the root structure concerns these four plants (Table 1). Roots of three other plants were not completely excavated due to time constraints, but some additional data, for instance on water isotopes and records of root morphology, were obtained from these.

Five plants were excavated in late 2012. Although no rain had fallen for 6-9 months before samples were collected from these plants, 17 mm rain had fallen in early 2012, and 98 mm in early 2011. Two more welwitschias were excavated in early 2014. Excavation was accomplished by careful manual removal of earth around each plant, starting at the stem and moving outwards along roots. Away from roots, soil was removed by using picks, shovels and jackhammer. Near roots, and particularly around fine roots, soil was cleared by using narrow metal rods of several sizes, a variety of paint brushes, and air puffers, ensuring that roots were not damaged before measuring.

2.3. Plant measurements

Excavation started by exposing fine roots near the surface (<30 cm depth). For two plants we dug trenches from the stem to 2 m away and counting fine roots in 3.75 cm² sample areas at 10 cm distances at depths of 10, 20 and 30 cm. Positions from the centre of the plant stem (horizontal distance) and the soil surface (vertical depth) were determined by tape measure (± 1 cm), and a compass, accurate to 1°, was used to plot direction. At each position two perpendicular thickness measurements of roots were taken with callipers (± 0.01 mm). The relative abundance of fine roots was scored: 0=absent, 1=present, 2=several fine roots extending <30 cm, 3= dense cluster (>1 cm²) or network of fine roots extending >30 cm from main root. A fine root index was derived from the sum of these scores. Using trigonometry, all positions were converted to x, y and z coordinates, with true north assigned to the positive y-axis and depth to the negative z-axis. These coordinates allowed mapping of roots, to calculate their length, and to relate the positions of fine roots to soil moisture and other soil characteristics, as well as generating 3D visual maps (Methods S1). Roots of one plant were mapped completely, for three others, all but one minor root was mapped, while the remaining three had several incompletely mapped roots (Table 1).

2.4. Soil samples

Samples (50-100 g) of freshly exposed bulk soil were taken outside the rhizosphere near roots at mapped positions. Each soil sample was placed in a sealed plastic bag and immediately placed in a portable freezer at -4 °C. Soil moisture was determined using gravimetric methods of weighing (± 0.05 g) 50-100g of soil before and after 24 h in 110 °C thermostatically controlled oven. Moisture content (%) was calculated relative to dry soil. This method of moisture determination may have somewhat overestimated water content of gypsum soils, since crystalline water would be released at temperatures above 42°C (Sofer, 1978; substantial releases at temperatures above 80°C, with total release only above 150°C).

At depths of 30-60 cm of the gypsum layer, temperatures daily fluctuate by about 1°C in the central Namib Desert (summer: 31-32°C, winter: 21-22°C; Lancaster *et al.*, 1984), and we therefore calculated potential amounts of water released for warming of 1°C. Two gypsum blocks were weighed (± 0.5 mg) before and after 24 h in an incubation chamber at 40% relative humidity, warmed from 27-39 °C then reweighed after cooling for 24 h to 33.5 °C. From changes in mass, we calculated the amount of water released from or gained by gypsum

blocks with warming or cooling respectively. From this, we estimated the volume of water daily released across the volume of gypsum penetrated by fine roots of study plants (Table S1).

2.5. Isotopic analyses of water

Leaf samples were taken from four plants. Three 1x10 cm strips were cut per leaf: “proximal” starting 5 cm from the meristem; “mid” being halfway along the green leaf; “distal” ending 5 cm from the end of the green portion of leaf. The distance from the meristem was recorded for each sample. Samples were sealed in a vacutainer, and frozen. Samples of roots were cut close to the stem, at intermediate depths, and from the deepest roots, and immediately sealed intact (bark not removed) and frozen in vacutainers. Samples of soil were duplicates of other soil samples collected between 10 and 115 cm depth from four plants, immediately placed into sealed vacutainers and frozen.

Frozen samples of roots (n=12), leaves (n=24) and soil (n=32) were exported to the Princeton Ecohydrology Laboratory (Mpala Research Centre, Kenya) for analyses of isotopic composition of the water to identify the water sources. Analyses followed the protocol of IAEA Moisture Isotopes in the Biosphere and Atmosphere (Twining *et al.*, 2006). Samples were distilled via cryogenic vacuum distillation using boiling water (~100 degrees C) as the heat source (West *et al.*, 2006), and not all samples yielded sufficient distillate to analyse (see Table S2). Isotope analyses were performed using integrated cavity output spectroscopy, either with in-line micropyrolysis (Picarro L2130i-MPM) or with post-processing for spectral interference by organics (Los Gatos Research LWIA; Schultz *et al.*, 2011; see Methods S2, Table S2). Fourteen samples were analysed by both methods, with an average difference of 0.5 ‰ for $\delta^2\text{H}$ and 0.1 ‰ for $\delta^{18}\text{O}$. Interpretation of the results took into account potential isotope fractionation occurring during water uptake by some xerophytic plants, with water becoming $\delta^2\text{H}$ -depleted (Ellsworth & Williams, 2007). The results are also placed into the framework of isotope compositions previously reported for water sources in the central Namib. Fog, dew and rare Atlantic rainfall are used as the Atlantic endmember, derived from 75 fog samples, 17 dew samples and 7 Atlantic rain samples (Table S3). Local runoff after heavy rains is used as the isotopically depleted Continental endmember, derived from samples of four runoff events (Table S4).

3. RESULTS

3.1. Soil characteristics

Soil moisture content changed with soil composition and depth in 102-178 cm deep excavations (Table 1). The top 10-30 cm thick layer of soil comprised dry, coarse sand and gravel (Table 2). Below that, there was a 20-53 cm thick layer of alluvial gravel with variable amounts of porous gypsitic matrix, containing blocks of translucent gypsum mesocrystal and microcrystal cobbles of 10-20 cm diameter. Although dry to the touch, the gypsum layer contained 10.0% crystalline water (Table 2). The content of water in gypsum changed by 0.031 mg kg^{-1} gypsum for $1 \text{ }^{\circ}\text{C}$ change in temperature, i.e. 73 ml of water released per m^3 of gypsum, amounting to $0.603 \pm 0.408 \text{ L}$ (0.146-1.024 L) water per plant (Table S1). Beneath the gypsum, the alluvial sand was dry except where it was sandwiched between calcrete layers, where moisture was 9.9% (Table 2).

3.2. Root architecture

Roots spread 1.8-8.9 times further laterally than vertically (Table 1; Figure 3, S1, S2). The total lengths of roots scaled allometrically to stem size ($r=0.90$; Table 1), as did the lateral spread of roots ($r=0.76$), but this relationship was not evident with the maximum depth reached by the roots ($r=-0.05$) (Figure S2).

Roots had at least two depth distribution peaks, one around 50 cm and a deeper level, varying from 70-130 cm for different plants (Figure 4). Most roots (63-99% of total length) were shallower than 100 cm (Figure 4). The deepest roots were orientated horizontally and there was little evidence of a prominent vertical tap root besides a single 12.9 mm thick root of plant F that projected downwards from 120-cm deep horizontal roots, penetrating bedrock at a depth of 178 cm, where it was lost (Figure 3).

The lateral distribution of roots differed between plants (Figure 3). The quantity of roots gradually declined with increasing distance from the stem, ending 240-904 cm away. Root systems of two plants had a wide horizontal spread and grew further from one side of the stem compared to the other side (upslope vs downslope, Plant A: 510 vs 85 cm; Plant G: 34 vs 904 cm; Figure 3, 4). The other two plants confined their roots to within a lateral radius of 240-450 cm of the stem and grew slightly deeper than Plants A and G (Figure 3, 4).

Branching and pathways of the main roots of all seven plants was complex (Figure 3, S1, S2; Notes S1): roots frequently merged with other roots, even across considerable distances, there were U-turns, thickenings with distance away from the stem before thinning again, and abrupt terminal dead ends of thick roots (Figure S3).

3.3. Fine roots

Fine roots (feeder roots; 0.4-1.4 mm diameter) were found either in networks projecting 10-50 cm laterally away from major roots, or in fine root clusters of up to 5 cm diameter around major roots. Near the surface at all seven plants, fine roots extended upwards and outwards from major roots that were located at depths of ca. 30 cm near the stem. These fine roots reached up to the surface (Figure 3), often branching extensively (Figure S4). The density of fine roots in the top 30 cm increased with distance from the centre of the plant, reaching maxima around 60-80 cm away from the stem, corresponding to the zone where the leaves would have touched the ground; fine root density decreased beyond that point (Figure 5).

Extensive fine root networks with prominent rhizome sheaths spread out from the main root system into gypsum at depths of 30-60 cm (Figure S5). Fine roots growing in this layer had an average density of $1.01 \pm 0.45 \text{ cm}^{-1}$ (measured along 30 cm-long lines; $n=7$). Deeper down, another dense network of fine roots spread out from main roots that had levelled out horizontally between calcrete layers (Figure S6).

Below 20 cm depth, the distribution of fine root networks was associated with the occurrence of moisture in the soil beneath each plant (Figure 4), either in the form of moisture in gypsum, or moist sand sandwiched between calcrete horizons at greater depths (Table 2; Figure 6, S6). Although the nature of water sources differed (moisture in a widespread layer of gypsum cf. moist sand in a thin horizon between calcrete layers) and the fine root index was not quantified, the depth levels of high and low densities of fine roots at each plant corresponded with moister and drier levels respectively (Table 2; $r=0.75$, $p=0.001$; Figure S7).

3.4. Plant water isotopic composition

Roots contained $51.7 \pm 9.4\%$ water ($n=12$), similar to the water content of proximal leaf samples ($49.9 \pm 1.7\%$, $n=2$). Values of $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of root water fell along a fairly well-defined line with a slope of 2.4, aligned with water of Continental source (Figure 7). This differed minimally between individuals, e.g., the root water of Plant A ($6.6 \pm 1.4 \text{ ‰}$ for $\delta^{18}\text{O}$

and -17.9 ± 4.8 ‰ for $\delta^2\text{H}$) was within the same range of Plant B (4.4 ± 0.9 ‰ for $\delta^{18}\text{O}$ and -20.8 ± 3.1 ‰ for $\delta^2\text{H}$). Soils showed much more variability (Table 3) and were significantly enriched relative to the root water despite being collected from similar depths below the ground surface. The proximal leaf samples (closest to the stem) were statistically similar to the soil samples ($P > 0.05$) and slightly enriched relative to the root samples ($P < 0.05$; Table 3). The more distal leaf samples were highly enriched and fell along a slope of 2.9 with the proximal samples (Figure 7).

4. DISCUSSION

The root architecture of the seven plants we excavated showed some generalities. We note a lack of any taproots growing deep into groundwater. The few roots that were not followed to their ends were thin, $15.7 \pm 5.6\%$ the diameter of the root at its beginning. It is therefore unlikely that these un-excavated roots would have continued much further. In this respect the root architecture of the *welwitschias* in our study was similar to that described by Kutschera (1997) and fits the general pattern for root systems of plants growing in hyperarid areas which tend to be wide rather than deep (Schenk & Jackson, 2002; Fan *et al.*, 2017).

Welwitschia roots in our study were confined to depths shallower than 2 m, but extended laterally to up to 9 m, comparable to the 15 m previously recorded for one plant by Kutschera (1997; maximum depth 1.6 m). This reflects a strategy of opportunistically “foraging” for water in relatively shallow soil layers.

The complex root structure, with twists, circular connections, thickened sections, dead ends and disproportionately many thick roots in large plants, has the effect of packing root material densely into confined space, consistent with the suggestion of *welwitschia* roots being water storage organs (Giess, 1969; Kutschera, 1997). Such storage could help explain the depleted root water relative to typical soil water found in the present study, with the soil water subjected to additional evaporative enrichment. We estimate the roots of our study plants to have contained 1.2-4.7 L water (Table S1).

The idea that *welwitschia* is a phreatophyte is not supported. The roots are too shallow and isotopic analyses showed indistinct traces of groundwater (present study, Soderberg *et al.* 2014). The isotopic signature of root water suggests that it originated from rain coming from the east across the sub-continent. In addition, the perched water that we recorded in petrocalcic horizons at 93-125 cm depths also showed isotopic Continental

signatures of rain. There was no evidence that *welwitschia* roots were able to span the big depth gap (> 50 m) beneath this perched water horizon and the groundwater table. To reach groundwater, desert phreatophytes have major root structures growing downwards (Fan *et al.*, 2017) rather than sideways as is the case for *welwitschia*.

It may seem surprising for a plant endemic to gravel plains of a hyperarid desert, where effective rainfall is extremely rare and variable, to rely on rainwater, but it appears to be a common strategy for plants of the Namib gravel plains. Soderberg (2010) and Eckardt *et al.* (2013) showed that the dwarf shrubs *Arthroerua leubnitziae*, *Zygophyllum stapfii*, and *Calicorema capitata* also bore predominantly Continental isotopic signatures, although in certain locations these species also showed Atlantic signatures, indicating uptake of fog, vapour or exceptional Atlantic rainfall. Like with *welwitschia*, the root architecture of *A. leubnitziae* furthermore suggests a shallow water source (Loris *et al.*, 2001) in addition to its direct uptake of fog (Gottlieb, 2018).

The hydro-pedology of the gravel plains is poorly studied. Evaporites such as calcretes form thick consolidated, subsurface layers that can block deep infiltration. A calcrete layer is widespread across the Namib gravel plains (Heine & Walter, 1996), but is incised by drainage lines towards which they decline (Wilkinson, 1990). We found cracks and pockets of moister soil within calcrete layers, where local rainwater can infiltrate and presumably be retained for long periods or be replenished from upslope. We recorded that *welwitschias* expand fine root networks into these narrow perched water horizons, as Loris *et al.* (2001) had observed for *A. leubnitziae*.

Our results imply that fog is not the principal source of water of *welwitschia*. Previous studies of long-term leaf growth patterns (Henschel & Seely, 2000) and isotope composition (Soderberg, 2010) already indicated that fog is not an important water source for *welwitschia*, although it could still be a supplementary water source for sustaining leaf and stem growth. The current study presents some evidence that it plays at least a partial role. The *Welwitschia* Plains root waters (5.6 ± 1.6 ‰ for $\delta^{18}\text{O}$ and -19.2 ± 4.2 ‰ for $\delta^2\text{H}$) were isotopically enriched along a slope of 2.6 relative to stem water reported for a previous study at the Hope *welwitschia* field (0.0 ± 0.9 ‰ for $\delta^{18}\text{O}$ and -33.8 ± 6.6 ‰ for $\delta^2\text{H}$, $n=13$) (Soderberg, 2010). This relationship between the two *welwitschia* fields implies a similar Continental source of water that has experienced slightly more evaporative enrichment at *Welwitschia* Plains than at Hope (slope values of 2-6 indicate evaporative enrichment, with lower values commonly found in drier climates; Gat, 1996). Previous studies of gypsum hydration water, soil and

plant water enrichment found slopes between 2-3 for the central Namib Desert, with an average of 2.6 (Sofer, 1978; Soderberg, 2010). The proximal leaf water isotopes fall above this line (Figure 7), raising the possibility that the leaf water is somewhat influenced by an Atlantic isotopic signature. The welwitschias of Welwitschia Plains, therefore, showed a predominantly Continental water source signature, with a slight influence of an Atlantic source possible in the leaf water. The latter could be due to passive uptake of some fog and dew water through the stomata when these open at dawn (Eller *et al.*, 1983; Krüger *et al.*, 2017). Some isotopically depleted fog and dew samples have been reported (see Table S3), possibly due to the recycling of locally transpired water vapor into night time fog or dew deposition (Kaseke *et al.*, 2017). However, the typical isotope composition of these water sources is enriched as reflected in the Atlantic endmember.

Additional evidence for the possible role of fog and dew as a source of water comes from the dispersion of dense networks of fine roots extending upwards from a depth of 30 cm to the ground surface at all seven of our study plants. Much of this surface network occurred under leaf canopies, where fog and dew runoff would be blocked off, though not its vapour, and daytime relative humidity would likely be higher than ambient atmospheric conditions, including from moisture originating from leaf transpiration (Shuuya, 2016). Some fine roots did extend beyond the ends of leaves, where fog and dew deposition and runoff could reach the ground. A one-year study at Gobabeb using leaf wetness sensors and weather station data indicated an average of 2.7 day-time hours and 2.6 night-time hours each day with some degree of moisture on the leaf wetness sensor. At least 88% of the wet hours were the result of fog or dew (Soderberg, 2010). Leaf runoff of fog and dew can potentially be extremely important in this nutrient-impoverished environment, as was demonstrated for the Namib dwarf shrub *A. leubnitziae* (Gottlieb, 2018), where fog rinsed mineral-rich dust, deposited onto plants during dry conditions, onto the ground, enabling surface roots to assimilate this nutrient-rich mixture.

The high concentrations and wide extent of fine roots in the layer of unconsolidated gypsum at 30-60 cm depth was unexpected, as gypsum is hydrophilic and poor in nutrients besides sulphur (Palacio *et al.*, 2014a), creating conditions which few plants can tolerate (Bolukbasi *et al.*, 2016). Some plants do however succeed in obtaining water when gypsum heats up during the day and releases small amounts of water (Palacio *et al.*, 2014b). The spatial distribution of the fine roots that we recorded suggests that welwitschia possibly does the same. According to our calculations, the daily warming of the gypsum layer by 1 °C, may

release 0.1-1.0 L water within the gypsum layer surrounding welwitschia roots (Table S1), which is comparable to a plant's daily needs if all this water were available.

Water taken by welwitschia from gypsum could be replenished daily as gypsum rehydrates during the coolness of night when soil vapour pressure increases (Palacio *et al.*, 2014b). The source of replenishment could be fog, atmospheric vapour, or, according to Külls *et al.* (2015), who measured water isotopes from the gypsum layer next to our Plant A, from upward diffusion of rainwater from lower levels. We hypothesise that the daily rehydration/hydration of gypsum, with water drawn from different sources, represents a reliable source of water for welwitschia. This would facilitate the observed ability of this evergreen to survive long dry spells without rain.

Welwitschia's rhizomal microbes may be involved in the uptake of water from gypsum, as was suggested for a gypsophyllic dwarf shrub in Spain (Palacio *et al.*, 2014b). The rhizospheres of welwitschia have distinctive and particularly species-rich communities of bacteria and fungi (Valverde *et al.*, 2016), suggested to be important for plant health and productivity. High abundances of mycorrhiza are associated with gypsophily (Palacio *et al.*, 2012; Moore *et al.*, 2014) and may be instrumental in offsetting the low nutrient conditions (van der Heijden *et al.*, 2014).

The only one of our seven excavated welwitschias that survived replanting was where gypsum blocks were packed around the roots. There is not yet sufficient information to test whether welwitschia is a gypsophile, dependent on gypsum (Drohan & Merkler, 2009), or merely a gypsovag, having the ability to tolerate and make use of the properties of gypsum (Escudero *et al.*, 2015). Association with gypsum would reduce competition, as many plant species do not tolerate gypsic conditions (Bolukbasi *et al.*, 2016).

The occurrence of gypsum in different welwitschia fields across its distribution range (northern half of the Namib Desert; Kers, 1967) has not been determined, and it would be of interest to see how the patchy distribution of this species relates to the patchy distribution of gypsum in the middle and eastern zones of the Namib. Such patchy associations are observed for other gypsophiles (Moore *et al.*, 2015). High salt content of soils closer than 50 km from the Namib coast could be the reason why welwitschia cannot occur there, despite abundant gypsum (Eckardt & Spiro, 2001).

5. CONCLUSIONS

Our study confirms that *welwitschia* can tap into several different water sources, but most water comes from rainfall which it obtains with fine roots in petrocalcitic perched water horizons or from evaporites. Fine roots at the surface extending beyond the canopy could access fog at night, this being either advective moisture, or moisture recycled from local evapotranspiration as dew (Kaseke *et al.*, 2017). It remains to be determined what water source the fine roots at the surface under the canopy of transpiring leaves are tapping into. Likewise, the water source in several cubic metres of gypsum infused by dense networks of fine roots at each *welwitschia* remains to be established. We conclude that *welwitschia*'s dynamic root system appears to be a key characteristic enabling this extremely long-lived evergreen to reduce risks of running out of water even in the driest phases of a hyperarid desert.

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AUTHOR CONTRIBUTION

J.R.H., T.W., A.K. and M.K.L. planned and designed the research. T.W. and M.K.L. secured funding and permission. A.K. supervised fieldwork. J.R.H., T.W., A.K., M.K.L., G.N. and

T.S. conducted fieldwork. J.R.H., G.N. and T.S. compiled root datasets. K.S. conducted laboratory analyses of isotopic composition. J.R.H., T.W., K.S. analysed data and wrote the manuscript. There are no conflict of interests.

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REFERENCES

- 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. *Journal of Arid Environments*, 35, 29–38.
- Agam, N., & Berliner, P. (2006). Dew formation and water vapor adsorption in semi-arid environments – a review. *Journal of Arid Environments*, 65, 572–590.
- Bolukbasi, A., Kurt, L., & Palacio, S. (2016). Unravelling the mechanisms for plant survival on gypsum soils: an analysis of the chemical composition of gypsum plants from Turkey. *Plant Biology*, 18, 271–279.
- Bornman, C.J., Botha, C.E.J., & Nash, L.J. (1973). *Welwitschia mirabilis*: observations on movement of water and assimilates under föhn and fog conditions. *Madoqua Series II*, 2, 25–31.
- Canadell, J., Jackson, R. B., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E-D. (1996). Maximum rooting depth of vegetation types at the global scale. *Oecologia*, 108, 583–595.
- Cermak, J. (2012). Low clouds and fog along the South-Western African coast - Satellite-based retrieval and spatial patterns. *Atmospheric Research*, 116, 15–21.
- Drohan, P. J., & Merkler, D. J. (2009). How do we find a true gypsophile? *Geoderma*, 150, 96–105.
- Duniway, M. C., Herrick, J. E., & Monger, C. (2010). Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. *Oecologia*, 163, 215–226.
- 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 Surface Processes and Landforms*, 26, 1177–1193.
- Eckardt, F.D., & Schemenauer, R.S. (1998). Fog water chemistry in the Namib Desert Namibia. *Atmospheric Environment*, 32, 2595–2599.
- Eckardt, F. D., Soderberg, K., Coop, L. J., Muller, A. A., Vickery, K. J., Grandin, R. D., Jack, C., Kapalanga, T. S., & Henschel, J. R. (2012). The nature of moisture at Gobabeb, in the central Namib Desert. *Journal of Arid Environments*, 93, 7–19.

- Eller, B. M., von Willert, D. J., Brinckmann, E., & Baasch, R. (1983). Ecophysiological studies on *Welwitschia mirabilis* in the Namib Desert. *South African Journal of Botany*, 2, 209–223.
- Ellsworth, P. Z. & Williams, D. G. (2007). Hydrogen isotope fractionation during water uptake by woody xerophytes. *Plant Soil*, 291, 93–107.
- Escudero, A., Palacio, S., Maestre, F. T., & Luzuriaga, A. L. (2015). Plant life on gypsum: a review of its multiple facets. *Biological reviews of the Cambridge Philosophical Society*, 90, 1–18.
- Esler, K., & Rundel, P. W. (1999). Comparative patterns of phenology and growth form diversity in two winter rainfall deserts: The Succulent Karoo and Mojave Desert ecosystems. *Plant Ecology*, 142, 97–104.
- Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences*, 114, 10572–10577.
- Gat, J. R. (1996). Oxygen and hydrogen isotopes in the hydrologic cycle. *Annual Review of Earth and Planetary Sciences*, 24, 225–262.
- Giess, W. (1969). *Welwitschia mirabilis* Hook.fil. *Dinteria*, 3, 3–55.
- Gottlieb, T. R. (2018). The contribution of fog to the moisture and nutritional supply of *Arthroa leubnitziae* in the central Namib Desert, Namibia. MSc Thesis, University of Cape Town, South Africa, 126 pp.
- Hachfeld, B., & Jürgens, 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.
- Heine, K., & Walter, R. (1996). Gypcrete soils of the central Namib desert (Namibia) and their palaeoclimatological significance. *Petermanns Geographische Mitteilungen*, 140, 237–253.
- Henschel, J. R. (2012). *Welwitschia's World*. Windhoek, Namibia: Wordweaver Publishing House.

- Henschel, J. R., Burke, A., & Seely, M. K. (2005). Temporal and spatial variability of grass productivity in the Central Namib Desert. *African Study Monographs Supplement*, 30, 43–56.
- Henschel, J. R., Eller, B. M., Seely, M. K., & von Willert, D. J. (2000). Bibliography *Welwitschia mirabilis* J.D.Hooker. *Plant Ecology*, 150, 19-26.
- Henschel, J. R., & Seely, M. K. (2000). Long-term growth of *Welwitschia mirabilis*, a long lived plant of the Namib Desert. *Plant Ecology*, 150, 7–18.
- Henschel, J. R., & Seely, M. K. (2008). Ecophysiology of atmospheric moisture in the Namib Desert. *Atmospheric Research*, 87, 362–368.
- Hill, A. J., Dawson, T. E., Shelef, O., & Rachmilevitch, S. (2015) The role of dew in Negev Desert plants. *Oecologia*, 178, 317–327.
- Jolly, J., & Smith, G. (2010). *Husab Project Hydrogeology*. Specialist report by Aquaterra to Swakop Uranium as part of the Environmental Impact Assessment for the Husab Mine. Swakopmund, Namibia: Swakop Uranium.
- Kaseke, K. F., Mills, A. J., Henschel, J. R., Seely, M. K., Esler, K., & Brown, R. (2011). The effects of desert pavements (gravel mulch) on soil micro-hydrology. *Pure and Applied Geophysics*, 169, 873–880.
- Kaseke, K. F., Wang, L., & Seely, M. K. (2017). Nonrainfall water origins and formation mechanisms. *Science Advances*, 3, e1603131.
- Kers, L. E. (1967). The distribution of *Welwitschia mirabilis* Hook. f. *Svenska Botanisk Tidskrif*, 61, 97–125.
- Krüger, G. H. J., Jordaan, A., Tiedt, L. R., Strasser, R. J., Kilbourn-Louw, M., & Berner, J. M. (2017). Opportunistic survival strategy of *Welwitschia mirabilis*: recent anatomical and ecophysiological studies elucidating stomatal behaviour and photosynthetic potential. *Botany*, 95, 1109–1123.
- Külls, C., Marx, V., & Kambinda, W. (2015). *Moisture and isotope study in the Welwitschia mirabilis Area-EPL3138. Report No. 2014-G65*. Swakopmund, Namibia: Swakop Uranium.
- Kutschera, L., Lichtenegger, E., Sobotik, M., & Haas, D. (1997). *Die Wurzel das neue Organ: Ihre Bedeutung für das Leben von Welwitschia mirabilis und anderer Arten*

der Namib sowie von Arten angrenzender Gebiete mit Erklärung des geotropen Wachstums der Pflanzen. Klagenfurt, Austria: Pflanzensoziologisches Institut.

Laliberté, E. (2017). Below-ground frontiers in trait-based plant ecology. *New Phytologist*, 213, 1597–1603.

Lancaster, J., Lancaster, N., & Seely, M. K. (1984). Climate of the central Namib Desert. *Madoqua*, 14, 5–61.

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, e0164982.

Lindesay, J. A., & Tyson, P. D. (1990). Climate and near-surface airflow over the central Namib. *Transvaal Museum Monograph*, 7, 27–37.

Loris, K., Jürgens, N., & Veste, M. (2001). Zonobiom III: Die Namib-Wüste im südwestlichen Afrika (Namibia, Südafrika, Angola). In S-W. Breckle, M. Veste, & W. Wucherer (Eds.), *Sustainable land use in deserts* (pp. 441–498). Berlin, Germany: Springer Verlag.

Lynch, J. (1995). Root architecture and plant productivity. *Plant Physiology*, 109, 7–13.

Mills, A. J., Fey, M. V., Gröngroft, A., Petersen, A., & Medinski, T. V. (2006). Unravelling the effects of soil properties on water infiltration: segmented quantile regression on a large data set from arid south-west Africa. *Australian Journal of Soil Research*, 44, 783–797.

Moore, M. J., Mota, J. F., Douglas, N. A., Olvera, H. F., & Ochoterena, H. (2015). The ecology, assembly and evolution of gypsophile floras. In N. Rajakaruna, R. S. Boyd, & T. B. Harris (Eds.), *Plant Ecology and Evolution in Harsh Environments* (pp. 97–128). Hauppauge, NY, USA: Nova Science Publishers.

Müller, M. (2004). Seed dispersal ecology of the !nara melon. In J. R. Henschel, R. Dausab, P. Moser, & J. Pallett (Eds.), *!NARA fruit for development of the !Khuseb Topnaar* (pp. 77-84). Windhoek, Namibia: Namibia Scientific Society.

Palacio, S., Aitkenhead, M., Escudero, A., Montserrat-Marti, G., Maestro, M., & Robertson, A. H. J. (2014a). Gypsophile chemistry unveiled: Fourier transform infrared (FTIR) spectroscopy provides new insight into plant adaptations to gypsum soils. *PlosONE*, 9, e0107285.

- Palacio, S., Azorin', J., Montserrat-Marti', G., & Ferrio, J. P. (2014b). The crystallization water of gypsum rocks is a relevant water source for plants. *Nature Communications*, 5, e4660.
- Rössing Uranium Ltd. (2013). *Annual Environmental Report*. Swakopmund, Namibia: Rössing Uranium Limited, <http://www.rossing.com/reports-research.htm>.
- Schachtschneider, K., & February, E. C. (2010). The relationship between fog, floods, groundwater and tree growth along the lower Kuiseb River in the hyperarid Namib. *Journal of Arid Environments*, 74, 1632–1637.
- Schachtschneider, K., & February, E. C. (2013). Impact of *Prosopis* invasion on a keystone tree species in the Kalahari Desert. *Plant Ecology*, 214, 597–605.
- Schenk, H. J., & Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/ above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, 90, 480–494
- Schmitz, A. U. (2004). Transmission losses and soil moisture dynamics in the alluvial fill of the Kuiseb River, Namibia. MSc Thesis, Albert-Ludwigs-Universität, Freiburg i. Br., Germany, 75 pp.
- Schulze, E.-D., Ziegler, H., & Stichler, W. (1976). Environmental control of Crassulacean Acid Metabolism in *Welwitschia mirabilis* Hook. Fil. in its range of natural distribution in the Namib Desert. *Oecologia*, 24, 323–334.
- Schultz, N. M., Griffis, T. J., Lee, X., & Baker, J. M. (2011). Identification and correction of spectral contamination in $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ measured in leaf, stem, and soil water. *Rapid Communications in Mass Spectrometry*, 25, 3360–3368.
- Schwinning, S. (2010) The ecohydrology of roots in rocks. *Ecohydrology*, 3, 238–245.
- Shuuya, T. (2016). Investigating the environmental and anthropogenic spatio-temporal patterns of plant health of *Welwitschia mirabilis* in the central Namib Desert. MSc Thesis, Namibia University of Science and Technology, Windhoek, Namibia, 60 pp.
- Soderberg, K. (2010). The role of fog in the ecohydrology and biogeochemistry of the Namib Desert. PhD Thesis, University of Virginia, Charlottesville, VA, USA, 200 pp.

- Soderberg, K, Henschel, J. R., Swap, R. J., & Macko, S. A. (2014). Sulphur isotopes in the central Namib Desert ecosystem. *Transactions of the Royal Society of South Africa*, 69, 217–223.
- Sofer, Z. (1978). Isotopic composition of hydration water in gypsum. *Geochimica et Cosmochimica Acta*, 42, 1141-1149.
- Twining, J., Stone, D., Tadros, C., Henderson-Sellers, A., & Williams, A. (2006). Moisture isotopes in the biosphere and atmosphere (MIBA) in Australia: a priori estimates and preliminary observations of stable water isotopes in soil, plant and vapour for the Tumberumba Field Campaign. *Global and Planetary Change*, 51, 59–72.
- UNEP. (1992). *World Atlas of Desertification*. Edward Arnold, London: United Nations Environment Programme.
- Valverde, A., De Maayer, P., Oberholster, T., Henschel, J. R., Louw, M. K., & Cowan, D. (2016). Specific microbial communities associate with the rhizosphere of *Welwitschia mirabilis*, a living fossil. *PLoS ONE* 11: e0153353
- van der Heijden, M. G. A., Martin, F. M., Selosse, M. A., & Sanders, I. R. (2014). Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist*, 205, 1406–1423.
- Van Jaarsveld, E. J., & Pond, U. (2013). *Welwitschia mirabilis – uncrowned monarch of the Namib*. Cape Town, South Africa: Penrock Publications.
- Von Willert, D. J., Armbrüster, N., Drees, T., & Zabarowski, M. (2005). *Welwitschia mirabilis*: CAM or not CAM – what is the answer? *Functional Plant Ecology*, 32, 389–395.
- Von Willert, D. J., Eller, B. M., Werger, M. J. A., Brinckmann, E., & Ihlenfeldt, H-D. (1992). Life strategies of succulents in deserts: with special reference to the Namib Desert. Cambridge, UK: Cambridge University Press.
- Von Willert, D.J., & Wagner-Douglas, U. (1994). Water relations, CO₂ exchange, water-use efficiency and growth of *Welwitschia mirabilis* Hook. fil. in three contrasting habitats of the Namib Desert. *Botanica Acta*, 107, 291–299.
- Warren, J. M., Hanson, P. J., Iversen, C. M., Kumar, J., Walker, A. P., & Wullschleger, S. D. (2015). Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations. *New Phytologist*, 205, 59–78.

Wassenaar, T. D., Henschel, J. R., Pfaffenthaler, M. M., Mutota, E. P., Seely, M. K., & Pallet, J. R. (2013). Ensuring the future of the Namib's biodiversity: ecological restoration as a key management response to a mining boom. *Journal of Arid Environments*, 93, 126-135.

West, A. G., Partrickson, S. J., & Ehleringer, J. R. (2006). Water extraction times for plant and soil materials used in stable isotope analysis. *Rapid Communications in Mass Spectrometry*, 20, 1317–1321.

Wilkinson, M. J. (1990). Palaeoenvironments in the Namib Desert. *University of Chicago Geography Research Paper*, 231, 1–196.

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TABLE 1 Dimensions of four welwitschia plants that were extensively (plants A, E, F, G) or incompletely (B, C, D) excavated

Individual welwitschia plant	A	B	C	D	E	F	G
Gender	M	F	F	M	F	M	M
Stem width maximum (cm)	25	54	34	21	17	75	108
Stem width perpendicular (cm)	17	28	26	10	6	42	97
Leaf 1 length (cm)	99	105	129	40	61	198	116
Leaf 2 length (cm)	97	98	109	35	52	195	115
Leaf 1 width at meristem (cm)	31	107	44	27	23	148	267
Leaf 2 width at meristem (cm)	31	17	46	22	23	125	184
Root maximum depth (cm)	116	65	83	71	133	178	102
Root maximum spread (cm)	560	280	150	100	240	414	904
Lateral spread to depth ratio	4.83	4.31	1.81	1.41	1.80	2.33	8.86
Number of positions mapped	133	26	69	38	102	236	171
Number of main root branches mapped	35	6	16	18	22	37	19
Number of fine root branches mapped	81	5	27	9	46	73	51
Length of main roots mapped (m)	35.82	10.11	9.58	3.63	22.31	62.31	58.49
Main roots incompletely mapped	1	2	4	8	1	1	0
Diameter of last root (mm)	6.0	9.3	28.8	10.0	4.3	12.9	-

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TABLE 2 Depths of soil layers, the proportion of each plant's major and fine roots in that layer, and each layer's percentage soil moisture

Soil layer	Depth of layer bottom (cm)				Major roots (% for plant in layer)				Fine roots (% for plant in layer)				Soil moisture (% of soil mass)				Soil moisture (%) mean (range) N
	A	E	F	G	A	E	F	G	A	E	F	G	A	E	F	G	
Individual plants																	
Aeolian sand and gravel	25	10	15	30	3	0	0	13	9	15	19	13	0.2	0.2	0.9	0.4	0.8 (0.1-2.1) 33
Gypsum in alluvial gravel	66	63	60	57	50	54	43	78	51	56	48	66	6.2	9.9	7.7	9.1	10.0 (6.5-14.9) 29
Calcrete with alluvial gravel	116	134	178	102	10	19	18	9	6	9	7	7	3.3	4.4	2.3	3.3	3.2 (1.9-4.2) 17
Moist sand in calcrete layer	114	125	93	-	37	26	39	0	35	21	26	14	11.2	7.1	6.8	-	9.9 (5.2-13.4) 16

TABLE 3 O and H isotope values (mean±SD) of plant and soil samples from Welwitschia Plains

Sample Group	$\delta^{18}\text{O}$ (‰)	$\delta^2\text{H}$ (‰)	n	Individual Plants
roots	5.6 ± 1.6	-19.2 ± 4.2	11	A,B
leaves – All	23.7 ± 13.1	40.5 ± 39.4	13	A,B,C,D
Proximal	7.5 ± 0.7	-7.1 ± 2.0	4	A,D
Mid leaf	26.8 ± 3.4	44.8 ± 9.3	5	A,B,C,D
Distal	36.1 ± 10.3	82.7 ± 25.7	4	B,C,D
soils	8.0 ± 3.0	-13.3 ± 7.4	20	A,B,C,D



FIGURE 1 *Welwitschia mirabilis* plants growing in typical habitat on the Welwitschia Plains in the central Namib Desert.

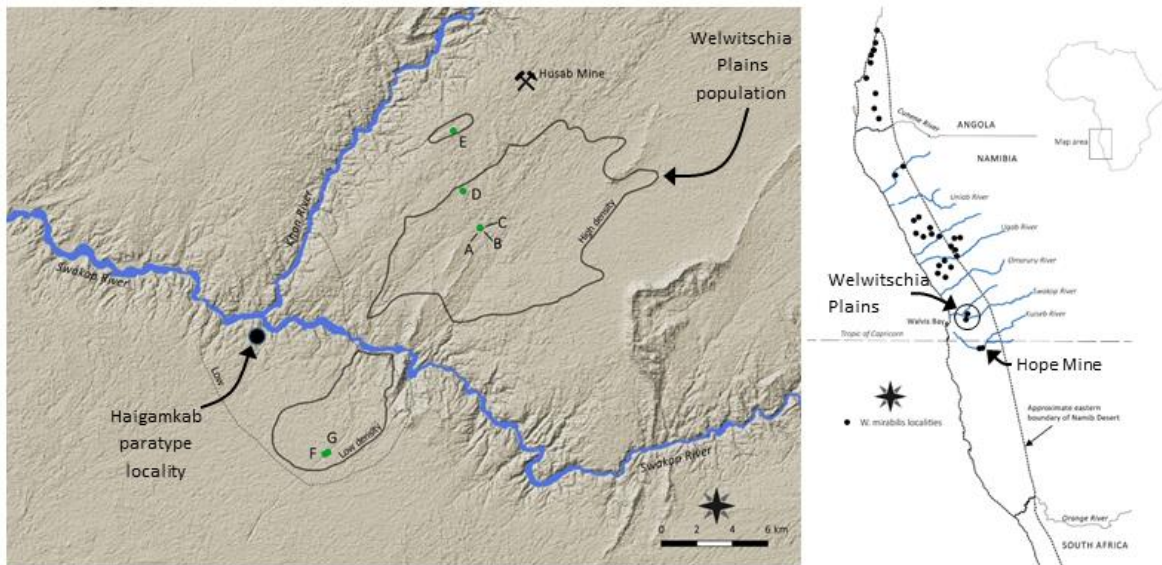


FIGURE 2 Location of the seven study plants (A-G) of the Welwitschia Plains population near Husab Mine in the central Namib Desert (left) in relation to the species distribution (right). The distribution map on the right was reproduced from Kers (1967).

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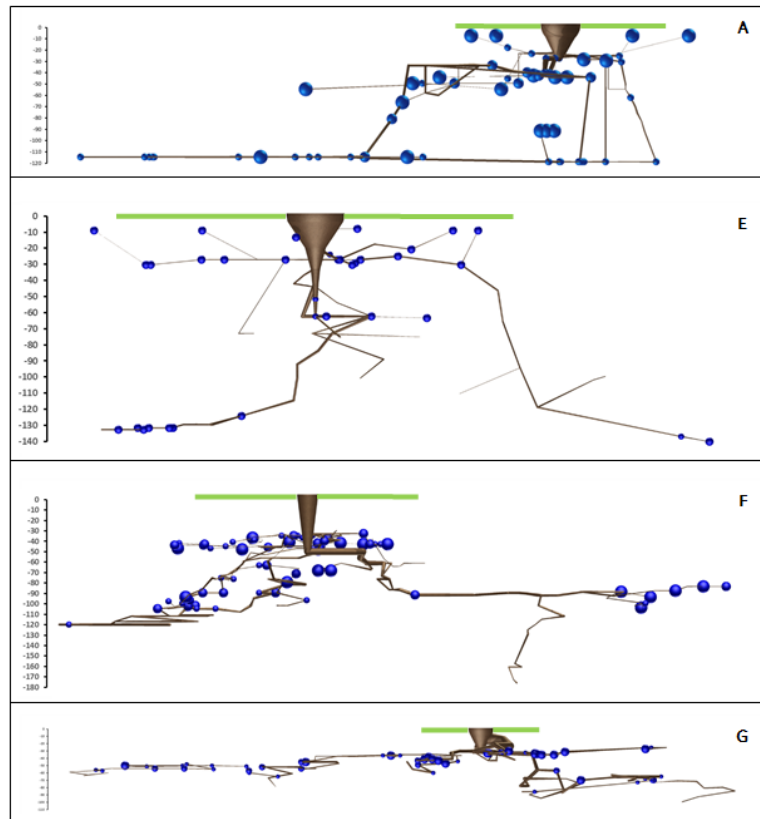


FIGURE 3 Three-dimensional depictions of plants A, E, F and G viewed from the side, showing the mapped pathways of major roots starting at stem (highest point), on either side of which is a 1 m long green bar (horizontal scale). Blue spheres depict locations of fine roots, with the size of the sphere related to the relative number of fine roots at that location (see methods). Dense networks of fine roots in the upper 30 cm of plants F and G are not mapped. The scales on the left show 10 cm intervals of depth into the ground. Rotating 3D images are shown in Figure S1 (click on image).

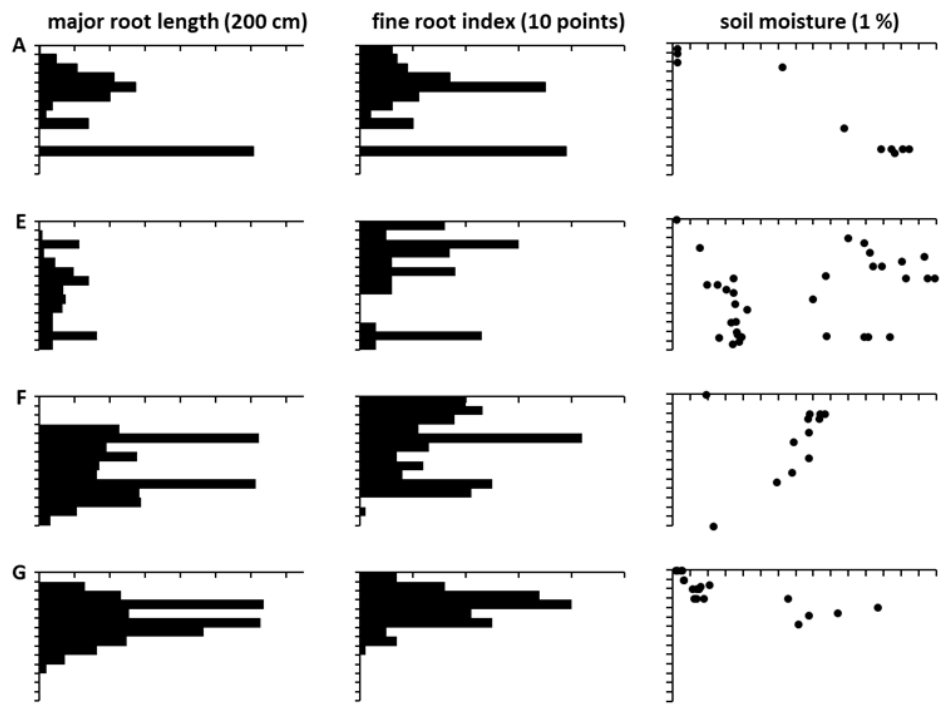


FIGURE 4 Distribution of major roots (left, total length in 10-cm layers from the surface to 140 cm below ground), fine roots (middle, index for layer) and soil moisture (right) for four welwitschia plants. Intervals of tick mark intervals are indicated in the top axis labels.

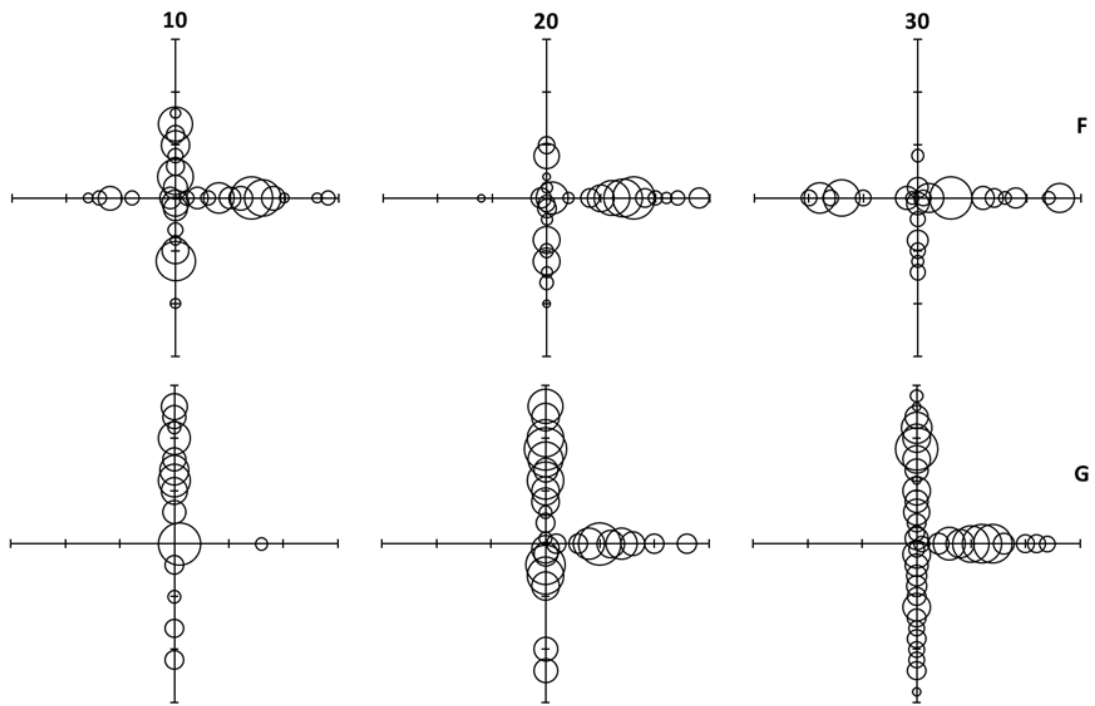


FIGURE 5 Relative density of fine roots in four directions around plants F and G at 0-150 cm distances from stems (mid-point) at depths of 10, 20 and 30 cm. Bubble area depicts densities ranging from 0.25-4 fine roots cm^{-2} .

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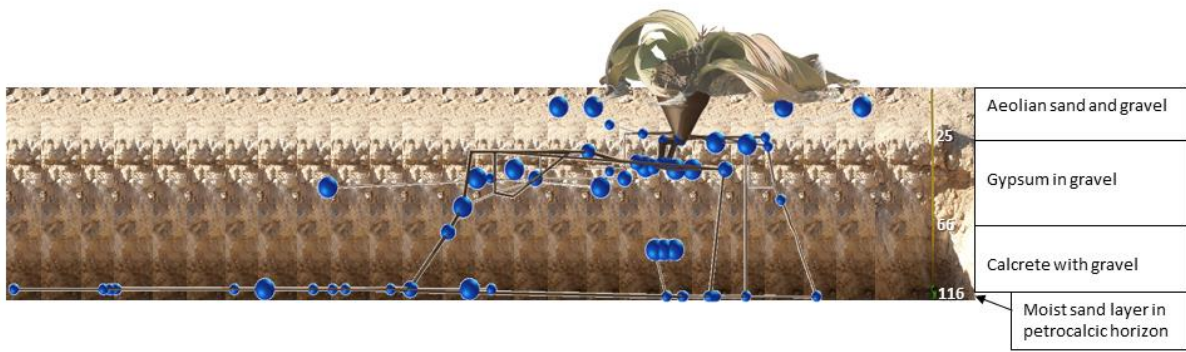


FIGURE 6 Depiction of the root structure (lines) and location of fine roots (blue spheres) of a welwitschia (plant A) in different layers of the ground at this plant (the photograph at the right was repeatedly cloned across the space). The tape measure at right indicates depth from 0-116 cm below ground. Stem and leaves illustrate the above-ground perspective.

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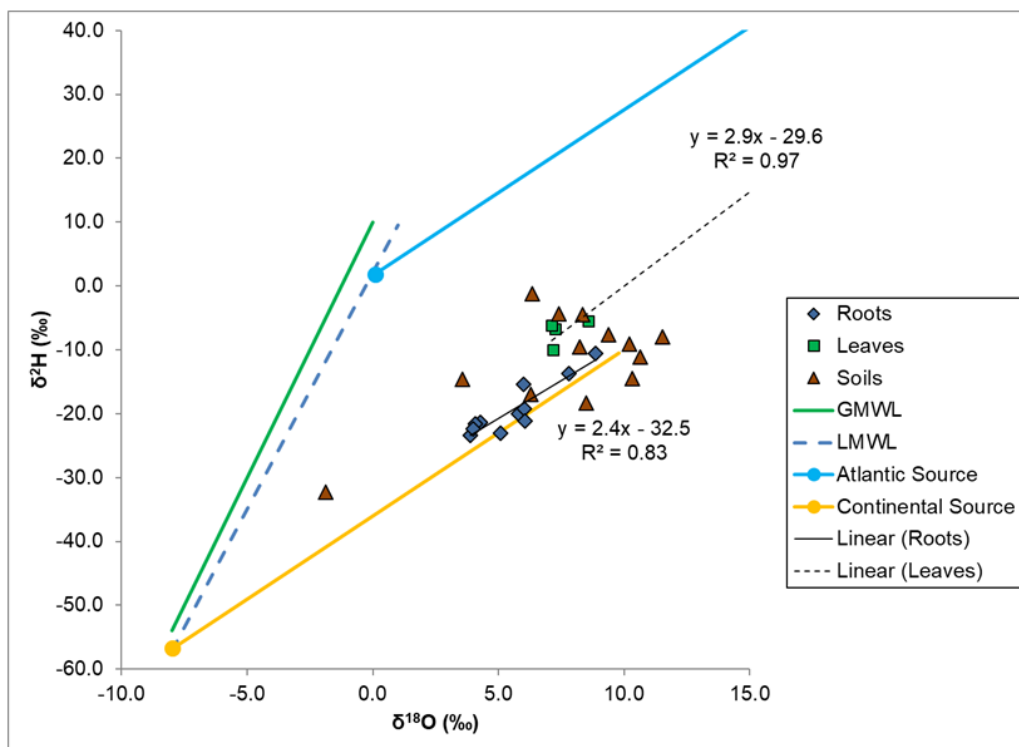


FIGURE 7 Stable isotopic composition of stems, leaves and soils collected from plants A and B. Only proximal leaf samples (closest to the stem) are shown at this scale, but the linear regression between these samples and the more distal leaf samples is provided. The “Atlantic” and “Continental” source lines reflect the isotopically enriched and depleted source water end members, respectively, in the central Namib as recorded by several studies conducted over the past two decades (see Tables S3 and S4 for original data) (Eckardt & Schemenauer, 1998; Schmitz, 2004; Soderberg, 2010; Schachtschneider & February, 2010; Eckardt *et al.*, 2013; Külls *et al.* 2015; Kaseke *et al.*, 2017). The Local Meteoric Water Line (LMWL) is taken as the average of three studies (Soderberg, 2010; Schachtschneider & February, 2010; Kaseke *et al.*, 2017), with a slope of 7.4 and an intercept of 2.1, falling to the right of the Global Meteoric Water Line (GMWL).