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Non rainfall moisture interception by dwarf succulents and their relative abundance in an inland arid South African ecosystem

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ABSTRACT

Dwarf succulents persist in the arid Succulent Karoo despite the low-water storage capacities of their contracted leaves and stems that are inadequate for enduring severe and prolonged drought. We examined the contribution of non-rainfall moisture (fog, dew, water vapour) to the water budgets and relative abundance of two endemic dwarf succulents *Agyroderma pearsonii* and *Cephalophyllum spissum*. Non-rainfall moisture was measured with automated lysimeters containing bare quartz-gravel soils and introduced *A. pearsonii* and *C. spissum* individuals at hourly intervals spanning an 8-month wet winter to dry summer period. Total non-rainfall atmospheric moisture intercepted by the bare quartz-gravel substrate of 137·6 mm, of which water vapour adsorption contributed 56·2 mm, fog 78·2 mm and dew 3·4 mm, was virtually equivalent to the rainfall amount of 142·7 mm. *Agyroderma pearsonii* intercepted 228·4 mm of non-rainfall moisture of which water vapour adsorption contributed 117·1 mm, fog 104·4 mm and dew 6·9 mm. This was nearly three times the non-rainfall amount of 88·7 mm y^{-1} intercepted by *C. spissum*, of which water vapour contributed 44·3 mm, fog 41·3 mm and dew 3·1 mm. The greater quantity of non-rainfall moisture intercepted by *A. pearsonii* corresponded with its threefold greater leaf abundance and twofold greater canopy cover than that of *C. spissum*. We conclude that non-rainfall moisture, especially the absorption of atmospheric water vapour by soils and its uptake by the extensive network of superficial roots of dwarf quartz-field succulents are vital in sustaining their growth and survival and in determining their distributions and relative abundance.

KEY WORDS fog; dew; water vapour; dwarf-succulent; inland-arid; interception

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INTRODUCTION

Non-rainfall atmospheric moisture, which includes dew, fog and atmospheric water vapour, has been identified as a crucial water source for plants in a variety of ecosystems worldwide (Dawson, 1998; Corbin *et al.*, 2005; Gabriel and Jauze, 2008), including several global biodiversity hotspots, where it is particularly important in species distributions (Olson and Dinerstein, 1998). Fog-dependent ecosystems include tropical montane cloud forests and arid coastal areas with high levels of species diversity and endemism, such as Mediterranean-climate regions of Chile (Cereceda and Schemenauer, 1991), south-western Australia (Hutley *et al.*, 1997), southern Africa (Olivier, 2002; Maphangwa *et al.*, 2012) and California (Ingraham and Matthews, 1995; Fischer and Still, 2007). Changes in global climate and land cover have already altered fog patterns in fog-dependent ecosystems (Barbosa *et al.*, 2010; Ponette-González *et al.*, 2010), with as yet unknown effects on the range dynamics of rare species (Pounds *et al.*, 1999). Despite this, the interception and utilisation of non-rainfall atmospheric moisture sources by plant canopies remains one of the least considered aspects of vegetation studies at any scale (Andrade, 2003). The studies that have been reported include the utilisation of fog drip by vegetation in a coniferous ecosystem (Dawson, 1998), and the interception of fog and dew by *Tillandsia* sp and *Sophora* sp inhabiting cloudy montane areas in Mexico (Martorello and Ezcurra, 2002) and Reunion (Gabriel and Jauze, 2008) and elfin cloud forests in Venezuela (Cavelier and Goldstein, 1989; Cavelier *et al.*, 1996). Also, in the semi arid regions of Chile, it has been reported that forests are largely dependent on the deposition of fog water (Del-Val *et al.*, 2006). In southern Africa, only a few studies have examined the role of non-rainfall atmospheric moisture as an ecological factor in natural ecosystems (Agam and Berliner, 2006). Some of the earliest studies examined fog interception by plants of the family Restionaceae on Table Mountain (Marloth, 1904, 1907; Nagel, 1956). These include an unpublished investigation of mist interception by natural vegetation on Table Mountain in Cape Town (Snow, 1985), fog, dew and atmospheric water vapour utilisation by lichens along the west coast (Lange *et al.*, 1990; Maphangwa *et al.*, 2012), and several other studies emanating from the Gobabeb Training and Research Centre in the Namib Desert, which have investigated fog and dew exploitation by some plants and animals (Seely, 1979; Louw and Seely, 1980; Henschel and Seely, 2005).

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Non-rainfall atmospheric moisture is an important source of moisture for hyper-arid coastal ecosystems, such as the Namib and Atacama deserts, where it supplies a relatively predictable source of free water for biota (Louw and Seely, 1980; Westbeld *et al.*, 2009). Soil surface hydration by either dew or fog is readily accepted, but theoretical conditions for water vapour adsorption by soils in arid environments, coupled with their low energy fluxes, have led to this process being disregarded in these environments (Berkowicz *et al.*, 2001; Jacobs *et al.*, 2002). However, there is mounting experimental evidence that this process does occur in arid environments (Kosmas *et al.*, 1998; Ninari and Berliner, 2002). Non-rainfall atmospheric moisture normally accrues on leaf surfaces where it drips, or is funnelled via stem-flow, onto the soil (Hutley *et al.*, 1997) where it is absorbed by plant root systems (Martin and von Willert, 2000). However, pathways for foliar absorption of this moisture are poorly understood. In certain *Crassula* species, epidermal hydathodes have been reported to play a role in water absorption by leaves from their wetted surfaces (Yates and Hutley, 1995; Martin and von Willert, 2000) or from a vapour-saturated atmosphere (Breazeale *et al.*, 1950), although cuticular wettability, integrity and permeability vary considerably among species (Schreiber *et al.*, 2001). Despite these findings, quantitative data on the interception of fog, dew and water vapour by soils and plants in arid ecosystems remain scant; and consequently, this study sought to advance this understanding. The following hypotheses were tested: (i) that non-rainfall atmospheric moisture provides as important source of water as rainfall for shallow rooted dwarf succulents; (ii) that water vapour adsorption comprises the largest component of the non-rainfall atmospheric moisture intercepted by soils and dwarf succulents in the dry season; and (iii) that the quantities of non-rainfall atmospheric moisture intercepted by dwarf succulents determine their relative abundance and local distribution.

METHODS AND MATERIALS

Study site and species

The study site was located on the farm Quaggaskop at an elevation ±160 m situated in the Knersvlakte (30°45′–31°40′S, 18°15′–19°00′E), a semi-arid winter rainfall region within the South African Succulent Karoo Biome (Rutherford and Westfall, 1986). Listed as a global biodiversity hot spot (Myers *et al.*, 2000), the area has a mean annual precipitation and daily maximum air temperature recorded at the nearby Vredendal weather station between 1957 and 1984 of 145 mm and 25·7 °C, respectively (Anonymous, 1990). Large parts of the Knersvlakte, an acknowledged centre of diversity and endemism (Hilton-Taylor, 1996), are covered by quartz-gravel fields, an extra-zonal special habitat, which houses a globally unique specialised flora dominated by chamaephytes among which nano-chamaephytes (dwarf succulents) represent the most important growth form group (Schmiedel, 2001). Two dwarf succulents with different canopy morphologies common on quartz-gravel substrates were selected for study. They were *Agyroderma pearsonii* N.E.Br. Schwantes with silvery to grey–green spherical leaves, rounded at their lower surface with the upper surface flat or slightly convex and *Cephalophyllum spissum* H.E.K. Hartmann with dark green, three-angled spindle-shaped leaves. Both of these species, included in the subfamily Ruschioideae, are endemic to the Knersvlakte and most abundant on saline quartz substrates with moderate to rare abundances on non-saline acid quartz substrates (Schmiedel, 2002).

Dwarf succulent leaf abundance and canopy cover

To determine the relative abundance of *A. pearsonii* and *C. spissum*, $10 \times m^2$ quadrats were randomised on quartz gravel substrates at eight different locations at the study site (80 quadrats in total). The dwarf succulent populations present in each quadrat were photographed with a high resolution 3·4 effective mega pixel (Sigma SD10) digital camera with a three-band Foveon X3 sensor (three sensor photo detectors per pixel location). The camera was fitted with a semi-wide angle lens (24–70 mm zoom, 20 mm fixed) and suspended 1·5 m above ground surface on a tripod. A graduated ruler placed on the ground provided an indicator of scale. For each dwarf succulent species in each quadrat, the total numbers of visible leaves present (leaf abundance) and total leaf areas (canopy cover) were precisely determined in the digital images with the aid of image analysis software (Image-J ver.1·34I, National Institute of Health, USA (Abramoff *et al.*, 2004).

Non-rainfall moisture interception by soils and dwarf succulents

A variety of techniques have been applied to quantify the amount and frequency of non-rainfall atmospheric moisture input. They include leaf wetness resistance sensors, cloth-plates and Duvdevani gauges (Kidron, 2000) and various fog collectors (Schemenauer and Cereceda, 1994; Olivier, 2002; Fischer and Still, 2007) that rely on artificial collecting surfaces. Such collecting surfaces provide unreliable estimates of moisture inputs into natural receiving surfaces (Berkowicz *et al.*, 2001; Ninari and Berliner, 2002; Heusinkveld *et al.*, 2006) and relevant therefore only as proxies for inter-site comparisons (Berkowicz *et al.*, 2001). Also, the reliance of many of these traditional methods on human observation renders them unsuitable for studies in remote or sparsely populated areas (Jacobs *et al.*, 2002). More recently, portable weighing micro-lysimeters, originally used for quantification of evapo-transpiration (Starr *et al.*, 2004), have been developed that allow for automated recording of fog and dew accumulation and evaporation from soil surfaces (Heusinkveld *et al.*, 2006). These appear most promising (Ninari and Berliner, 2002) as they directly measure gains and losses and residence times of water (Heusinkveld *et al.*, 2006) derived from non-rainfall atmospheric sources (Brown *et al.*, 2008). They have been successfully applied in measuring dew deposition in the Negev Desert from which simple physical models simulating dew deposition and evaporation have been developed (Jacobs *et al.*, 2002).

Quantities of non-rainfall atmospheric moisture intercepted by the quartz gravel soils and dwarf succulents in this study were measured hourly with automated weighing micro-lysimeters modified from Heusinkveld *et al.* (2006). Each lysimeter comprised a 240 mm diameter weighing pan constructed from non-porous, low thermal conducting, polyvinyl chloride to minimise material influence on sample temperature (Evett *et al.*, 1995; Heusinkveld *et al.*, 2006). The weighing pan's 35 mm depth was in compliance with reports that the daily moisture cycle is confined to the upper 20 mm to 30 mm of the soil profile (Jacobs *et al.*, 2002). The weighing pans straddled load cells (Model 535QD-D20-6Kg, RS485, DSEnet protocol, DS-Europe, Milano, Italy) manufactured without a silicon gel filler to reduce hysteresis. The load cell resolution was 0·1 g, equivalent to 0·0022 mm of water, which was well below the recommended minimum resolution of 0·1 mm of water for measurement of non-rainfall atmospheric moisture (Agam and Berliner, 2006). A thermocouple was attached to the load cell that constantly monitored its temperature. Both the thermocouple and load cell were connected to a programmable micro-controller sealed inside the lysimeter housing, which was energised by an external battery connected to a solar panel.

Six cylindrical soil cores of similar dimension to that of the lysimeter weighing pans were carefully excavated at the study site. Two comprised bare quartz gravel soil cores, two contained quartz gravel soil cores with growing *A. pearsonii* plants and two contained quartz gravel soil cores with growing *C. spissum* plants. One of each of the three aforementioned duplicated quartz gravel soil cores were dried in a forced draft oven at 60 °C to a constant mass and weighed. The remaining duplicates were placed individually into three lysimeter weighing pans positioned 35 cm above the soil surface at the apex of a slope at the study site (Figure 1 (A, B, D)). The weighing pans were not positioned at the ground surface under aerodynamic conditions (soil surface temperatures and ventilation) similar to those to which dwarf succulents are exposed to in the natural environment (Kidron *et al.*, 2000). The rationale was the disruption of the weighing pans at the soil surface by rodents and other fauna, their operative impediment by wind-blown soils and their contamination by moisture from adjacent soils recharged by capillary rise and overnight distillation processes (Francis *et al.*, 2007). Also, the placement of the weighing pans slightly (5 cm) below the outer lysimeter housing prevented wind induced loss of finer soil particles. Solar panels were located beneath the weighing pans thereby providing no obstruction to the soils and dwarf succulents in the lysimeter weighing pans from non-rainfall moisture deposition. Despite these engineering limitations, the soil and dwarf succulents in the weighing pans of all three lysimeters were exposed to identical environmental conditions. This allowed comparison of the relative quantities of non-rainfall atmospheric moisture intercepted and evaporated by the soils and dwarf succulents in the lysimeter weighing pans, even though the measured quantities of moisture may not have precisely reflected those at the ground surface.

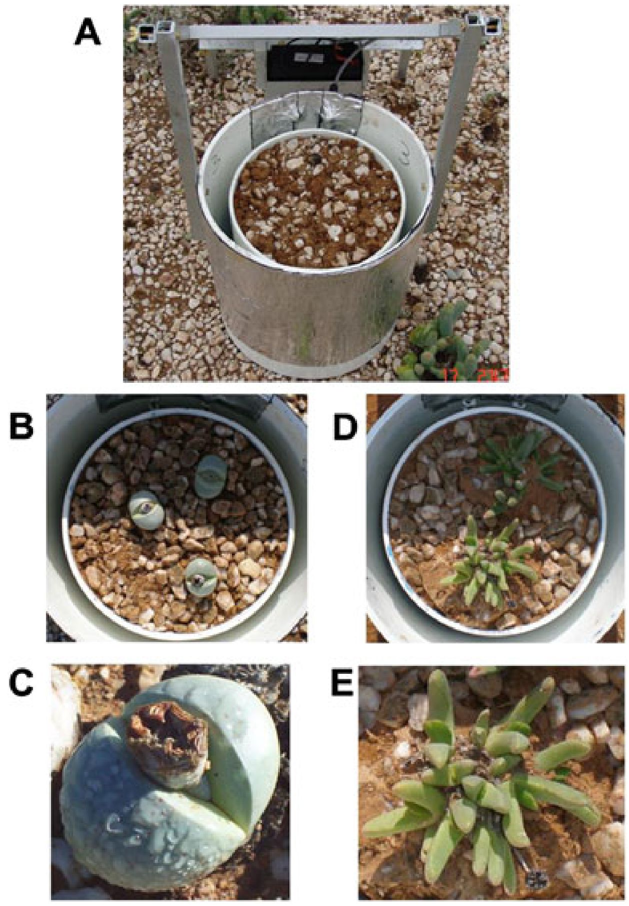

Figure 1. (A) Portable lysimeter containing bare quartz gravel soil in weighing pan, (B) *A. pearsonii* present in weighing pan, (C) distinct dew condensation on *A. pearsonii* leaf surface, (D). *C. spissum* present in weighing pan, (E) indistinct dew condensation on *C. spissum* leaf surface.

Replication of the lysimeters and other automated environmental sensors at the study site was prohibited by their cost. However, the frequency and duration of non-rainfall atmospheric moisture deposition recorded by the lysimeters were corroborated against simultaneous proxy measurements of non-rainfall atmospheric moisture monitored by a leaf wetness resistance sensor. This sensor was positioned at the same height above the soil surface as the lysimeter weighing pans and interfaced with a Watch Dog 450 data logger (Spectrum Technologies Inc., Plainfield, IL, USA). Also, in the initial calibration process, a generalised linear model analysis of variance revealed no statistically significant differences in the net quantities of non-rainfall atmospheric moisture intercepted daily by each of the three lysimeters containing only quartz gravel soils. This was also reported for replicated weighing lysimeters of similar design used in another study of non-rainfall atmospheric moisture interception by soils in the Central Namib Desert (Kaseke, 2009). In addition, all automated temperature, relative humidity and rainfall measurements were corroborated against those recorded concurrently at two nearby meteorological stations.

Changes in mass of moisture (recorded fresh mass minus measured dry mass) of the bare quartz gravel soil cores and those containing the dwarf succulent test species were logged by the lysimeter micro-controller units at hourly intervals over 8 months starting in mid-winter (July) and terminating at the end of summer (February). Measured moisture masses were standardised at 20 °C by applying a calibration function, predetermined for each lysimeter, that corrected for temperature deviations in load cell output (Figure 2(B)). Lysimeter measurements that coincided with incidences of rainfall recorded hourly with a tipping bucket rain gauge interfaced with the Watch Dog 450 data logger were omitted.

The differences between the net quantities of non-rainfall atmospheric moisture intercepted hourly by the quartz-gravel soil cores containing the attached dwarf succulents and that containing only the bare quartz gravel soil provided estimates of the net quantities of non-rainfall atmospheric moisture intercepted hourly solely by each dwarf succulent species. The net quantities of non-rainfall atmospheric moisture intercepted daily by the bare quartz gravel soil cores and the two dwarf succulent species were computed from the differences between the highest and lowest recorded values over each 24-h period and these converted to millimetre of precipitation by dividing them by the weighing pan surface area (Figures 2(C) and 3)

The following criteria were applied to separate the three components of non-rainfall atmospheric moisture intercepted by the quartz gravel soils and dwarf succulents. For fog, the diagnostic developed by Guidard and Tzanos (2007) was applied in which fog occurs at a relative humidity above 90% at a wind speed of less than 7 m s^{-1}, although a satellite-based fog detection model developed by Gultepe *et al.* (2007) did report an average 80% relative humidity during fog episodes. Our observed saturation of the leaf wetness resistance sensor at a relative humidity ≥90% (Figure 2(A)) concurred with the fog diagnostic of Guidard and Tzanos (2007). Consequently, fog was presumed where daily maximum relative humidity was equal to or exceeded 90%. The diagnostic applied for dew was the natural condensation of water vapour into liquid droplets at a relative humidity below 90% when the receiving surface temperature equalled or fell below the ambient dew point temperature (Agam and Berliner, 2006). Dew point temperatures were computed from hourly records of atmospheric relative humidity and air temperature measured with a miniature Watch Dog 450 data logger and compared with simultaneously measured soil surface temperatures using radiation shielded thermocouples interfaced with the data logger. The equation of Berry (1945) was applied for computing dew point temperatures, namely:

$$\text{Dew point} = ((0.66077 - \text{EW}) \times 237.3)/(\text{EW} - 8.16077), \quad (1)$$

where $\text{EW} = 0{\cdot}66077 + (7{\cdot}5 \times \text{T}/(237{\cdot}3 + \text{T})) + \log_{10}(\text{RH})$ 2 T = air temperature (°C) and RH = relative humidity (%).

Dew was presumed where measured minimum daily soil surface temperatures fell below computed minimum daily dew point temperatures. However, this premise may not have strictly applied to leaf surface temperatures of dwarf succulents that were assumed to closely approximate soil surface temperatures. Where fog and dew diagnostics were inapplicable, water vapour adsorption was assumed because this occurs when a water vapour gradient is established between the atmosphere and the soil and is independent of dew-point temperature (Brown *et al.*, 2008).

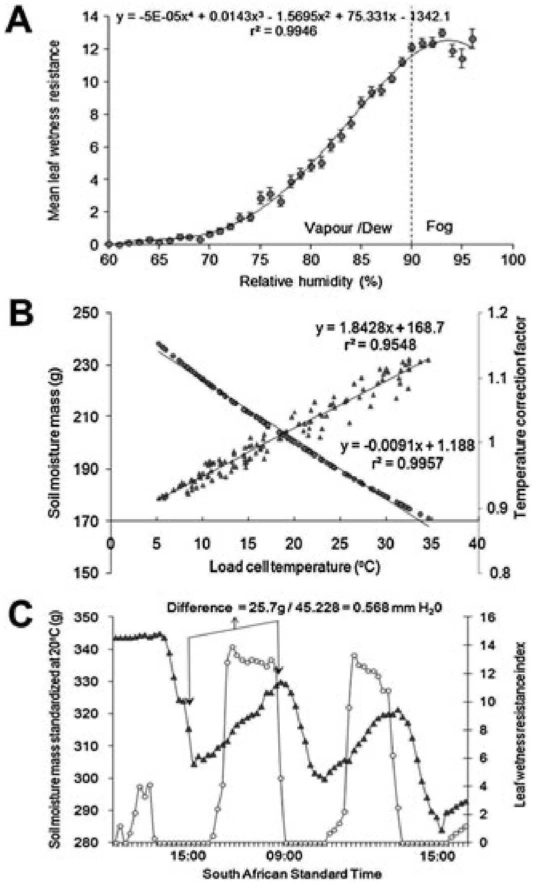

Figure 2. (A) Mean leaf wetness resistance ± standard errors (bars) versus atmospheric relative humidity, (B) regression functions applied for correcting measured moisture masses for load cell deviations due to temperature variation, (C) net quantities of moisture present in weighing pans containing quartz gravel soils and dwarf succulents computed from the difference between the largest and smallest recorded moisture masses over each 24-h period with simultaneous leaf wetness resistance measurements corroborating lysimeter records. The factor 45·228 (pan surface area in mm × 10^{-3}) applied to convert moisture mass (g) to millimetre precipitation.

Data synthesis and statistical analysis

An analysis of variance tested for differences in leaf abundance and canopy cover between the two dwarf succulent test species. A Wilcoxon Sign Rank *Z*-test tested the measured net quantities of fog, dew and water vapour intercepted monthly by the bare quartz gravel soil and the two dwarf succulent test species for significant difference.

RESULTS

Dwarf succulent leaf abundance and canopy cover

A. pearsonii leaf abundance (112·5 leaves ± 9·8 m^{-2}) and canopy cover (199·1 ± 17·8 cm^2 m^{-2}) were significantly greater ($P \leq 0{\cdot}001$) than *C. spissum* leaf abundance (39·0 ± 3·2 m^{-2}) and canopy cover (92·7 ± 8·6 cm^2 m^{-2}).

Non-rainfall moisture interception by soils and dwarf succulents

The net quantity of non-rainfall atmospheric moisture (Figure 2(B)) intercepted over the 8-month period by the

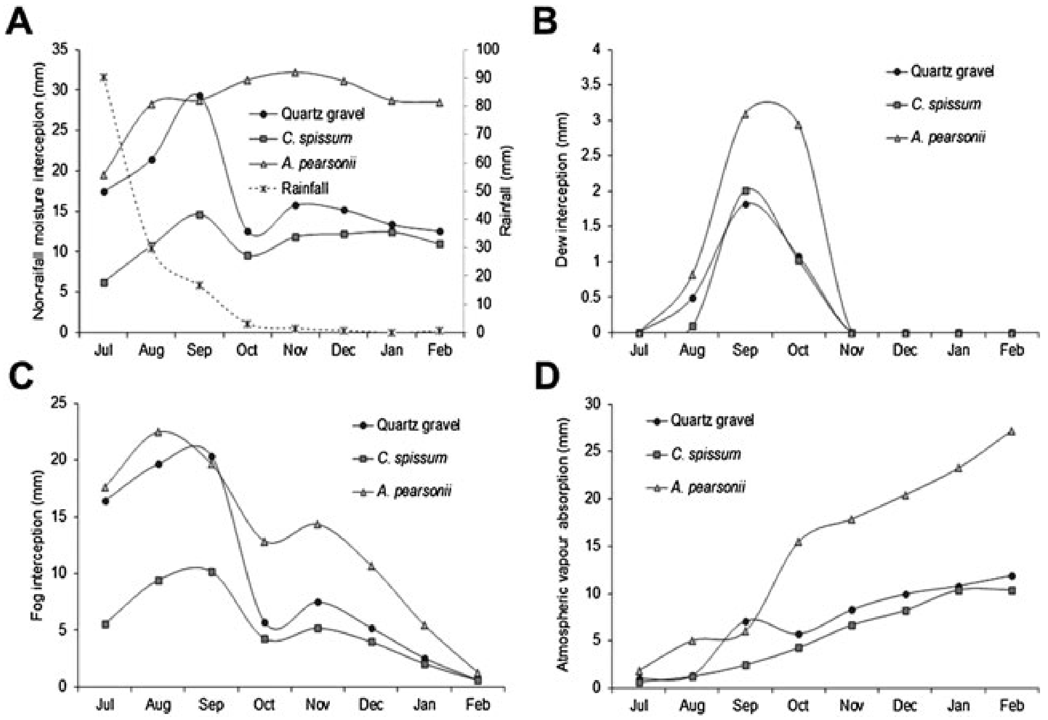

Figure 3. Monthly quantities of (A) total non-rainfall atmospheric moisture, (B) dew, (C) fog and (D) atmospheric water vapour intercepted by quartz gravel soils and the dwarf succulents *A. pearsonii* and *C. spissum*.

quartz gravel soil was 137·6 mm. Water vapour adsorption contributed 56·2 mm (40·8%), fog 78·2 mm (56·7%) and dew 3·4 mm y^{-1} (2·5%) to the non-rainfall amount, which was virtually equivalent to the rainfall amount of 142·7 mm. Moisture input into the quartz gravel soil by fog was greatest during winter and early Spring (July to September), by dew greatest in early Spring (September) and by water vapour absorption greatest during summer (December to February). However, over the entire 8-month monitoring period, moisture input into the quartz gravel soil by fog was not significantly different to that by water vapour adsorption (Wilcoxon *Z*-statistic = 0·3501, *P* = 0·3631), but moisture input into the quartz gravel soil by dew was significantly less (Wilcoxon *Z*-statistic = 2·4505, *P* = 0·007) than that by fog and water vapour adsorption.

The net quantity of non-rainfall atmospheric moisture intercepted over the 8-month period solely by *A. pearsonii* of 228·4 mm, of which water vapour adsorption contributed 117·1 mm (51·3%), fog 104·4 mm (45·7%) and dew 6·9 mm (3·0%), was significantly greater (Wilcoxon *Z*-statistic = 2 3805, *P* = 0·009) and nearly three times the amount of 88·7 mm intercepted by *C. spissum*, of which water vapour adsorption contributed 44·3 mm y^{-1} (49·9%), fog 41·3 mm (46·5%) and dew 3·1 mm (3·5%).

DISCUSSION

Non-rainfall atmospheric moisture interception by quartz gravel soil at this study's arid inland study site of 137·6 mm over the 8-month monitoring period was virtually equivalent to the rainfall amount of 142·7 mm. However, much greater non-rainfall atmospheric moisture inputs relative to rainfall have been reported in other arid ecosystems. An eddy covariance method recently estimated 25 mm y^{-1} of moisture deposited by fog in the hyper-arid Atacama desert, which is over 25 times the annual rainfall of 0·8 mm y^{-1} (Westbeld *et al.*, 2009). Also, recent lysimeter based measurements of non-rainfall atmospheric moisture interception by bare gypsum soils in a South African coastal desert indicated an annual deposition 510 mm y^{-1} that is over ten times greater than the rainfall amount of 43 mm y^{-1} (Maphangwa *et al.*, 2012), a consequence of the higher frequency of fog at this coastal site and the hygroscopic nature of gypsum soils (Pavlík *et al.*, 2008). Other examples include the up to 154% of the annual rainfall contributed by fog in a tropical montane cloud forest (Bruijnzeel, 2001), and the up to 34% of the total hydrological input contributed by fog in a California redwood forest (Dawson, 1998). The measured 3·4% of the total non-rainfall atmospheric moisture input contributed by dew to the quartz gravel substrate in this study conformed with a similar 3% contribution by dew to gypsum soils in a South African coastal desert at Alexander Bay (Maphangwa *et al.*, 2012) and the >1–2% contribution by dew to dune and river sand in the Central Namib Desert at Gobabeb and Kleinberg (Kaseke, 2009). Large diurnal fluctuations in temperature under clear skies and high humidity favour dew formation (Malek *et al.*, 1999), which were mainly attained at the arid inland study site in early spring. However, generally, environmental conditions are more conducive to atmospheric water vapour adsorption than dew formation (Agam and Berliner, 2006). This was clearly apparent in this study where atmospheric water vapour adsorption comprised as high a percentage of the total non-rainfall atmospheric moisture input into the quartz gravel soils as fog and was the main source of moisture during the dry late spring and summer months. Similar findings were reported in the Central Namib Desert (Kaseke, 2009), thus confirming that atmospheric water vapour adsorption is a significant feature of areas characterised by high oscillations in air humidity (Kosmas *et al.*, 2001), despite it being discounted in arid areas (Berkowicz *et al.*, 2001; Jacobs *et al.*, 2002) and therefore less extensively studied (Agam and Berliner, 2006).

Schmiedel and Jürgens (1999) argued that a combination of shallow, quartz debris-covered, and fine-grained soils, with a clear gradient of decreasing stone content by volume and increasing salinity, explained the gradients in plant growth-form composition in quartz-field landscapes. This argument, however, does not explain the persistence of dwarf succulent growth forms in the arid Succulent Karoo with its unreliable seasonal rains (Desmet and Cowling, 1999; Esler and Rundel, 1999) as the low water storage capacity in their contracted leaves and stems are not adequate for enduring severe and prolonged droughts (von Willert *et al.*, 1992). This argument applies generally to subglobose and subterranean nano-chamaephytes in the Succulent Karoo, with quartz patches, especially saline ones, representing an extreme case (Schmiedel, 2002). Midgley and van der Heyden (1999) pointed out the importance of regular fog precipitation in the western part of the Succulent Karoo for shallow rooting miniaturised plants on quartz fields. This argument applies generally to dwarf plants and not exclusively to the quartz-field flora as quartz fields outside the influence of fog show a similar dominance of dwarf plants as in the western part of the Succulent Karoo (Schmiedel, 2002). It was argued that the high importance of ground-level growth forms on quartz fields is enabled by a decreased thermal impact due to the specific reflective properties of quartz, because maximum daily air temperatures at quartz field surfaces are up to 10 °C lower during summer than on adjacent shales (Schmiedel and Jürgens, 2004). Also, measured leaf temperatures of a dwarf succulent *A. pearsonii* on quartz substrates were observed close to that of the ambient air temperature of 35 °C, and up to 3 °C lower on quartz substrates than on adjacent shales (von Willert *et al.*, 1992; Schmiedel and Jürgens, 2004). Despite these arguments, the limited physiological data available indicate that dwarf quartz-field succulents are resilient to high temperatures with an abrupt 28% loss in the catalytic efficiency of the photosynthetic enzyme Rubisco only measured in *C. spissum* at daytime temperature extremes exceeding 54 °C, although this was preceded by a decrease in Photosystem II electron transport at a lower temperature of 44 °C (Musil *et al.*, 2009).

Interception of non-rainfall atmospheric moistures do assist plants in preventing thermo-regulation by enhancing leaf turgor (Hanba *et al.*, 2004) and suppressing water loss from leaves by delaying day time transpiration (Burgess and Dawson, 2004) as well as minimising nocturnal transpiration water loss in succulents with a crassulacean acid metabolism (CAM) photosynthetic mode, a common feature in the Ruschioideae. Recent studies show that CAM may not only serve in water conservation but also in moisture collection (Herrera, 2009; Matimati *et al.*, 2012). For instance, the accumulation of malate in the vacuole of *Kalanchoe daigremontiana* causes a reduction in bulk-leaf turgor pressure, which favours water absorption (Smith and Luttge 1985). Furthermore, it was demonstrated that the induction of CAM in *Clusia minor* assisted in water absorption through a decrease in leaf sap osmotic potential (Herrera *et al.*, 2008). Noteworthy, was that the measured non-rainfall atmospheric moisture interception by *C. spissum* (88·7 mm) and especially *A. pearsonii* (228·4 mm) were substantial when compared with the rainfall amount of 142·7 mm. Similar substantial amounts of non-rainfall moisture interception have been reported for the lichens *Ramalina* sp (88 mm y^{-1}) and *Teloschistes capensis* (152 mm y^{-1}) at an arid coastal site in the Succulent Karoo with a high frequency of oceanic fog but a low rainfall amount 43 mm y^{-1} (Maphangwa *et al.*, 2012). Also, it has been reported that the ball moss (*Tillandsia recurvata*) in the Mexican Central Highlands (Guevara-Escobar *et al.*, 2011) intercepts up to three times greater fog (0·56 mm) than rainfall (0·19 mm), and that as much as 5 mm per fog event is intercepted by a medium-sized mound of the endemic grass *Stipagrostis sabulicola* in the Central Namib Desert (Ebner *et al.*, 2011). In this study, the observed approximately three times greater non-rainfall atmospheric moisture intercepted by *A. pearsonii* (228·4 mm) than by *C. spissum* (88·7 mm) was reflected in *A. pearsonii's* approximately three times greater leaf abundance and two times greater canopy cover than that of *C. spissum*. This was attributed to *A. pearsonii's* structural and morphological attributes that seem more conducive to moisture interception and conservation than those of *C. spissum*.

Photographic evidence indicated greater water repellence and dew condensation on *A. pearsonii* leaves than *C. spissum* leaves (Figures 1(C, E)), a known adaptation among plants inhabiting dry climates for channelling hydrological inputs underneath their canopies (Holder, 2007). This is attributed to the paler silvery to grey–green leaves of *A. pearsonii* leaves than the dark green leaves of *C. spissum* indicating less radiation and heat absorption by *A. pearsonii* leaves resulting in lower leaf temperatures and consequently more frequent dew condensation. This suggestion is corroborated by observations on epiphytic bromeliads in Mexican dry forests that have shown that the greater amounts of dew intercepted by *Tillandsia elongata* than *T. brachycaulos* during both dry and rainy seasons are due to *T. elongata*'s consistently lower leaf temperatures (Andrade, 2003). Also, potentially lower leaf temperatures in *A. pearsonii* than *C. spissum* would result in less water loss through transpiration, an effective means of cooling leaf surfaces (Von Willert *et al.*, 1992) that may partly explain why *A. pearsonii's* seasonal pattern in total non-rainfall moisture interception was less distinct than those of *C. spissum* and the bare quartz gravel soil.

Atmospheric water vapour absorption comprised the highest fraction of the total quantity of non-rainfall moisture intercepted during the dry summer season by both the quartz gravel soils and dwarf succulents. This indicated that the most important benefit to plants was the uptake of atmospheric water vapour absorbed by the soils by superficial plant roots (Batanouny, 2001). This suggestion concurs with *A. pearsonii*'s extensive network of superficial roots that ramify in the top soil layer, coupled with its water repellent leaf surfaces. Such adaptations have been reported in the fog zone of the Namib Desert, where certain plants such as *Salsola sabulicola* have well-developed superficial root networks (Danin, 1991) or efficient mycorrhizal relationships that enable them to benefit from alternative moisture sources such as fog and dew.

We conclude that non-rainfall moisture sources, especially the absorption of atmospheric water vapour by soils, are vital in sustaining growth and survival of dwarf quartz-field succulents and in determining their distributions and relative abundance.

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