

**THE RELEVANCE OF FOG AND DEW PRECIPITATION TO
SUCCULENT PLANT HYDROLOGY IN AN ARID SOUTH
AFRICAN ECOSYSTEM**

IGNATIUS MATIMATI



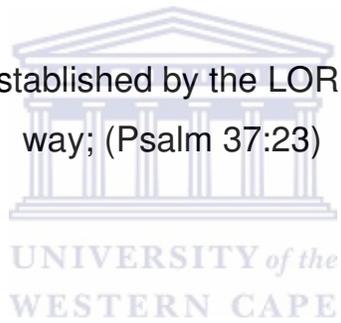
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Supervisors: Dr Charles F. Musil
Prof. Lincoln Raitt
Dr. Edmund February

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To Mikayla and Shekinah

The steps of a man are established by the LORD, when he delights in his
way; (Psalm 37:23)



Keywords

CAM and C₃ photosynthetic mode

Fog and dew precipitation

Foliar Nitrogen

Foliar Phosphorous

Malate accumulation

PSII function

Stem diameter variation sensor

Succulent karoo

Succulent plants

Vapour pressure deficit



Abstract

Fog and dew interception and utilization by plant canopies remains one of the least considered aspects of vegetation studies at any scale yet the few studies that have been conducted point to their considerable influence on ecological processes and a critical role in modulating climate in southern African arid ecosystems. Their relevance to succulent plant hydrology was investigated in this study.

The first study measured stable $\delta^{18}\text{O}$ and $\delta^2\text{H}$ isotope ratios in samples of rain, fog and dew water and compared these with those assayed monthly in stem xylem water of six succulent shrub species over a one year period. Negative $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ratios were observed in the stem xylem water of all six species signifying a predominance of water derived from fog and dew precipitation which was most conspicuous during the wet winter. This implied that fog and dew are even more important sources of water than rain and corroborated by significant correspondence found between fog and dew frequencies, succulent foliar water contents and quantum yields of photochemistry.

The second study monitored variations in stem diameter at 2-hourly intervals in 8 succulent shrub species of diverse growth form over a 9-month period. Two groups of species were distinguished based on whether their daily amplitudes in stem diameter were consistently positively correlated with daily fluxes in vapour pressure deficit, which were indicative of a persistent CAM photosynthetic mode, or intermittently correlated with daily fluxes in vapour pressure deficit, which were indicative of mixed CAM and C_3 photosynthetic modes. Among species displaying a persistent CAM photosynthetic mode, high nocturnal fog and dew precipitation amounts corresponded with low daily amplitudes in stem diameter, and vice versa, which pointed to reduced nocturnal stomatal water loss. These patterns, which were indistinct among species displaying mixed CAM and C_3 photosynthetic modes, were corroborated by small daily amplitudes in stem diameter also consistently observed in one species displaying a CAM photosynthetic mode in ambient than artificially fog and dew excluded environments.

The third study monitored changes in water mass at hourly intervals of quartz gravel substrates with different dwarf succulent species assemblages over an 8-month period. Consistently greater net amounts of water were intercepted daily by quartz gravel substrates containing *Agyroderma pearsonii* than *Cephalophyllum spissum* plants as well as those without plants. These attributed to a high water repellence of *A. pearsonii* leaves and less radiation absorbed by the paler silvery to grey-green leaves of *A. pearsonii* leaves than the dark green leaves of *C. spissum* resulting in lower leaf temperatures and less water loss by transpiration. Quartz gravel soils devoid of plants intercepted nearly 5-times greater amounts of precipitation contributed by fog and dew than that contributed by rain. These precipitation

amounts exceeding the high percentages of total hydrological input contributed by fog and dew reported in other ecosystems.

The study concludes that fog and dew are a vital source of water for succulent shrubs in arid South African ecosystems and imply that diminished fog and dew frequencies associated with elevated night time temperatures accompanying global warming could exacerbate plant drought stress.



Declaration

I declare that *The Relevance of Fog and Dew Precipitation to Succulent Plant Hydrology in an Arid South African Ecosystem* is my own work, that it has not been submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Ignatious Matimati

May 2009



Ignatious Matimati

Signed :

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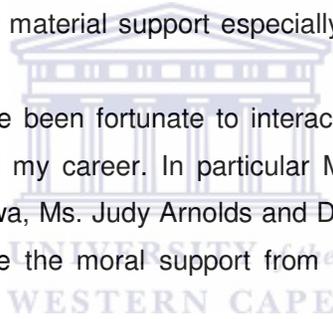


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Abbreviations

AFD	Apparent fog and dew precipitation
BIOTA	Biodiversity Monitoring Transect Analysis
CAM	crassulacean acid metabolism
DSMS	dry soil mass of sample
e	vapour pressure
e_s	saturation vapour pressure
FSMC	fresh soil mass of sample
IDSMS	initial dry mass of core
IPCC	International Panel on Climate Change
ISWC	initial soil water content
PSII	photosystem II
VPD	vapour pressure deficit
V-SMOW	Vienna Standard Mean Ocean Water



Chapter 1

A review of fog and dew precipitation effects on succulent plant hydrology

1.1. Background

Over the last 200 years, there has been a lack of sustained investigations on dew and fog and their utilization by plants. This is partly due to a predilection by biologists towards investigating limiting rather than contributing environmental factors that enable plants to survive and compete in ecosystems where water resources are limiting (Stone, 1957). Dew and fog are known to have considerable influence on ecological processes (Vermeulen, et al., 1997; Weathers, 1999; Burgess & Dawson, 2004) and have a critical role in moderating climate in southern African arid ecosystems. This readily acknowledged with several studies having assessed the viability of harvesting fog to supplement water supplies to rural communities (Olivier, 2002). However, as a key ecological resource there remains much that is unknown about the dynamics of both dew and fog occurrence and their contribution to regional moisture availability. Cowling & Hilton-Taylor (1999) noted that dew and fog are likely to have a large and potentially controlling influence on soil water availability, and therefore plant water balance in the South African succulent karoo biome, especially during the dry summer months. Variation in soil surface wetting by dew and fog at a landscape scale is likely to result in variation in soil water and nutrient supply to roots. This is caused by nutrient input within this precipitation (Kulshrestha, et al., 2005), and effects of soil moisture on soil microbial activity and nutrient cycling (Biederbeck, et al., 1977).

However, the frequency of occurrence and spatial extent of dew and fog is poorly documented, intra and inter-annual variability of their spatial extent is unclear and historical trends are unknown. Also, finer-scale features such as the diurnal timing of dew and fog formation and its incursion, and the amounts used by different plant species to maintain metabolism and hydration require examination (Smith & McClean, 1989). Also requiring understanding is the potential impact of anticipated changes in global climate (IPCC, 2001) on fog and dew precipitation (Schulze, 1995; Yates & Hutley, 1995; Andrade, 2003) in a predicted more arid and hotter climate in the succulent karoo biome (Rutherford, et al., 1999a,b; Midgley, et al., 2002; Midgley, et al., 2003).

1.2. Dew and fog effects on plants

Dew and fog, collectively defined as occult precipitation, constitute a considerable portion of the hydrologic input into ecosystems in tropical montane, desert and coastal

regions (Azevedo & Morgan, 1974; Cereceda & Schemenauer, 1991; Yates & Hutley, 1995; Ingraham & Matthews, 1995; Dawson 1998; Burgess & Dawson, 2004; Scholl, et al., 2007; Fischer & Still, 2007) including the southern African West coast (Desmet & Cowling, 1999a) where spatial and temporal distribution patterns have been measured (Olivier, 2002).

Plant canopies are ideal dew and fog interceptors (Kerfoot, 1968), the quantities influenced by plant size, phenology and habitat type (Shure & Lewis, 1973), with water in excess of canopy-storage capacity transferred to the soil surface *via* stem flow or leaf drip where it is absorbed by plant root systems (Hutley, et al., 1997). Plants with rosette growth forms comprising flexible narrow leaves are particularly efficient as fog interceptors. This demonstrated in *Tillandsia spp.* where the total amount of fog intercepted by the rosettes correlated with total leaf area, the narrow leaves maximizing interception efficiency per unit area (Martorello & Ezcurra, 2007). Based on micrometeorological measurements Martorello & Ezcurra (2002) found that rosette plants inhabiting cloudy montane areas in Mexico could increase their water supply by between 10 and 100% by intercepting fog. Other studies have estimated that fog interception by plant canopies may account for up to 34% of hydrological input in some ecosystems (Dawson, 1998), and also plays as an important role as rain in depositing essential ions such as NO_3^- , SO_4^{2-} , NH_4^+ (Thalmann, et al., 2002; Takenaka, et al., 1999).

Coalesced dew and fog may also influence the internal water balance of the plant (Martin & von Willert, 2000; Slatyer, 1967) with the frequency and duration of water on leaf surfaces having important consequences for plant growth and photosynthetic gas exchange (Brewer & Smith, 1997). Surface leaf wettability has been reported to modify leaf photosynthesis (Hanba, et al., 2004). Among alpine and subalpine plants, it was observed that natural dew depressed leaf CO_2 assimilation in species with wettable leaves by 77%, but stimulated leaf CO_2 assimilation by 14% in species with non-wettable leaves (Smith & Mclean, 1989), this due to differences in stomatal regulation in the two leaf types (Hanba, et al., 2004). Also, dew and fog enhance leaf turgor necessary to maintain photosynthesis (Hanba, et al., 2004) and suppress water loss from leaves by delaying transpiration thereby ameliorating daily water stress (Burgess & Dawson, 2004). Heavy dew also assists in the conservation of soil water resources which is crucial in areas where semi-arid agriculture is practised (Monteith, 1957; Duvdevani, 1964; Baier, 1966) and has a significant impact on the restoration of degraded vegetation after forest fires (Mileta, et al., 2006).

There exists substantial anecdotal evidence, and some experimental data largely from laboratory studies (Kerfoot, 1968), that leaves of some succulent species can also absorb water vapour directly from a saturated atmosphere (Breazeale, et al., 1950; Haines, 1952; 1953) or from wetted leaf surfaces (Yates & Hutley, 1995; Martin & von Willert, 2000) with greater absorption possible from the latter than the former (Breazeale, et al., 1950;

Yates & Hutley, 1995). However, for both processes quantitative data are generally lacking, particularly for plants growing under field conditions and, in addition, the pathways of foliar absorption of water are poorly understood. In certain *Crassula* species, epidermal hydathodes have been reported to play a role (Martin & von Willert, 2000), but in their absence a cuticular pathway is usually presumed though cuticular wettability, integrity and permeability vary considerably among species (Boyce, et al., 1991; Jagels, 1991; Schreiber, et al., 2001).

In southern Africa, the earliest documented experiments aimed at determining dew and fog deposition volumes were conducted on Table Mountain in the early twentieth century (Marloth, 1904; 1907). Since then, several similar studies have been conducted in South Africa and Namibia primarily with the objective of examining the feasibility of harvesting dew and fog precipitation as a source of drinking water and irrigation for small-scale agricultural projects to generate income for local impoverished communities. The most noteworthy of these include Nagel (1959; 1962), Schutte (1971), Schulze (1975), Nieman et al. (1978), and more recently Olivier (2002). All these experiments indicate a considerable potential of dew and fog as a water source, supported by the substantial water yields generated in established fog water collection projects in Chile and other developing countries (Schemenauer & Cereceda, 1991; 1994). In contrast, there is a paucity of studies examining the role of dew and fog as an ecological factor in southern African natural ecosystems. The exceptions including an unpublished study of mist interception by natural vegetation on Table Mountain (Snow, 1985), and several other studies emanating from the Gobabeb Training & Research Centre in the Namib Desert which have investigated dew and fog exploitation by some plants and animals (see review by Henschel & Seely, 2005).

1.3. Dew and fog measurement

A variety of techniques have been applied to quantify the amount and frequency of moisture deposited by dew and fog. These include both direct systems using leaf wetness resistance sensors, weighing lysimeters, dew gauges, Duvdevani blocks and indirect systems using stem flow sensors, stem microvariation sensors (dendrometers) and isotopic discrimination (Noffsinger, 1965; Agam & Berliner, 2005).

Single measurements taken on proxy surfaces (wood or cloth) have been applied extensively to quantify dew and fog amounts (Duvdevani, 1947; Trautner & Eiden, 1988; Scherm & Van Bruggen, 1993; Kidron, 2000) but these provided little information on dew onset, its rate of accumulation and subsequent evaporation (Heusinkveld, et al., 2004). Leaf wetness resistance sensors comprising rectangular epoxy-fiberglass printed circuit boards etched with a grid network of gold-copper lines (Scherm & Van Bruggen, 1993; Kidron, 2000; Kidron, et al., 2000) are relatively simple to install but only provide a means of detecting the

frequency and duration of dew and fog but not the total amounts deposited (Agam & Berliner, 2005).

Various types of mesh screens which are more efficient at fog interception than smooth solid surfaces (Walter, 1986) have been developed to collect fog moisture (Desmet & Cowling, 1999b) and these interfaced with rain gauges provide reliable instantaneous measurements of fog (Olivier, 2002; Cereceda, et al., 2002).

More recently portable weighing micro-lysimeters, originally used for quantification of evapotranspiration (Evelt, 1995; Yunusa, et al., 2004; Marek, et al., 2004; Starr, et al., 2004), have been developed that allow for automated recording of dew formation, accumulation and evaporation (Kidron, 1998; 2000; Heusinkveld, et al., 2004). These have been successfully applied in measuring dew deposition in Negev Desert from which simple physical models simulating the dew deposition and evaporation have been developed (Jacobs, et al., 1999).

Thermometric sap flow sensors are widely used to measure xylem water flow in roots, stems and branches of plants (Hinckley, 1971; Jian Hua, et al., 2007; Burgess & Dawson, 2007) with average sap flow velocity showing a significant linear correlation with net radiation, air temperature and relative humidity (Jian Hua, et al., 2007). However, such sensors are difficult to install and insensitive to changes in sap flow direction (Burgess & Dawson, 2007). In contrast, stem micro-variation sensors are more reliable and easily installed and have been successfully applied in monitoring plant water stress in horticultural crops (Ton & Kopyt, 2003; Kopyt, et al., 2005; Gurovich, et al., 2006).

Isotopic discrimination provides an indirect measure of the fraction of total precipitation contributed by fog and dew. Numerous studies (e.g. Dawson, 1993; 1998; Burgess & Dawson, 2004; Ingram & Mark, 2000) have confirmed that fog, a condensate of saturated air close to the earth's surface, has a higher proportion of the heavy isotopes than rain, a condensate from saturated air higher levels in the atmosphere (Ingram & Mark, 2000). Stable isotopic compositions (^2H and ^{18}O) of fog are more enriched than those of rain (Gonfiantini & Longinelli, 1962; Ingraham & Mark, 2000), these differences consistent and predictable (Ingraham & Mathews, 1990; Ingraham, 1998; Dawson, 1998). This allows for the discrimination of the different sources of precipitation absorbed by vegetation from analyses of stable hydrogen (^2H) and/or oxygen isotope (^{18}O) composition of water extracted from plant stems (Flanagan & Ehleringer, 1991; Ehleringer & Dawson 1992; Dawson, 1993; Gat 1996; Dawson & Ehleringer, 1993; 1998). Indeed assays of the stable isotope composition of fog, rain, shallow and deep soil water, and xylem water have been successfully applied to determine how much of these water sources were used by plants inhabiting coastal ecosystems (Dawson, 1998; Ingram & Mark, 2000; Dawson, 1993; Phillips & Gregg, 2001; Corbin, et al., 2005). Other documented examples where stable isotope assays have been applied include the interception of fog water by redwood (*Sequoia sempervirens*) forests of

northern California (Dawson, 1998), fog water utilization by *Didymopanax pittieri* in Costa Rica (Field & Dawson, 1998) and snow tussock grass (*Chionochloa rigida*) in New Zealand (Ingraham & Mark, 2000) and summer fog water use by prairie grasses in California (Corbin, et al., 2005). Also isotopic discrimination assays have also been applied in determining dew deposition and fog water input into hydrological cycles in California (Dawson, 1998; Fischer & Still, 2007) and New Zealand (see Ingraham & Mark, 2000).

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Chapter 2

Study area and sites, project objectives, hypotheses and key questions

2.1. Study area

The study area was the succulent karoo biome (Rutherford & Westfall, 1986) which has the highest species diversity recorded for semi-arid vegetation type and listed among 34 global biodiversity hot spots (Myers, et al., 2000; Mittermeier, et al., 2004). This biome contains more than 6356 species with 168 families and 1 002 genera, 80 of which are endemic, confined within an area of 116 000 km². Forty percent (40%) of the 6356 species are either strict (26%) or near (14%) endemics (Milton, et. al., 1997; Driver, et al., 2003) and 15% are “Red Data” listed. Chamaephytes and geophytes are predominant in the biome, and there is a scarcity of tall trees, grasses and shrubs (Evenari, et al., 1985). Approximately 18% of the flora comprises geophytes and 29% succulents belonging mainly to the Crassulaceae and the subfamily Ruschioideae of the Aizoaceae (Milton, et al., 1997; Driver et al., 2003).

The climate for the biome is very different from that of other arid desert ecosystems in that it receives a dependable winter precipitation (Milton, et al., 1997; Cowling & Pearce, 1999). One theory has related the diversification of some species, especially in sub family Ruschioideae to the onset of a winter rainfall regime during the Pleistocene some 5 million years ago (Klak, et al., 2004; Hendey, 1982; Axelrod, et al., 1978). Annual rainfall varies from 20 mm in the northwest to more than 400 mm in the south on the escarpment, but the majority of the biome receives less than 150 mm. The biome also receives a substantial amount of precipitation from heavy dews and fog (Desmet & Cowling, 1999a). The fog is generated by the cold Benguela Current of the Atlantic Ocean, and summer heat in coastal parts of this region. However, some of the hottest days, when temperature may rise to 40°C, occur in winter as a result of hot “berg” or mountain winds (Cowling, 2001). Nocturnal fogs and/or dew deposition are quite common during summertime (Milton, et al., 1997; Cowling, 2001; Martin & von Willert, 2000; 2002; Olivier, 2002), these caused mainly by advection of moist sea air (Heydoorn & Tinley, 1980; Henderson-Sellers & Robinson, 1986) but also by temperature inversion and cloud interception.

There are concerns that increased anthropogenic activities and anticipated increases in temperature and aridity with climate warming may threaten biodiversity patterns in the biome over the short-term. Bio-climatic models predict large reductions in species richness in the biome with climate warming (Rutherford, et al., 1999a; 1999b; Midgley, et al., 2002; 2003) with five of its conservation areas expected to lose 40% of their endemic species

(Rutherford, et al., 2000). These findings validated by empirical studies that have revealed massive increases in mortalities of dwarf succulents on quartz-fields following artificial warming consistent with future African climate scenarios (Musil, et al., 2005; 2009). Therefore, new biodiversity conservation strategies are essential to accommodate human induced changes in climate (Hannah, et al., 2002). Successful biodiversity conservation and ecosystem restoration strategies hinge on an in-depth understanding of the relationships between both biotic and abiotic factors influencing plant growth and survival. The importance of fog and dew for plant survival, especially during the dry summer season has been recognized (Desmet & Cowling, 1999b; Musil, et al., 2005; 2009) and their potential as drivers of biodiversity is indispensable for any conservation or restoration programs within the biome.

2.2. Study sites

The principal study site (Figure 2.1) comprised the farm Quaggaskop ($31^{\circ}24.6'$ S, $18^{\circ}37.8'$ E) at an elevation ± 160 m situated in the Knersvlakte, with 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 (Climate of South Africa, 1986). Large parts of the Knersvlakte, an acknowledged centre of diversity and endemism (Hilton-Taylor, 1994; 1996), are covered by quartz-gravel fields, an extra-zonal special habitat, which houses a globally unique specialized flora (Schmiedel & Jürgens, 1999; Schmiedel, 2001; 2002). Inter-dispersed among the quartz-gravel fields are areas devoid of quartz covered with shale, phyllite and limestone derived substrates of the Nama Group (Schmiedel & Jurgens, 1999) where larger succulent shrubs dominate.

Some fog exclusion observations were also conducted at one other study site in the Richtersveld, namely Numees ($28^{\circ}18'07.6''$ S / $16^{\circ}57'50.4''$ E) which occurs approximately 12 km south-east of the Orange River at an altitude of 377 m (Figure 2.2). Maximum daily summer temperatures reach 50°C with a predominantly winter rainfall averaging 70 mm annum^{-1} supplemented by coastal fogs occurring 40–50 days annum^{-1} (Jürgens, et al., 1999). Soils constitute meta-sediments of the Gariep Supergroup which include quartzite, limestone and dolomite. The vegetation type is classified as Central Richtersveld Mountain Shrubland (Mucina & Rutherford, 2006) comprising diverse dwarf shrub communities with many leaf succulent species (Jürgens, et al., 1999; Gotzmann, 2002).

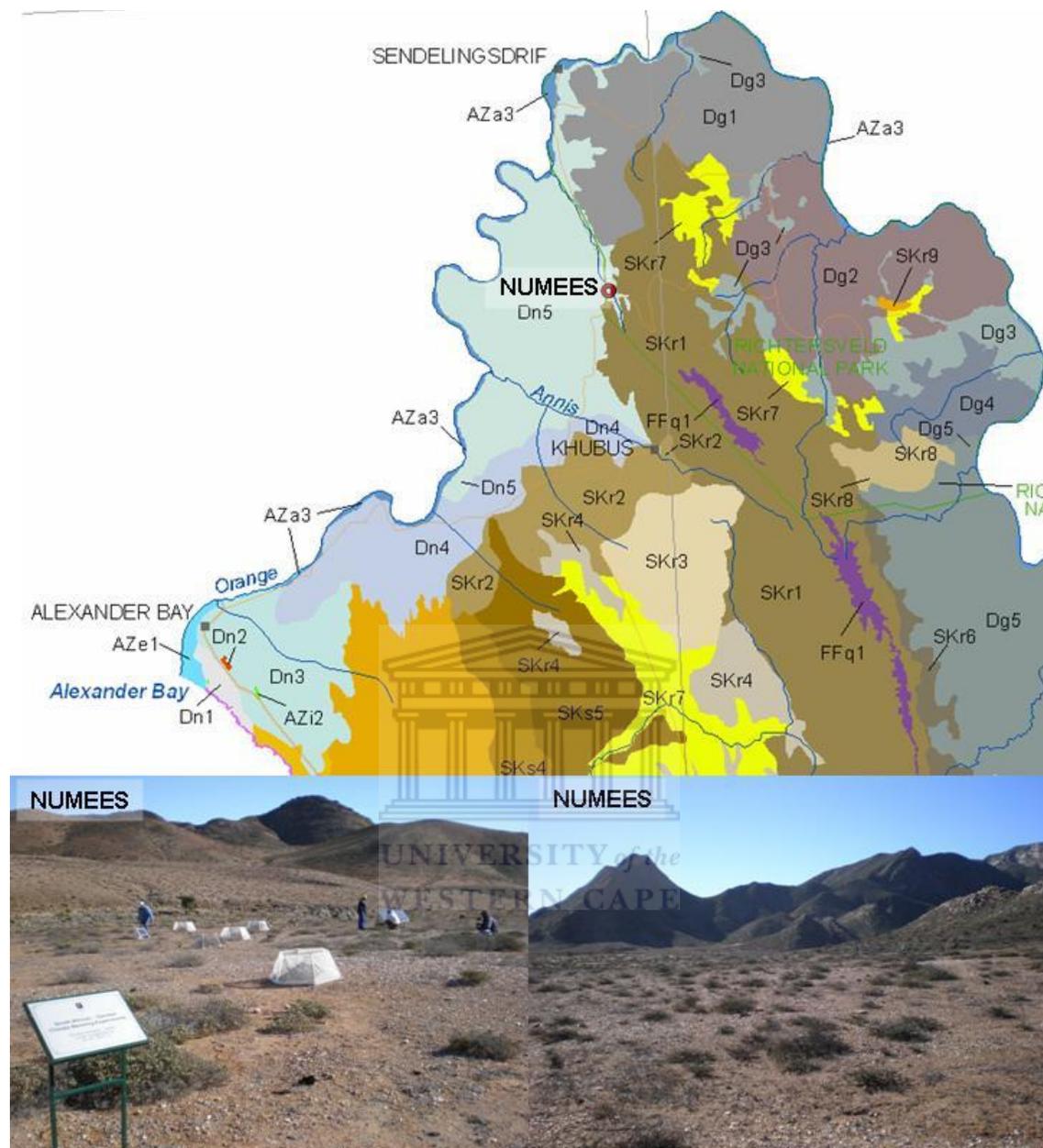


Figure 2.2. Location, typical topography and vegetation of the Numees experimental site

2.3. Study objectives, hypotheses and key questions

This study's main objective was to establish the relevance of fog and dew precipitation to succulent plant hydrology.

The hypotheses tested were as follows:

1. Dew and fog contribute significant proportions of the water requirements of succulent species;
2. Dew and fog moderate transpiration water loss especially in succulent species displaying a CAM photosynthetic mode;
3. Succulent plants with different canopy morphology intercept differential amounts of fog and dew precipitation.

The key questions examined were as follows:

1. What fractions of dew, fog and rain water are absorbed by succulent plants (Chapter 3)?
2. Do the fractions of dew, fog and rain water absorbed differ in succulent plants of different life form (Chapter 3)?
3. Do the fractions of dew, fog and rain water absorbed by succulent plants change seasonally or with prevalent climatic conditions and are these changes reflected in leaf photosynthetic efficiency and water content (Chapter 3)?
4. Do fog and dew precipitation moderate transpiration water loss in succulent plants and does this differ in plants with C₃ and CAM photosynthetic modes (Chapter 4)?
5. Do dwarf succulent plants with different canopy morphology intercept different amounts of fog and dew (Chapter 5)?

2.4. Thesis organisation

The bulk of this thesis has been written as independent manuscripts according to the guidelines of the Journal of Arid Environments. Thus a certain amount of repetition between chapters is unavoidable.

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Chapter 3

Evidence that fog and dew are essential sources of moisture for succulent shrubs in an arid South African ecosystem

Abstract

The hypothesis that fog and dew are essential sources of water for succulent shrubs in arid South African ecosystems was tested by comparing $\delta^{18}\text{O}/\delta^{16}\text{O}$ and $\delta^2\text{H}/\text{H}$ isotope ratios in samples of rain, fog and dew water with those assayed monthly in stem xylem water of six succulent shrub species over a one year period. All six species displayed negative $\delta^{18}\text{O}/\delta^{16}\text{O}$ and $\delta^2\text{H}/\text{H}$ ratios in their stem xylem water along the local meteoric water line. This signified a predominance of water derived from fog and dew precipitation which was most conspicuous during the winter rainy months. It implied that fog and dew are even more important sources of water than rain for these succulent shrubs which was substantiated by the significant correlations found between fog and dew frequencies, foliar water contents and quantum yields of photochemistry. The evergreen leaf succulents *Cephalophyllum framesii*, *Ruschia stricta*, *R. bolusiae* and *Zygophyllum cordifolium* displayed clear separation in δ -space between winter and summer $\delta^{18}\text{O}/\delta^{16}\text{O}$ and $\delta^2\text{H}/\text{H}$ ratios. This explained by an increased evaporative loss of the lighter ^{16}O and ^1H isotopes from plant-stored xylem water during the dry summer months and supported by the large fluctuations in their stem xylem water $\delta^{18}\text{O}$ ratios with changes in atmospheric vapour pressure deficit. In contrast, the two partly drought deciduous shrubs *Tripteria sinuata* and *Lyceum cinereum* exhibited indistinguishable separation in δ -space between winter and summer $\delta^{18}\text{O}/\delta^{16}\text{O}$ and $\delta^2\text{H}/\text{H}$ ratios in their xylem water. This attributed to reduced stomatal water loss of the lighter ^{16}O and ^1H isotopes caused by partial leaf defoliation in these species during the dry summer months and supported by the smaller fluctuations in their stem xylem water $\delta^{18}\text{O}$ ratios with changes in atmospheric vapour pressure deficit.

Keywords: $\delta^{18}\text{O}$, $\delta^2\text{H}$ isotopes, fog, dew, PSII function, N, P, malate accumulation

3.1. Introduction

Dew and fog have been reported to constitute a considerable portion of the hydrologic input into ecosystems in tropical montane, desert and coastal regions (Burgess & Dawson, 2004; Scholl, et al., 2008; Fischer & Still, 2007). However, the interception and utilization of fog and dew precipitation by plant canopies remains one of the least considered aspects of

vegetation studies at any scale (Schulze, 1995; Yates & Hutley, 1995; Andrade, 2003). In southern Africa, the earliest documented experiments aimed at determining dew and fog deposition volumes were conducted on Table Mountain in the south-western Cape in the early twentieth century (Marloth, 1904; 1907). Since then, several similar studies have been conducted in South Africa and Namibia primarily with the objective of examining the feasibility of harvesting dew and fog precipitation as a source of drinking water and irrigation for small-scale agricultural projects to generate income for local impoverished communities. The most noteworthy of these include Nagel (1956), Schutte (1971), Schulze (1975), Nieman, et al. (1978), and more recently Olivier (2002). All these experiments indicated a considerable potential of dew and fog as a water source. These findings supported by the substantial water yields generated in established fog water collection projects in Chile and other developing countries (Schemenauer & Cereceda, 1991; 1994).

Only a few studies have examined the role of dew and fog as an ecological factor in southern African natural ecosystems. These include an unpublished study of mist interception by natural vegetation on Table Mountain (Snow, 1985), and several other studies emanating from the Gobabeb Training & Research Centre in the Namib Desert which have investigated dew and fog exploitation by some plants and animals (see review by Henschel & Seely, 2005). The role of supplementary precipitation by fog and dew, estimated at as much as 38% of the annual hydrological input (Dawson, 1998), is considered a crucial factor in ameliorating summer water deficits in semi-arid and arid Mediterranean-climate ecosystems and preventing thermoregulation problems due to reduced transpiration (von Willert, et al., 1992; Turner & Picker, 1993; Musil, et al., 2005; 2009). This supplementary precipitation accrued on leaf surfaces drips, or is funnelled via stem-flow, onto the soil (Hutley, et al., 1997) where it can be absorbed by plant root systems or directly by leaves from their wetted surfaces (Yates & Hutley, 1995; Martin & von Willert, 2000) or from the vapour-saturated atmosphere (Breazeale, et al., 1950). However, pathways of foliar absorption of water are poorly understood. In certain *Crassula* species, epidermal hydathodes have been reported to play a role (Martin & von Willert, 2000), but in their absence a cuticular pathway is usually presumed though cuticular wetability, integrity and permeability vary considerably among species (Boyce, et al., 1991; Jagels, 1991; Schreiber, et al., 2001). Also, apart from enhancing leaf turgor (Hanba, et al., 2004), fog and dew deposit ions like NO_3^- , SO_4^{2-} , NH_4^+ and PO_4^{2-} essential for plant growth (Thalmann, et al., 2002; Takenaka, et al., 2003; Olivier, 2002) and play an important role in conserving soil water resources where semi-arid agriculture is practiced (Monteith, 1957; Duvdevani, 1964; Baier, 1966). However, quantitative data as to the importance of fog and dew precipitation for plant photosynthesis, growth and survival especially under field conditions are lacking.

Isotopic discrimination provides a means of determining the fraction of total precipitation contributed by fog and dew. Studies have demonstrated that fog and dew condensates of saturated air close to the earth's surface usually have a higher proportion of heavy oxygen and hydrogen isotopes than rain, a condensate from saturated air from higher levels in the atmosphere (Dawson, 1993; 1998; Burgess & Dawson, 2004; Ingram & Mark, 2000). Stable isotope ratios ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) of fog and dew are more enriched than those of rain (Gonfiantini & Longinelli, 1962; Ingraham & Mark, 2000), these differences are consistent and predictable (Ingraham & Mathews, 1990; Dawson, 1998). This feature allows for the discrimination of different sources of precipitation absorbed by vegetation from assays of the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ ratios in water extracted from plant stems (Ehleringer & Dawson, 1992; Dawson, 1993; Gat, 1996; Dawson & Ehleringer, 1993; 1998).

In view of these findings, the hypothesis that fog and dew are an essential source of water for succulent shrubs in arid South African Mediterranean-climate ecosystems was tested empirically.

3.2. Materials and Methods

3.2.1. Study area and site

The study site was located on the farm Quaggaskop at an elevation ± 160 m situated in the Knersvlakte ($30^{\circ}45'-31^{\circ}40'S$, $18^{\circ}15'-19^{\circ}00'E$), a semi-arid winter rainfall region within the South African Succulent Karoo Biome (Rutherford & Westfall, 1986). Listed among 34 global biodiversity hot spots (Myers, et al., 2000; Mittermeier, et al., 2004), 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 (Climate of South Africa, 1986). Large parts of the Knersvlakte, an acknowledged centre of diversity and endemism (Hilton-Taylor, 1994; 1996), are covered by quartz-gravel fields, an extra-zonal special habitat, which houses a globally unique specialized flora dominated by chamaephytes among which nano - chamaephytes represent the most important growth form group (Schmiedel & Jürgens, 1999; Schmiedel, 2001; 2002). Inter-dispersed among the quartz-gravel fields are areas devoid of quartz covered with shale, phyllite and limestone derived substrates where chamaephytes and phanerophytes of the Aizoaceae dominate.

3.2.2. Species selection

Six shrubs of different growth form dominant in areas with shale, phyllite and limestone derived substrates were selected for study. They comprised the erect evergreen leaf succulents *Ruschia bolusiae* Schwantes, *Ruschia stricta* L. Bolus var. *turgida* L. Bolus, the under-story prostrate dwarf succulents *Zygophyllum cordifolium* L.f. and *Cephalophyllum*

framesii L. Bolus, the partly drought deciduous microphyllous succulent *Lycium cinereum* Thunb and mesophyllous succulent *Tripteris sinuata* (DC) (see Appendix 3.1).

3.2.3. Plant measurements

3.2.3.1. PSII function, water and chemical contents

Measurements were conducted monthly under clear skies between 1100 and 1300 SAST (solar zenith) on fully expanded apical leaves on randomly selected plants of each species at the study site. Foliar chlorophyll contents were determined with a chlorophyll content meter (CCM200, Opti-Sciences Inc., Hudson, USA). Foliar quantum yields at a steady-state (Y_s) were determined with a modulated fluorometer (OSI-F1, Opti-Sciences Inc., Hudson, USA) following a 0.8s light pulse of 15 000 μE . Y_s is a sensitive indicator of photosystem II (PS II) efficiency and drought stress (Golding & Johnson, 2003). In healthy leaves, Y_s values have been reported consistently close to 0.8, this independent of plant species (Bolhar-Nordenkamp, 1989; Maxwell & Johnson, 2000). A diminished Y_s value indicates that a proportion of PSII reaction centers are damaged, a phenomenon often observed in plants under stress conditions (Ogaya & Penuelas, 2003; Percival, 2005; Ibaraki & Murakami, 2007).

On completion of the above measurements, batches of fresh leaf samples were randomly harvested from each species at sunrise, midday and sunset. The leaf samples were sealed in plastic bottles of predetermined mass, packed in dry ice and transported in insulated containers to the laboratory. On arrival, masses of fresh leaf samples were determined. Frozen leaf samples collected at sunrise and sunset were ground in 150 ml of de-ionized distilled water with a blender, centrifuged for 10 minutes at 186 x g at 25°C (SC-158, Scilab Instruments Co., Jhonghe City, Taiwan) and the clear supernatants titrated to pH 7.00 using 0.01 N NaOH and a phenolphthalein indicator (Woerner & Martin, 1999). The values of sunset samples were subtracted from corresponding values of sunrise samples in order to obtain foliar nocturnal malate accumulation (see Appendix 3.2).

The frozen leaf samples collected at midday were dried in a forced draft oven at 60°C, weighed on a fine electronic balance and their percentage water contents determined. Relative leaf water contents (Smart & Bingham, 1974) were not determined as leaves of some succulent species, such as *Z. cordifolium* and *R. stricta*, ruptured when they imbibed water. Sub-samples of the dry leaf tissues were weighed and analysed for percentage N and P content. N contents in the dry leaf samples were determined with an elemental analyser (FP-528, LECO Corporation, USA) at a combustion temperature of 900°C (Horneck & Miller, 1998). P was extracted from the dry leaf tissue samples with concentrated hydrochloric acid (Bray & Kurtz, 1945) and P contents determined with a Inductive Coupled Plasma Optical

Emission Spectrometer (700-ES, Varian Inc. Melbourne, Australia) at a wavelength of 213nm (Isaac & Johnson, 1998).

3.2.3.2. *Stable isotope ratios of stem xylem water*

Three separate batches of stem samples, each batch comprising approximately 10 stems of 0.5 to 1.0 cm in diameter and 6.0 to 7.0 cm in length, were collected monthly under clear skies at midday from randomly selected individuals of each species at the study site. Each batch of stem samples was sealed in a borosilicate tube (Kimax–Kimble, Vineland, NJ, and USA). Tubes were transported in an insulated container to the laboratory where these were inserted directly into a cryogenic vacuum extraction line to extract stem xylem water (February, et al., 2007). ¹⁸O/¹⁶O ratios and ²H/H ratios in the stem xylem water were measured with a mass spectrometer (Finnigan Mat 252, Bremen, Germany), the ¹⁸O/¹⁶O ratios using the CO₂ equilibrium method of Socki, et al. (1992) and the ²H/H ratios using the closed-tube zinc-reduction method of Coleman, et al. (1982) (see Appendix 3.3). Independently analyzed internal standards calibrated the measurements relative to the Vienna Mean Ocean Water Standard (V-SMOW) and corrected also for drift in the reference gas. The deviation from V-SMOW is denoted by δ and expressed as parts per thousand (‰) by the function:

$$\delta = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 10^3 \dots\dots\dots(1)$$

where: R = the ratio of ¹⁸O/¹⁶O or ²H/H

The error in measurement of δ was c. 2‰ for δ²H and c. 0.2‰ for ¹⁸O.

3.2.4. *Environmental measurements*

3.2.4.1. *Rain, dew and fog precipitation*

Daily rainfall precipitation amounts over the 12-month monitoring period were obtained from two meteorological stations (Moedveloeren and Luiperskop) located in close proximity (c. 10 km distant) to the study site. Rain and combined fog and dew precipitation measurements were both expressed as frequencies (numbers of rain, fog and dew incidences) as leaf wetness sensors only provided instantaneous but not cumulative amounts of precipitation contributed by fog and dew.

Atmospheric air temperatures, relative humidities and combined amounts of fog and dew were monitored hourly with thermocouples, relative humidity and leaf wetness resistance sensors respectively positioned 0.1 m above the soil surface which were interfaced with miniature data loggers installed in radiation shields (Watch Dog 450,

Spectrum Technologies Inc., Plainfield, Illinois, USA). Vapour pressure deficits were computed from air temperature and relative humidity measurements using the following functions (Snyder & Paw, 2006):

$$e = 0.6108 \exp (17.27T/T+265.5) \dots\dots\dots(2)$$

$$e_s = 100e/RH \dots\dots\dots(3)$$

$$VPD = e_s - e \dots\dots\dots(4)$$

where e is vapour pressure (kPa), T is air temperature ($^{\circ}\text{C}$), e_s is saturation vapour pressure (kPa), RH is relative humidity (%) and VPD is vapour pressure deficit (kPa).

3.2.4.2. Stable isotope ratios of rain, dew and fog water

One meter square sheets of plexiglass mounted at a 45° angles with gutters installed at the lower ends were used to collect samples of water from rain, fog and dew. As fog and dew precipitation occur predominantly under conditions of high humidity and low temperatures at night time, collections of rainwater were restricted to sporadic day time rain events and fog and dew collections to overnight collections. The different water samples were collected directly after a specific rain or fog incidence and immediately sealed in borosilicate tubes (Kimax–Kimble, Vineland, NJ, and USA). $^{18}\text{O}/^{16}\text{O}$ and $^2\text{H}/\text{H}$ were determined on the samples as previously described.

Atmospheric precipitation follows a Rayleigh distillation process resulting in a linear relationship between $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of meteoric water samples (Craig 1961). This relationship is called the Global Meteoric Water Line and can be described by the equation $\delta^2\text{H} = 8 \delta^{18}\text{O} + 10$ (Craig 1961). For plant water-source studies, in arid environments with shallow soils such as at our study site, these relationships are exceptionally useful as rain (evaporatively enriched), fog and dew (non-evaporative enriched) moisture sources can be readily distinguished. Evaporatively enriched waters, such as surface waters or shallow soil moisture, plot below the Global Meteoric Water Line in δ -space. Using the $^{18}\text{O}/^{16}\text{O}$ and $^2\text{H}/\text{H}$ values of rain, dew and fog water obtained a local meteoric water line was developed for the study site.

3.2.5. Statistical analyses

Pearson correlations tested for significant correspondence between measured plant and environmental variables.

3.3. Results

A least squares regression of $\delta^{18}\text{O}$ ratios plotted against $\delta^2\text{H}$ ratios for water obtained from rain, fog and dew produced a local meteoric water line described by the equation $y = 12.6x + 9.5$ which had a r^2 of 0.764, significant at $P \leq 0.01$. $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ratios in rain water had predominantly positive values and those in fog and dew water mostly negative values about the local meteoric water line.

In compliance with the consistently higher incidences of fog and dew than rain at the study site (Figure 3.1), all six study species displayed negative $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ratios in their stem xylem water about the local meteoric water line, this most conspicuous during the rainy winter season (Figures 3.2 A to F). The evergreen leaf succulents *C. framesii*, *R. stricta*, *R. bolusiae* and *Z. cordifolium* displayed clear separation in δ -space between winter and summer $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ratios of their xylem water (Figures 3.2 A to D) with $\delta^{18}\text{O}$ ratios in their stem xylem water exhibiting large fluctuations with changes in atmospheric vapour pressure deficit (Figure 3.3). In contrast, the two partly drought deciduous shrubs *T. sinuata* and *L. cinereum* exhibited indistinguishable separation in δ -space between winter and summer $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ratios in their stem xylem water (Figures 3.2 E & F) with $\delta^{18}\text{O}$ ratios in their stem xylem water displaying only small fluctuations with changes in atmospheric vapour pressure deficit (Figure 3.3).

$\delta^{18}\text{O}$ ratios in stem xylem water were significantly ($P \leq 0.01$) negatively correlated with fog and dew frequencies in all 6 study species, but $\delta^2\text{H}$ ratios in stem xylem water were only significantly ($P \leq 0.05$) negatively correlated with fog and dew frequencies in 3 of the 6 study species, namely *C. framesii*, *R. stricta* and *R. bolusiae* (Table 3.1). Gravimetric soil moisture (Figure 3.1B) was significantly ($P \leq 0.05$) positively correlated with fog and dew. Fog and dew frequencies in turn were significantly ($P \leq 0.05$) positively correlated with leaf water contents in all 6 study species as well as with steady state fluorescence yields but only in 4 of the 6 study species, namely *C. framesii*, *R. stricta*, *R. bolusiae* and *T. sinuata* (Table 3.1). With respect to other measured physiological parameters, significant ($P \leq 0.05$) positive correlations were only observed between fog and dew frequencies and *T. sinuata*'s foliar chlorophyll content and *L. cinereum*'s and *R. bolusiae*'s foliar P contents (Table 3.1).

3.4. Discussion

The regression of $\delta^2\text{H}$ against $\delta^{18}\text{O}$ ratios measured in samples of rain, fog and dew water fitted a linear distribution ($y = 12.6x + 9.5$) which compared favourably with the expected global meteoric water line ($y = 8x + 10$) presented by Craig (1961). This confirmed that the different precipitation sources were distinguishable by their stable hydrogen ($\delta^2\text{H}$) and oxygen ($\delta^{18}\text{O}$) isotope ratios (Gonfiantini & Longinelli, 1962; Ingraham & Matthews, 1990; Dawson, 1998).

The negative $\delta^{18}\text{O}$ and $\delta^2\text{H}$ ratios measured in stem xylem water about the local meteoric water line in all six study species signified a predominance of water derived from fog and dew precipitation which was most conspicuous during the winter rainy months. It implied that fog and dew are even more important sources of water than rain for these succulent shrubs which was substantiated by the significant correlations found between fog and dew frequencies, foliar water contents and quantum yields of photochemistry.

The observed seasonal changes in $\delta^{18}\text{O}$ ratios of stem xylem water at the study site 64km distant from the coast were similar to seasonal variations in $^{18}\text{O}/^{16}\text{O}$ isotope ratios measured in stem xylem water of *Pinus muricata* at Point Reyes Peninsula in California (Ingraham & Mathews, 1995). The distinctly higher fractions of positive $\delta^{18}\text{O}$ ratios measured in stem xylem water of the evergreen leaf succulents *C. framesii*, *R. stricta*, *R. bolusiae* and *Z. cordifolium* during the dry summer pointed to a progressive enrichment of their xylem water with the heavier ^{18}O isotope. In summer when soil moisture is limiting, these typical crassulacean acid metabolism (CAM) species open their stomata at night to conserve water (Luttge, 2002) resulting in a preferential loss of the lighter oxygen (^{16}O) isotope and a consequent more positive $\delta^{18}\text{O}$ signature (Helliker & Griffiths, 2007; Farquhar, et al., 2007). This proposal supported by the large fluctuations in $\delta^{18}\text{O}$ ratios measured in stem xylem water of these species with changes in atmospheric vapour pressure deficit. These results concur with similar findings in coastal prairie grasses at Bodega Marine Reserve in California (Corbin, et al., 2005) and more recently with observations on epiphytic bromeliads in a seasonally dry tropical forest of Mexico (Reyes-Garcia, et al., 2008). In contrast, the two partly drought deciduous typical C_3 species *T. sinuata* and *L. cinereum* showed indistinguishable fractions of positive $\delta^{18}\text{O}$ ratios in their stem xylem water between winter and summer. This attributed to a reduced loss of the lighter ^{16}O isotope during transpiration caused by partial defoliation of these plants in the drier summer season and supported by the small fluctuations in $\delta^{18}\text{O}$ ratios of the stem xylem water with changes in atmospheric vapour pressure deficit.

Both measured $\delta^{18}\text{O}$ ratios in stem xylem water and changes in foliar water content and steady state fluorescence yield corresponded with seasonal changes in fog and dew frequency which in turn was also significantly linearly correlated with soil gravimetric moisture content. This indicated that both leaf hydration and photosynthetic efficiency were linked to fog and dew sources of precipitation and associated soil moisture content. In fact, periods of reduced fog frequency corresponded with diminished steady-state fluorescence yields in all except two drought resilient species, namely the microphyllous, deep rooted shrub *L. cinereum* and the prostrate dwarf understory shrub *Z. cordifolium*.

Water stress may lead to decreased foliar chlorophyll and carotenoid contents as reported in maize (Sanchez, et al., 1982) and *Picea abies* seedlings (Pawe, et al., 2005) and

often results in increased malate accumulation in water stressed CAM plants (Peckmann & Herppich, 1998). However, in this study foliar chlorophyll contents were significantly correlated with fog and dew frequency in only one species, namely *T. sinuata* which is known to experience leaf senescence and defoliation when drought stressed (Wand, et al., 2001). However, no significant correlations between nocturnal malate accumulation and fog frequency were observed in any of the study species. Also, fog and dew have been reported to deposit essential ions such NO_3^- , NH_4^+ and PO_4 (Takenaka, et al., 2003; Thalmann, et al., 2002; Olivier, 2002), but significant correlations between fog and dew frequency and leaf chemical content were restricted to foliar P levels in 2 species only, namely *L. cinereum* and *R. bolusiae*, both containing extensive fibrous rooting systems which ramify in the upper soil layers.

In conclusion, these findings support the hypothesis that fog and dew are an essential source of water for succulent shrubs in this arid South African ecosystem. They also imply that diminished fog and dew frequencies associated with elevated night time temperatures accompanying global warming could exacerbate plant drought stress. However, finer-scale studies are required to elucidate the reliance of succulent shrubs with different photosynthetic mechanisms on fog and dew precipitation for ameliorating drought stress.

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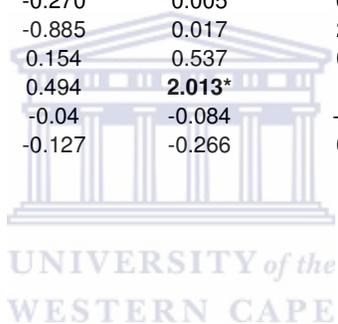
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Table 3.1. Correspondence (Pearson correlation coefficients r , and t-statistics) between fog and dew frequencies and various physiological parameters measured in 6 succulent shrub species. Values in bold denote significant correspondence at * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Parameter		Species					
		<i>C. framesii</i>	<i>R. stricta</i>	<i>R. bolusiae</i>	<i>Z. cordifolium</i>	<i>L. cinereum</i>	<i>T. sinuata</i>
$\delta^{18}\text{O}$	r	-0.802	-0.647	-0.775	-0.525	-0.664	-0.842
	$t_{1,10}$	-4.241***	-2.686**	-3.877***	-1.950*	-2.810**	-4.929***
$\delta^2\text{H}$	r	-0.812	-0.538	-0.681	-0.158	-0.360	-0.123
	$t_{1,10}$	-4.397***	-2.018*	-2.941**	0.505	-1.220	-0.391
Ys	r	0.753	0.758	0.703	0.326	0.265	0.542
	$t_{1,10}$	3.617**	3.669**	3.127**	1.090	0.868	2.037*
Leaf chlorophyll	r	0.023	0.448	0.023	0.246	0.047	0.596
	$t_{1,10}$	0.066	1.416	0.064	0.719	0.132	2.101*
Leaf water	r	0.808	0.647	0.636	0.890	0.748	0.723
	$t_{1,10}$	4.343***	2.683**	2.604*	6.164***	3.565**	3.310**
Leaf N	r	0.149	-0.270	0.005	0.358	0.403	0.431
	$t_{1,10}$	0.478	-0.885	0.017	2.111	1.391	-0.189
Leaf P	r	0.071	0.154	0.537	0.342	0.560	0.457
	$t_{1,10}$	-0.226	0.494	2.013*	1.091	-0.021*	1.624
Malate	r	0.336	-0.04	-0.084	-0.160	-0.01	0.187
	$t_{1,10}$	1.244	-0.127	-0.266	0.514	-0.03	0.603



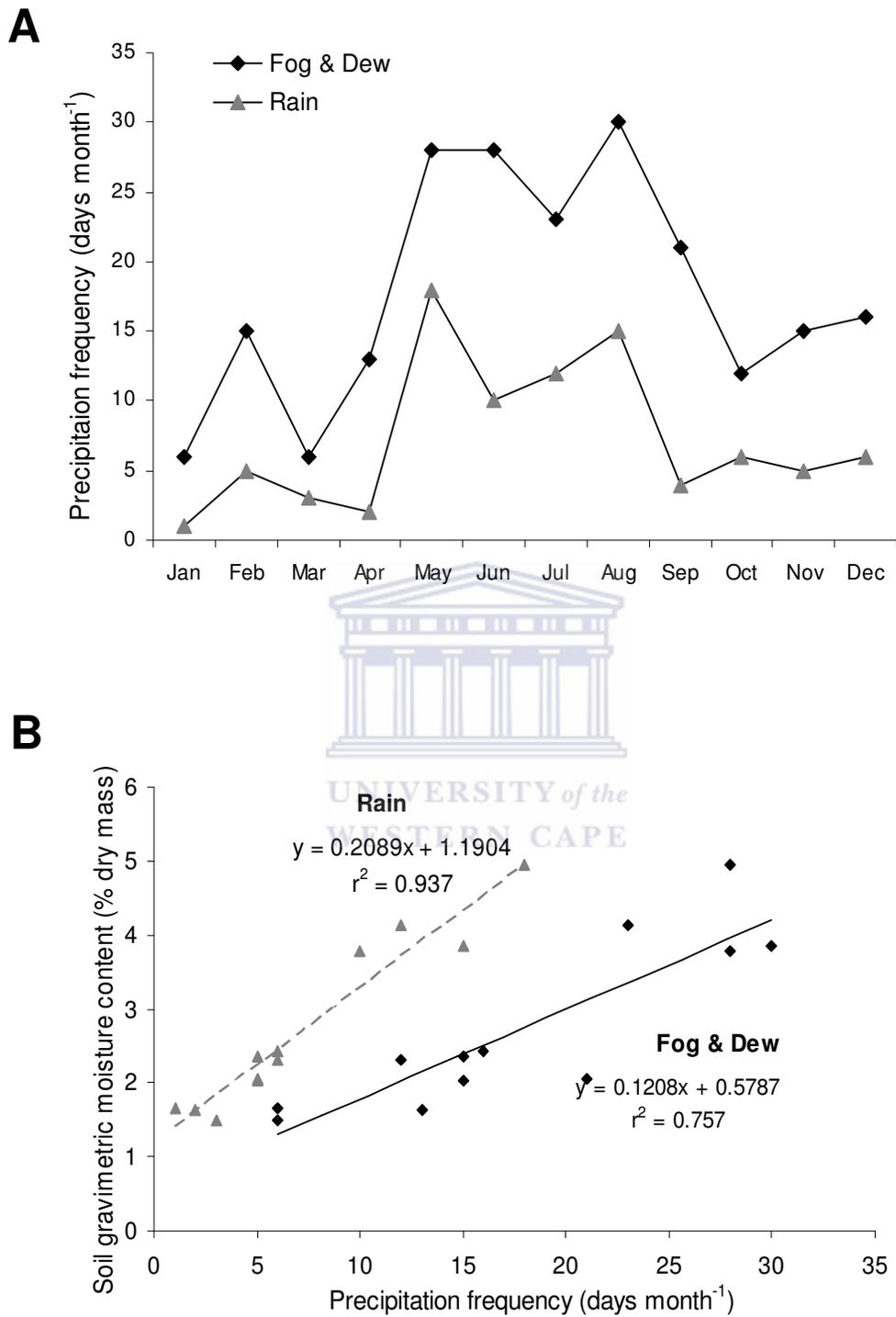


Figure 3.1. Monthly fog and dew and rain frequencies (A) and their correspondence with soil gravimetric moisture contents (B).

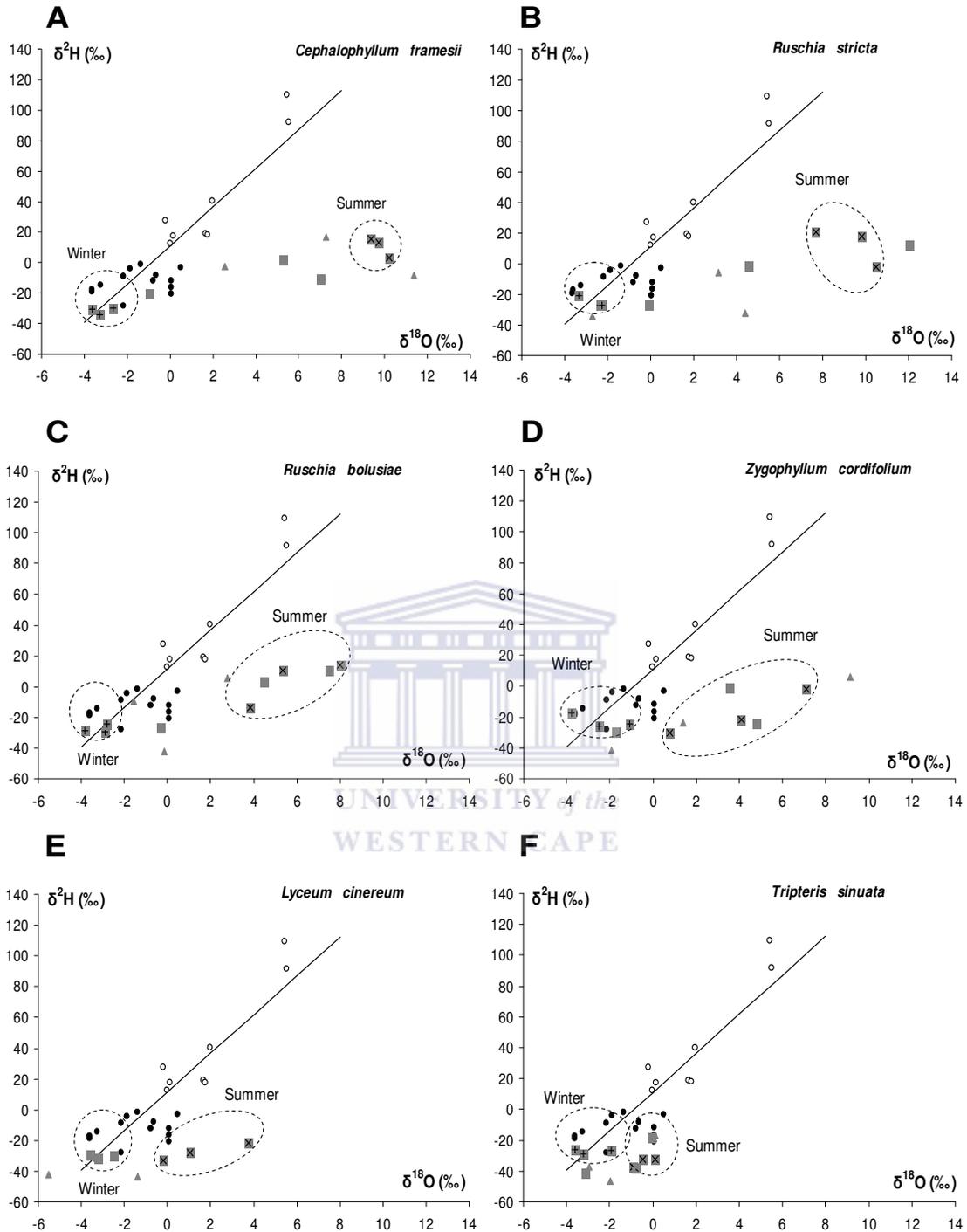


Figure 3.2. Comparison of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ isotope ratios in rain (○), fog and dew (●) water samples about the local meteoric water line ($y = 12.6x + 9.5$) with $\delta^2\text{H}$ and $\delta^{18}\text{O}$ ratios in stem xylem water of (A) *C. framesii*, (B) *R. stricta*, (C) *R. bolusiae*, (D) *Z. cordifolium*, (E) *L. cinereum* and (F) *T. sinuata* measured during winter(+), spring(■), autumn(▲) and summer(x).

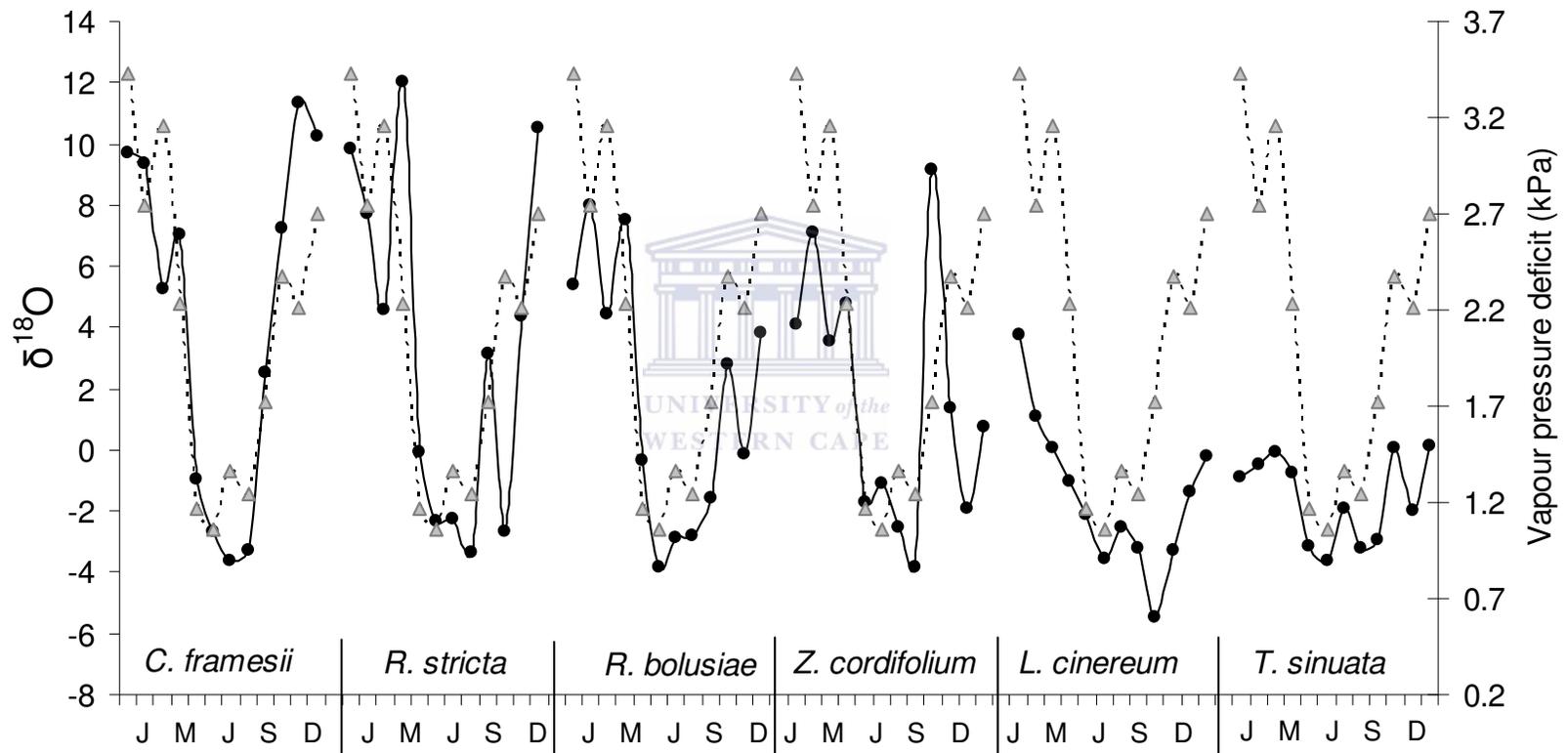


Figure 3.3. Correspondence of $\delta^{18}\text{O}$ isotope ratios in stem xylem water of 6 succulent shrubs (●) with atmospheric vapour pressure deficits (▲).

Chapter 4

Differential effects of fog and dew on the hydrology of succulents displaying CAM and C₃ photosynthetic modes in an arid South African ecosystem

Abstract

Variations in stem diameter were recorded at 2-hourly intervals in 8 succulent shrub species of diverse growth form over a 9-month period extending from early winter (June) through to mid summer (February) in an arid South African ecosystem. Two groups of species were distinguished based on whether their daily amplitudes in stem diameter were consistently positively correlated with daily fluxes in vapour pressure deficit, which were indicative of a persistent CAM photosynthetic mode, or intermittently correlated with daily fluxes in vapour pressure deficit, which were indicative of mixed CAM and C₃ photosynthetic modes. Plants in the CAM photosynthetic mode attained the smallest stem diameters during night time just prior to sunrise whereas those in the C₃ photosynthetic mode attained the smallest stem diameters during daytime around the solar noon. Instantaneous responses to sporadic rain and collective fog and dew events, evident from atypical peaks in diurnal stem diameter patterns, were evident among species displaying both persistent CAM and mixed CAM and C₃ photosynthetic modes. Also, transient switches in diurnal stem diameter patterns from a CAM photosynthetic mode to a C₃ photosynthetic mode in response to sporadic precipitation events were occasionally observed among species displaying a CAM photosynthetic mode. However, more frequently among species displaying a persistent CAM photosynthetic mode, high nocturnal fog and dew precipitation amounts corresponded with low daily amplitudes in stem diameter and vice versa which pointed to reduced nocturnal stomatal water loss. These patterns, which were indistinct among species displaying mixed CAM and C₃ photosynthetic modes, were corroborated by smaller daily amplitudes in stem diameter consistently observed in one species displaying a CAM photosynthetic mode in ambient than artificially fog and dew excluded environments.

Keywords

CAM and C₃ photosynthetic mode, fog and dew precipitation, stem diameter variation sensor, succulent plant, vapour pressure deficit

4.1. Introduction

Dew and fog precipitation are considered crucial in ameliorating plant water deficits in semi-arid and arid Mediterranean-climate ecosystems by reducing transpiration water loss and preventing thermoregulation problems (von Willert, et al., 1992; Turner & Picker, 1993; Musil, et al., 2005). However, the interception and utilization of fog and dew by plant canopies remains one of the least considered aspects of vegetation studies at any scale (Schulze, 1995; Yates & Hutley, 1995; Andrade, 2003).

Various direct and indirect techniques have been applied in quantifying fog and dew precipitation amounts and vegetation responses to these which present numerous measurement challenges (Ninari & Berliner, 2002). These include sap-flow sensors in *Sequoia sempervirens* (Burgess & Dawson, 2004), leaf thickness sensors in *Crassula spp* (Martin & von Willert, 2000) and stable water isotopes in *Sequoia sempervirens* and prairie grasses (Dawson, 1998; Corbin, et al., 2005). Assays of stable $\delta^{18}\text{O}$ and $\delta^2\text{H}$ isotope ratios in stem xylem water provide an effective means of detecting the relative contribution of fog and dew to plant hydrology. Such assays have shown that fog and dew are essential sources of water, even more important than rain, for succulent shrubs in arid South African ecosystems and corroborated by significant correspondence found between fog and dew frequencies, plant foliar water contents and quantum yields of photochemistry (Chapter 3). However, such assays are unsuitable in detecting instantaneous plant responses to fog and dew events and inapplicable in plants lacking non-photosynthetic above-ground parts due to isotopic fractionation of water in photosynthetic tissues (White, et al., 1985; Thorburn & Walker, 1993; February, et al., 2007).

Stem diameters fluctuate diurnally due to changes in stem water content (Kramer & Kozlowski, 1979), the amplitude of variation depending on the rate of transpiration and the elasticity of the shrinking and swelling stem tissue (Peramaki, et al., 2001). Several studies have demonstrated correspondence between diurnal stem diameter changes and shoot water potential, transpiration, relative humidity and other micro-meteorological measurements (Kozlowski & Winget, 1964; Klepper, et al., 1971; Zaerr, 1971; Kozlowski, 1972; Lassoie, 1973; Kramer & Kozlowski, 1979; Hellkvist, et al., 1980; Milne, et al., 1983; Wronski, et al., 1985; Herzog, et al., 1995; Offenthaler, et al., 2001). Therefore, sensors that accurately measure variations in stem diameter provide a means of quantifying plant responses to water supply (Ton, 1997; Ton, et al., 2001; Kopyt, et al., 2001; Ton & Kopyt, 2003) and have been successfully applied in horticultural irrigation systems linking the water status of plants to microclimatic conditions (Lee & Shin, 1998; Ton & Kopyt, 2003). They also provide a potential means of discriminating between C_3 and CAM plant photosynthetic types which display contrasting chronological opening of stomata (Black, 1973; Edwards & Walker,

1983; Luttge, 2004) that should essentially be reflected in opposing diurnal variations in stem diameter (Lee & Shin, 1998; Ton & Kopyt; 2003; McLaughlin, et al., 2003).

In view of this, this study examined whether stem variation sensors could discriminate between succulents displaying CAM and C₃ photosynthetic modes and quantify fog and dew effects on their hydrology.

4.2. Materials and methods

4.2.1. Study sites and species

There were two study sites, namely Quaggaskop and Numees located at the southern and northern extremities of the succulent karoo biome, a semi-arid winter rainfall region within South Africa (Rutherford & Westfall, 1986) ranked among 34 global biodiversity hot spots (Myers, et al., 2000; Mittermeier, et al., 2004). Quaggaskop (31° 24.6" S / 18° 37.8" E) is situated in the southern Knersvlakte bioregion at an elevation ±160 m and has a mean annual precipitation of 145 mm and mean daily maximum air temperature of 25.7°C determined at a nearby Vredendal weather station between 1957 and 1984 (Climate of South Africa, 1986). Numees (28° 18' 07.6" S / 16° 57' 50.4" E) is located in the northern Richtersveld bioregion 12 km south-east of the Orange River at an altitude of 377 m. The predominantly winter rainfall of 70 mm annum⁻¹ is supplemented by coastal fog during the summer months (Jürgens, et al., 1999).

Seven succulent species of different life form were examined. Those occurring on shale, phyllite and limestone derived substrates at Quaggaskop included the erect evergreen leaf succulent shrubs *Ruschia bolusiae* Schwantes and *Ruschia stricta* L. Bolus var. *turgida* L. Bolus, the under-story prostrate dwarf succulents *Zygophyllum cordifolium* L.f. and *Cephalophyllum framesii* L. Bolus, the partly drought deciduous microphyllous succulent shrub *Lycium cinereum* Thunb and the mesophyllous succulent shrub *Tripteris sinuata* (DC). Those occurring on quartz-gravel covered substrates at Quaggaskop included the specialized dwarf succulents *Monilaria pisiformis* Schwantes, *Agyroderma pearsonii* N.E.Br. Schwantes and *Cephalophyllum spissum* H.E.K. Hartmann. At Numees, the common erect evergreen leaf succulent shrub *Ruschia senaria* L. Bolus was examined.

4.2.2. Stem diameter measurement

Stem diameter variation sensors with a resolution of 5 µm interfaced with loggers (LS-SD-56 Phyttech Ltd., Israel) were used to measure changes in stem diameter in responses to precipitation events. These were installed on 10 mm to 15mm diameter woody stems on all 7 succulent shrub species and one dwarf succulent (*M. pisiformis*) and set to record at 2-hourly intervals. At the Richtersveld site, the stem diameter sensors were also installed on *R. senaria* plants enclosed in hexagonal, steel framed open top chambers (1.2m in diameter x

0.5 m high) which were clad with white 60% light transmitting (1 mm x 3 mm mesh) shade cloth that partly excluded fog and dew. Daily amplitudes (fluxes) in stem diameter were calculated as the differences between the recorded daily maximum and minimum values over each 24-h period (see Appendix 4.2).

4.2.3. Environmental measurements

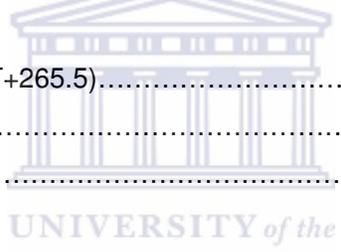
Hourly records of atmospheric air temperature, relative humidity, rain and apparent fog and dew precipitation amounts were obtained with thermocouples, relative humidity, leaf wetness resistance and tipping gauge sensors interfaced with miniature data loggers enclosed in ventilated radiation shields (Watch Dog 450, Spectrum Technologies Inc., Plainfield, Illinois, USA; see Appendix 4.1). Measured leaf wetness resistances (range: 0 to 15 units) were converted to apparent fog and dew precipitation amounts in mm using a published formula (Musil, et al., 2009).

Atmospheric vapour pressure deficits were computed from air temperature and relative humidity measurements applying the following functions (Snyder & Paw, 2006):

$$e = 0.6108 \exp (17.27T/T+265.5) \dots\dots\dots(3)$$

$$e_s = 100e/RH \dots\dots\dots(4)$$

$$VPD = e_s - e \dots\dots\dots(5)$$



where e is vapour pressure (kPa), T is air temperature ($^{\circ}\text{C}$), e_s is saturation vapor pressure (kPa), RH is relative humidity (%) and VPD is vapour pressure deficit (kPa).

Daily amplitudes in atmospheric vapour pressure deficit and apparent fog and dew precipitation amounts were calculated as the differences between the recorded daily maximum and minimum values over each 24-hr period

4.2.4. Statistical analyses

Pearson correlations tested for significant correspondence between daily stem diameter amplitudes and corresponding daily vapour pressure deficits and apparent fog and dew amplitudes. An analysis of variance (General Linear Model) tested for significant differences in the magnitude of stem diameter amplitudes in plants grown in ambient and artificially fog and dew excluded environments

4.3. Results

Two response groups of species were distinguished based on whether their daily amplitudes in stem diameter were consistently or intermittently positively correlated with daily amplitudes in vapour pressure deficit. The five species *M. pisiformis*, *R. stricta*, *R. bolusiae*,

R. senaria and *C. framesii*, displayed significantly ($P \leq 0.05$) positive correlations between their daily amplitudes in stem diameter and vapour pressure deficit during both the wet winter (June – August) and drier spring (September – November) and summer (December – February) months (Table 4.1, Figure 4.1 B1-B3), these indicative of a persistent CAM photosynthetic mode. The other three species *T. sinuata*, *L. cinereum* and *Z. cordifolium* displayed significant ($P \leq 0.05$) positive correlations between their daily amplitudes in stem diameter and vapour pressure deficit during the drier spring and summer months (Table 4.1, Figure 4.1 A2 & A3) but negative ($P \leq 0.05$) correlations during the wet winter months, these indicative of mixed CAM and C_3 photosynthetic modes.

Plants in the CAM photosynthetic mode attained the smallest stem diameters during night time just prior to sunrise (Figure 4.2A) whereas those in the C_3 photosynthetic mode attained the smallest stem diameters during daytime around the solar noon (Figure 4.2B). Instantaneous responses to sporadic rain and collective fog and dew events, evident from atypical peaks in diurnal stem diameter patterns, were evident among species displaying both persistent CAM and mixed CAM and C_3 photosynthetic modes (Figure 4.2C). Also, transient switches in diurnal stem diameter patterns from a CAM photosynthetic mode to C_3 photosynthetic mode in response to sporadic precipitation events were occasionally observed among species displaying a persistent CAM photosynthetic mode (Figure 4.2C). However, more frequently among species displaying a persistent CAM photosynthetic mode, high nocturnal fog and dew precipitation amounts corresponded with small daily amplitudes in stem diameter and vice versa, which pointed to reduced nocturnal stomatal water loss. These patterns, which were indistinct among species displaying mixed CAM and C_3 photosynthetic modes (Table 4.1: Figure 4.3), were corroborated by small daily amplitudes in stem diameter also consistently observed in one species displaying a CAM photosynthetic mode in ambient than artificially fog and dew excluded environments (Figure 4.4).

4.4. Discussion

This study is amongst the foremost in applying stem diameter sensors in succulent shrubs to monitor their instantaneous responses to sporadic precipitation events. The study results concur with similar observations on plum trees and grapevines (Intrigliolo & Castel, 2005; 2007), citrus trees (Velez, et al., 2007) and young almond trees (Nortes, et al., 2005). In addition, the results managed to discriminate between CAM and C_3 photosynthetic modes and transient switches between these modes.

Frequent measurements of stem diameters at high resolutions of 1 to 10 μ m are known to display variations that result from the action of several components. These include irreversible radial stem growth, reversible stem shrinking and swelling in relation to changing levels of hydration and thermal expansion (Kozlowski, 1971; Klepper, et al., 1971; McBurney

& Costigan, 1984; Améglio & Cruziat, 1992; Simonneau, et al., 1993; Zweifel, et al., 2000; Cochard, et al., 2001; Daudet, et al., 2005) and contraction and swelling of lifeless conducting elements due to the increase and relaxation of internal tensions (Irvine & Grace, 1997; Offenthaler, et al., 2001; Sevanto, et al., 2002). Clearly, whole stem diameter measurements do not provide precise information about water flow in the xylem because stem diameter changes are also effected by the shrinkage and swelling of phloem and bark cells (Sevanto, et al., 2002). As a consequence, fluctuations in trunk xylem diameters have been monitored in several tree species, such as *Pinus sylvestris* (Irvine & Grace, 1997; Sevanto, et al., 2003), *Acer rubrum*, *Alnus glutinosa*, *Betula lenta*, *Fagus sylvatica*, *Quercus rubra* and *Tilia vulgaris* (Sevanto, et al., 2008), as a more direct means of monitoring plant water dynamics. However, such measurements are also problematic since trunks require girdling that may result in xylem embolism and disruption of sugar transport due to phloem removal (Sevanto, et al., 2003), and the direct linkage of xylem diameter variations to actual sap flow and water tension requires knowledge of the radial elasticity of sap wood.

Despite all the components known to affect stem diameter amplitudes, the reversible stem shrinking and swelling observed in this study closely corresponded with changing levels of plant hydration from precipitation events. Positive correlations between night-time transpiration, VPD and air temperature have been reported for *Pinus ponderosa*, *Arctostaphylos manzanita*, *Ceanothus cordulatus* and *Quercus douglasii* in the Central Valley of California (Dawson, et al., 2007). Similarly, in this study the greatest stem shrinkages in species displaying a CAM photosynthetic mode were expected during night time (Black, 1973; Edwards & Walker, 1983; Luttge, 2004) but these were observed just prior to sunrise which pointed to an ostensible time lag between the smallest observed stem diameter and the expected maximum stomatal water loss at much earlier hours during the night. Such time-lags between transpiration and stem diameter extremes have been attributed to changes in stem and leaf water potentials (Hellkvist, et al., 1980; Sevanto, et al., 2003) and the dynamics of sap ascent regulated by active sugar transport (Sevanto, et al., 2002; 2003).

The negative correlations observed between daily amplitudes in stem diameter and vapour pressure deficit that characterized succulents in the C₃ photosynthetic mode have similarly been reported in the C₃ tree species *Liriodendron tulipifera* (McLaughlin, et al., 2003), and corroborate reports that xylem diameter variations closely follow diurnal transpiration patterns (Perämäki, et al., 2001). However, such patterns could potentially be distorted by patchy night-time transpiration which has recently been reported in some C₃ and C₄ species (Snyder, et al., 2003; Daley & Phillips, 2006; Caird, et al., 2007; Dawson, et al., 2007; Fisher, et al., 2007) though the effects would presumably be minor due to the absence of photosynthetically active radiation and other environmental driving forces during night time effecting transpiration water loss.

The observed transient switches in diurnal stem diameter patterns from CAM to C₃ photosynthetic modes have been reported in several other species (Ting, 1985; Monson & Moore, 1989; Raghavendra & Das, 1993; Ehleringer & Monson, 1993; Kraybill & Martin, 1996; Lüttge, 2002; 2004) based on chemical assay techniques. Examples include, the switch from C₃ to CAM photosynthesis in *Clusia minor* evoked during periods of high drought stress (De Mattos & Lüttge, 2001), the transition from C₃ to CAM photosynthesis in *Mesembryanthemum crystallinum* evoked by increased salinity and high irradiance (Hurst, et al., 2004), and the shift from C₃ to CAM photosynthesis in *Ananas comosus* and *Marrubium frivaldszkyanum* with increasing leaf age (Markovska & Dimitrov, 2001; Popp, et al., 2003).

Mitigation of drought effects by fog and dew has been reported at a coastal site in California (Corbin, et al., 2005). Likewise, the reduced stem diameter amplitudes observed during night-time incursion of fog and dew among species displaying a CAM photosynthetic mode, and the elevated stem diameter amplitudes noted where fog and dew were artificially excluded from plants, also pointed to the importance of fog and dew in limiting nocturnal plant water loss in such species. Both findings support the hypothesis that fog and dew assist plants in conserving water by eliminating the atmospheric vapour pressure deficit that drives evaporation and transpiration from plant surfaces (Burgess & Dawson, 2004).

4.5. Acknowledgements

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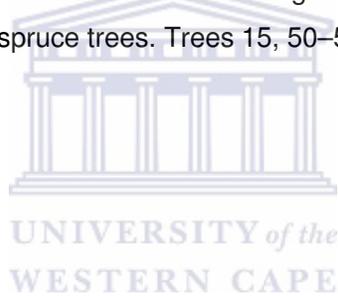


Table 4.1. t-statistics for statistical correspondence (Pearson correlations) between measured daily amplitudes in stem diameter of 8 succulent species and daily amplitudes in atmospheric vapour pressure deficit (VPD) and apparent fog & dew precipitation (AFD). Values in bold significant at *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001 for designated degrees of freedom (DF).

Month	Rainfall (mm)	Parameter	Persistent CAM photosynthetic mode					Mixed CAM & C ₃ photosynthetic modes		
			<i>M. pisiformis</i>	<i>R. stricta</i>	<i>R. bolusiae</i>	<i>C. framesii</i>	<i>R. senaria</i>	<i>T. sinuata</i>	<i>L. cinereum</i>	<i>Z. cordifolium</i>
Jun	32.8	DF	28	-	28	28	-	28	28	28
		VPD	4.414***	-	4.338***	2.072*	-	-2.637**	-1.514	-3.532***
		AFD	-1.735*	-	-1.996*	-0.356	-	3.408**	3.001**	2.280*
Jul	90.4	DF	29	29	29	29	-	29	29	29
		VPD	6.926***	2.247*	5.612***	0.954	-	0.267	-4.469***	-2.818**
		AFD	-2.617**	-1.261	-1.683	-0.324	-	1.546	2.808**	2.549**
Aug	29.6	DF	17	17	17	17	29	17	17	17
		VPD	7.287***	4.053***	8.613***	4.671***	2.622**	0.106	-5.364***	-0.073
		AFD	-4.174***	-2.594**	-3.934***	-4.284***	-3.623***	1.647	2.934**	0.315
Sep	16.6	DF	28	28	28	28	-	28	28	28
		VPD	4.438***	9.298***	7.135***	5.766***	-	0.999	0.164	-1.492
		AFD	-0.436	-1.401	-1.233	-1.127	-	2.851**	1.154	1.542
Oct	3.2	DF	29	29	29	29	29	29	29	29
		VPD	5.462***	8.061***	5.235***	8.908***	5.719***	2.818**	1.564	-2.951**
		AFD	-3.319**	-3.719***	-3.245**	-3.905***	-0.431	-1.069	-1.042	4.324***
Nov	1.5	DF	28	28	28	28	28	28	28	28
		VPD	3.179**	9.110***	5.116**	4.350***	3.282**	3.472***	7.130***	2.283*
		AFD	-1.973*	-2.752**	-0.721	-1.132	-0.720	-1.595	-3.109**	-1.592
Dec	0.8	DF	23	23	23	23	28	23	23	23
		VPD	6.009***	3.908***	4.913***	9.064***	5.190***	5.190***	7.028***	0.655
		AFD	0.124	-1.255	-0.121	-0.952	1.090	0.047	-1.706	1.909*
Jan	0.0	DF	25	25	25	25	27	25	25	25
		VPD	4.855***	7.780***	10.068***	7.637***	6.041***	6.052***	5.915***	6.195
		AFD ³	-	-	-	-	-	-	-	-
Feb	0.6	DF	24	24	24	24	22	24	24	24
		VPD	1.511 [†]	10.898***	9.860***	8.627***	3.077***	5.409***	5.596***	2.455***
		AFD	1.152	-0.799	-1.256	-0.355	-0.687	0.335	-0.150	-0.073

³ There was no fog or dew detected

[†] *M. pisiformis* lost all leaves in February

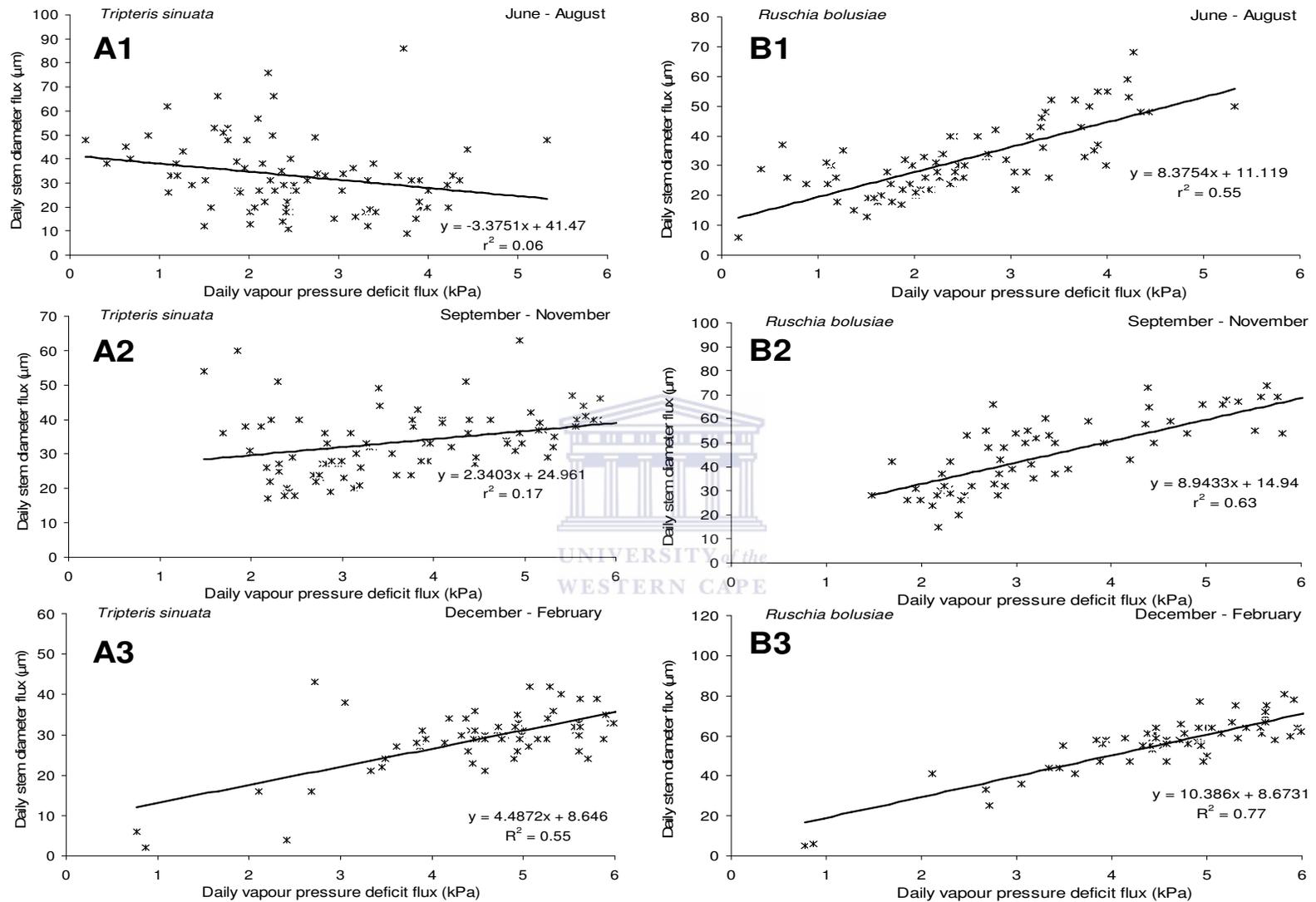


Figure 4.1. Relationships between daily amplitudes in vapour pressure deficit (VPD) and stem diameters of *T. sinuata* (A1- A3) and *R. bolusiae* (B1- B3) during the winter (June-August), spring (September- November 2008) and summer (December – February).

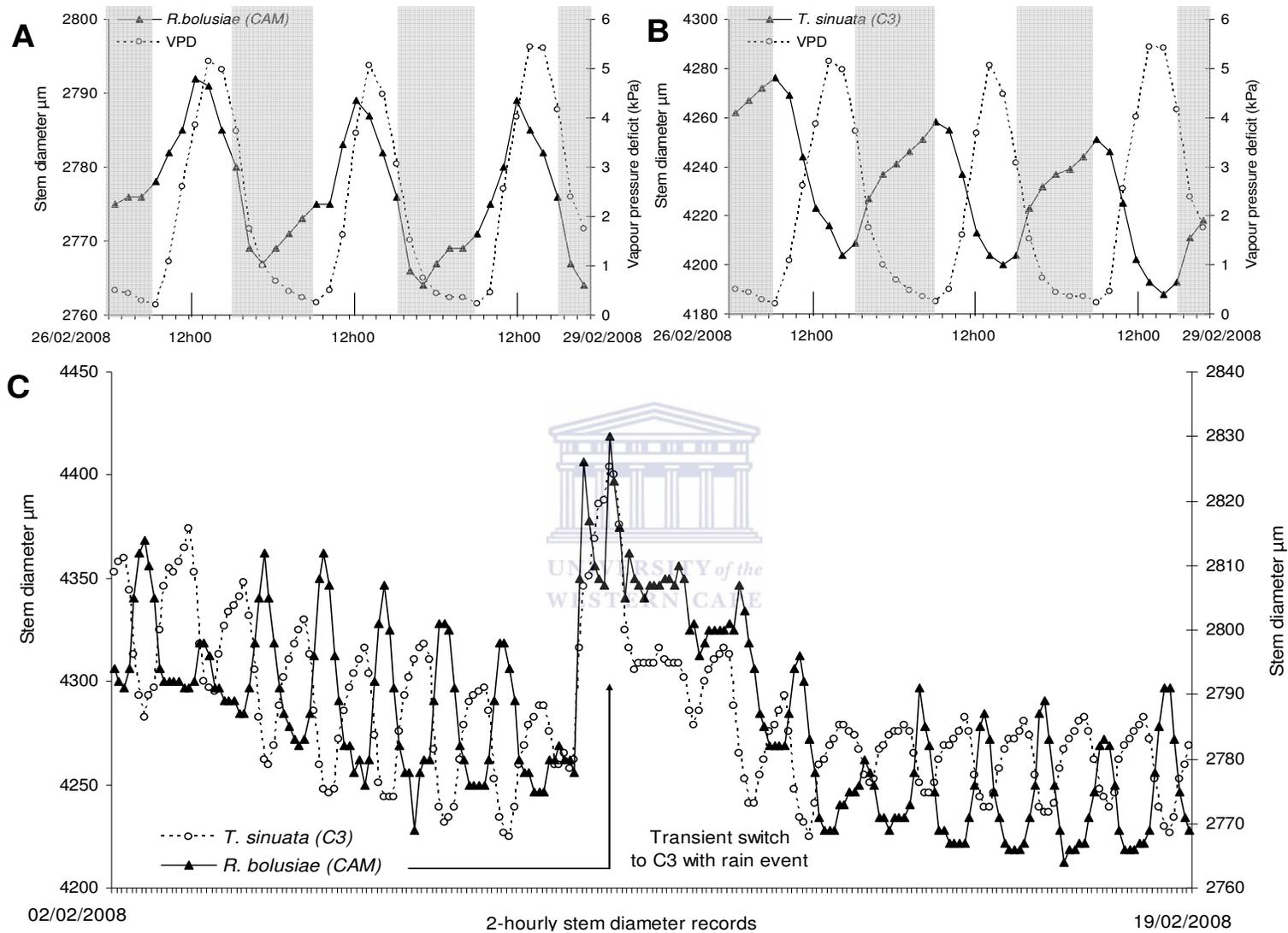


Figure 4.2. Diurnal variations in vapour pressure deficit (VPD) and stem diameters of *T. sinuata* (A) and *R. bolusiae* (B) (night-time shaded in grey) with a transient switch from a CAM to a C₃ photosynthetic mode evident in *R. bolusiae* after a sporadic rain event (C).

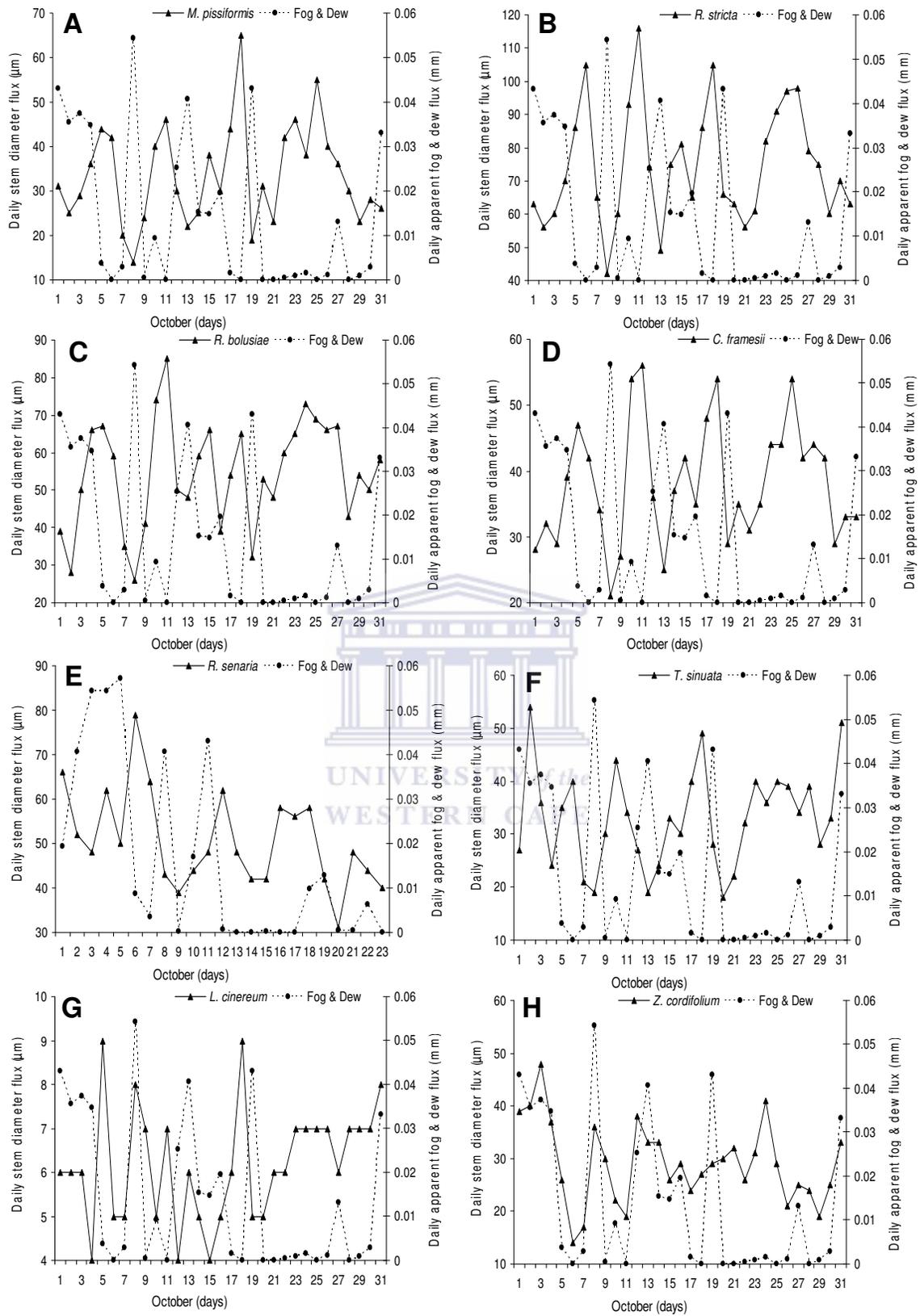


Figure 4.3. Relationships between daily amplitudes in apparent fog and dew precipitation amounts and stem diameters of *M. pissiformis* (A), *R. stricta* (B), *R. bolusiae* (C), *C. framesii* (D), *R. senaria* (E), *T. sinuata* (F), *L. cinereum* (G), *Z. cordifolium* (H).

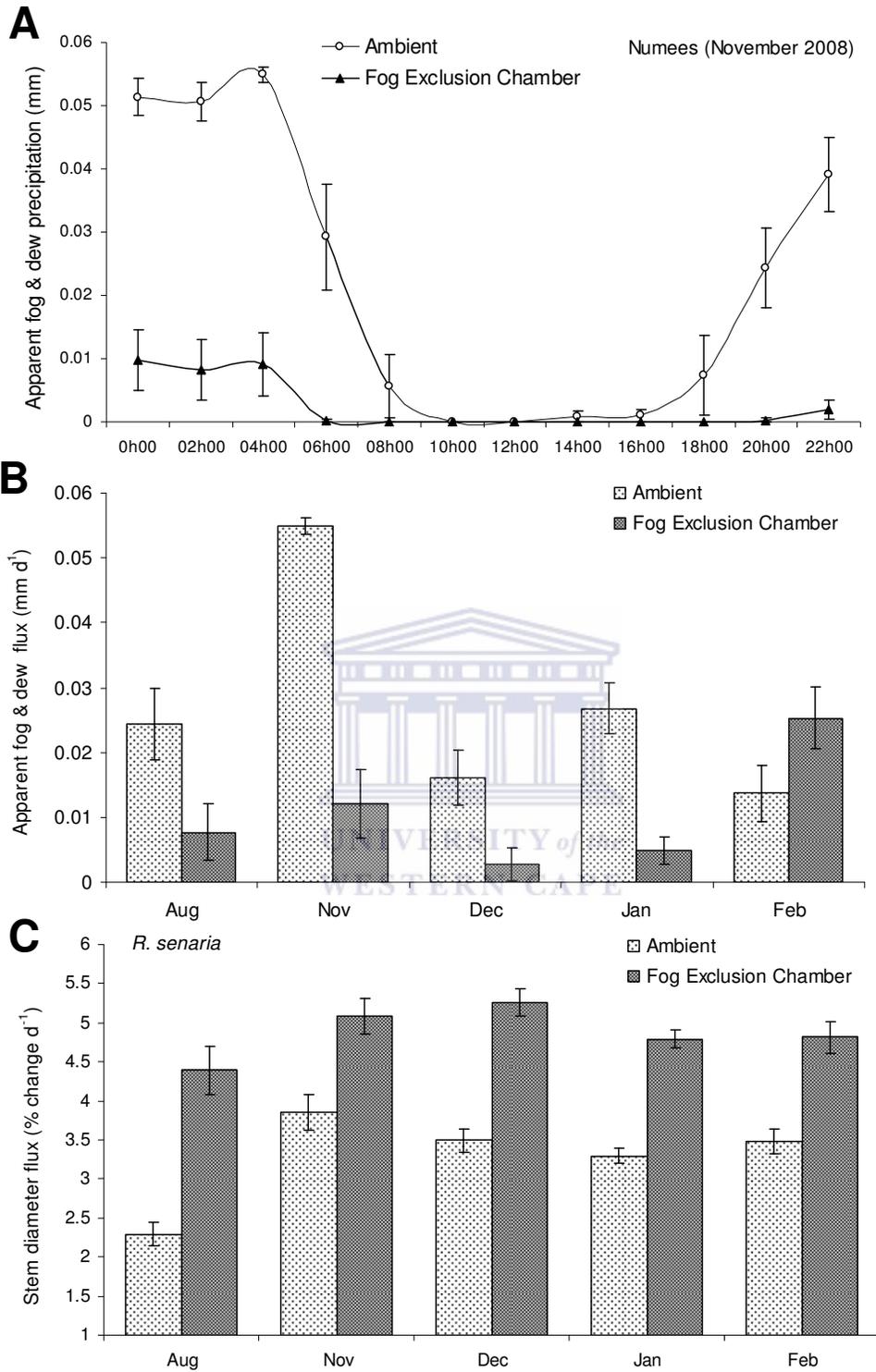


Figure 4.4. Diurnal changes in apparent fog and dew precipitation amounts under ambient and fog-excluded conditions (A). Average monthly fog and dew precipitation amounts and (B) average monthly stem diameter amplitudes of *R. senaria* (C) in ambient and artificially fog-excluded environments.

Chapter 5

Differential amounts of fog and dew intercepted by two dwarf quartz-field succulents with different canopy morphologies in an arid South African ecosystem

Abstract

Changes in water mass of quartz gravel substrates and those containing whole dwarf succulent species with different canopy morphologies were monitored at hourly intervals over an 8-month period with weighing lysimeters. Consistently greater net amounts of water were intercepted daily by quartz gravel substrates containing *Agyroderma pearsonii* than *Cephalophyllum spissum* plants as well as those containing no plants. These attributed to a high water repellence of *Agyroderma pearsonii* leaves and less radiation absorbed by the paler silvery to grey-green leaves of *Agyroderma pearsonii* leaves than the dark green leaves of *C. spissum* resulting in lower leaf temperatures and less water loss by transpiration. Quartz gravel soils devoid of plants intercepted nearly 5-times greater amounts of precipitation contributed by fog and dew than that contributed by rain. The presence of *Agyroderma pearsonii* elevated the amounts of fog and dew intercepted to values nearly 9-times higher than that contributed by rain. These precipitation amounts exceeding the high percentages of total hydrological input contributed by fog and dew reported for other ecosystems in tropical, montane, desert and coastal regions.

Keywords

transpiration, fog and dew precipitation, vapour pressure deficit, crassulacean acid metabolism, C₃, succulent karoo

5.1. Introduction

Dew and fog precipitation are considered crucial in ameliorating plant water deficits in semi-arid and arid Mediterranean-climate ecosystems by reducing transpiration water loss and preventing thermoregulation problems (von Willert, et al., 1992; Turner & Picker, 1993; Musil, et al., 2005; 2009). However, the interception and utilization of fog and dew by plant canopies remains one of the least considered aspects of vegetation studies at any scale (Schulze, 1995; Yates & Hutley, 1995; Andrade, 2003).

Various direct and indirect techniques have been applied in quantifying fog and dew precipitation amounts and vegetation responses to these which present numerous measurement challenges (Ninari & Berliner, 2002). Sensitive instrumentation with a minimum resolution of 0.1mm (Agam & Berliner, 2006) is required for quantifying especially dew precipitation amounts where the theoretical maximum does not exceed 0.4 mm d⁻¹ (Monteith & Unsworth, 1990; Jacobs, et al., 2000). Techniques applied include stable water isotopes in *Sequoia sempervirens* and prairie grasses (Dawson, 1998; Corbin, et al., 2005), sap-flow sensors in *Sequoia sempervirens* (Burgess & Dawson, 2004), leaf thickness sensors in *Crassula spp* (Martin & von Willert, 2000) and stem diameter variation sensors which are often linked to horticultural irrigation systems for monitoring the water status of plants in relation to microclimatic conditions (Lee & Shin, 1998; Ton & Kopyt, 2003).

Assays of stable $\delta^{18}\text{O}$ and $\delta^2\text{H}$ isotope ratios in stem xylem water provide an effective means of detecting the relative contribution of fog and dew to plant hydrology. Such assays have shown that fog and dew are essential sources of water, even more important than rain, for succulent shrubs in arid South African ecosystems and corroborated by significant correlations found between fog and dew frequencies, plant foliar water contents and quantum yields of photochemistry (Chapter 3). These assays were supplemented by automated stem diameter variation sensors installed on several succulent shrubs of diverse growth form which allowed discrimination between C₃ and CAM photosynthetic types, their immediate responses to and magnitude of transpiration water loss during fog and dew events (Chapter 4). However, assays of stable $\delta^{18}\text{O}$ and $\delta^2\text{H}$ isotope ratios in endemic dwarf succulent species are problematic as extraction of water from plant tissues requires non-photosynthetic portions in order to prevent isotopic fractionation (White, et al., 1985; Thorburn & Walker, 1993; February, et al., 2007). Also, the reduced stems and unique spherical and spindle leaf shapes of many South African dwarf succulents preclude the proper installation of sensors (linear variable displacement transducers) for detecting minute variations in stem diameter or leaf thickness.

Other techniques employed in quantifying fog and dew accumulation include measuring change in mass of whole plants such as in epiphytic bromeliads of a Mexican dry deciduous forest (Andrade, 2003). Automated weighing lysimeter provide useful devices in this regard and have been applied in determining the contribution of dew to the hydrological balances of strawberries (Glenn, et al., 1996), in quantifying subtle changes in soil moisture due to evaporation and transpiration (Yunusa, et al., 2004; Marek, et al., 2004; Johnson, et al., 2005) and more recently in quantifying non-rainfall moisture inputs in arid ecosystems in Israel (Heusinkveld, et al., 2006) and South Africa (Brown, et al., 2008). The potential of microlysimeters in quantifying fog and dew interception by substrates containing dwarf succulent species with different canopy morphologies was examined in this study.

5.2. Materials and methods

5.2.1. Study sites and species

The study site was Quaggaskop located at the southern extremity of the succulent karoo biome, a semi-arid winter rainfall region within South African (Rutherford & Westfall, 1986) ranked among 34 global biodiversity hot spots (Myers, et al., 2000; Mittermeier, et al., 2004). Quaggaskop (31° 24.6" S / 18° 37.8" E) is situated in the southern Knersvlakte bioregion at an elevation ±160 m and has a mean annual precipitation of 145 mm and mean daily maximum air temperature of 25.7°C determined at a nearby Vredendal weather station between 1957 and 1984 (Climate of South Africa, 1986).

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.

5.2.2. Soil lysimeters

Portable soil lysimeters with measuring accuracy of 0.002 mm, designed and constructed (Musil & Mulder, pers. com.) for the BIOTA South Phase III Project (Figures 5.1 A-B,) were used to quantify changes in water mass of quartz gravel substrates containing each of the two study species in response to precipitation events. Three quartz gravel soil cores (240 mm diameter x 45 mm deep) with different dwarf succulent plant species assemblages were carefully excavated with accompanying root systems and transferred into similar dimension lysimeter weighing pans. The first quartz gravel soil core comprised no plants and served as a control. The second quartz gravel soil core comprised three individuals of the dwarf succulent *C. spissum* with dark green, three angled spindle shaped leaves. The third quartz gravel soil core comprised three individuals of the dwarf succulent *A. pearsonii* with silvery to grey-green spherical leaves, rounded at their lower surface with the upper surface flat or slightly convex. Changes in mass of the quartz gravel substrates containing different soil-plant-species assemblages as well as load cell temperatures were logged at hourly intervals by a programmable circuit board installed in each microlysimeter.

Initial soil core water contents were determined from fresh samples of soil collected from the three different soil-plant-species assemblages as follows:

$$\text{ISWC} = [(\text{FSMS} - \text{DSMS})/(\text{FSMS})] \times 100 \dots\dots\dots(1)$$

where: ISWC = initial soil water content (% dry mass)

FSMS = fresh soil mass of sample

DSMS = dry soil mass of sample after drying at 60°C to a constant mass

These initial soil core water contents were used to calculate the initial soil dry masses in the different soil-plant-species assemblages as follows:

$$\text{IDSMC} = \text{FSMC} \times [(100 - \text{ISWC})/100] \dots\dots\dots(2)$$

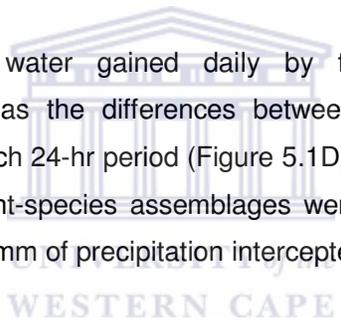
where: IDSMC = initial dry soil mass of core

FSMC = fresh soil mass of core

ISWC = initial soil water content

Subtraction of the initial soil dry masses of the three different soil-plant-species assemblages from their respective fresh masses recorded at hourly intervals provided the total masses of water present in the soils and plants of each soil core at each specific time and date. These measured water masses were adjusted to a uniform temperature of 20°C using correction factors derived from regressions of load cell output against temperature for each lysimeter.

The net amounts of water gained daily by the different soil-plant-species assemblages were calculated as the differences between the recorded maximum and minimum water masses over each 24-hr period (Figure 5.1D). These daily net fluxes in water content of the different soil-plant-species assemblages were divided by the lysimeter pan surface area to convert them to mm of precipitation intercepted.



5.2.3. Precipitation, humidity and temperature measurements

Hourly records of atmospheric air temperature, relative humidity and rain at the study site were obtained with thermocouples, relative humidity and tipping gauge sensors interfaced with miniature data loggers enclosed in ventilated radiation shields (Watch Dog 450, Spectrum Technologies Inc., Plainfield, Illinois, USA).

5.2.4. Statistical analyses

An analysis of variance (General Linear Model) tested for significant differences between the average amounts of fog and dew precipitation intercepted monthly by the quartz gravel substrates with the different dwarf succulent species. Significantly different treatment means were separated with a Duncan's multiple range test.

5.3. Results

Significantly greater ($F_{2,653} = 214.1$; $P \leq 0.001$) net amounts of fog and dew precipitation were intercepted by quartz gravel substrates containing *A. pearsonii* plants than those intercepted by quartz gravel substrates containing *C. spissum* plants as well as the

quartz gravel controls containing no plants (Figure 5.1). These greater amounts of fog and dew intercepted by quartz gravel substrates containing *A. pearsonii* plants were consistent over the 8-month recording period with no significant interaction ($F_{14,653} = 1.2$; $P \leq 0.05$) apparent between species assemblage and month. In contrast, the net amounts of water intercepted daily by the quartz gravel substrates containing *C. spissum* plants were not significantly ($P \leq 0.05$) different from those intercepted by the quartz gravel controls during the wetter mid-winter to early spring (July to September) period, but were significantly ($P \leq 0.05$) smaller than those intercepted by the quartz gravel controls during the drier mid spring to late summer (October to February) period.

The combined precipitation values over the 223-day monitoring period indicated that quartz gravel soils devoid of plants intercepted nearly 5-times greater amounts of precipitation contributed fog and dew than that contributed by rain. The presence of *A. pearsonii* elevated the amounts of fog and dew intercepted to values nearly 9-times higher than that contributed by rain.

5.4. Discussion

The consistently greater amounts of rain and fog and dew precipitation intercepted by quartz gravel soils containing *A. pearsonii* than those containing *C. spissum* over the entire 223-day monitoring period (Figure 5.2) was attributed to a high water repellence of *A. pearsonii* leaves, a known adaptation among plants inhabiting dry climates for channelling hydrological inputs underneath their canopies (Holder, 2007), and supported by photographic evidence showing a high water repellence of *A. pearsonii* leaves (Figure 5.1C). Also, the much paler silvery to grey-green leaves of *A. pearsonii* leaves pointed to less radiation absorption than by the dark green leaves of *C. spissum* resulting in potentially lower leaf temperatures and transpiration water loss, an effective means of cooling leaf surfaces (Von Willert, et al., 1992), as well as greater moisture interception. The latter suggestion supported by studies on epiphytic bromeliads in Mexican dry forests which have demonstrated that the lower leaf temperatures of *Tillandsia elongata* than its close relative *T. brachycaulos* with its relatively thicker and narrower leaves, explain the greater amounts of dew intercepted by this species during both dry and rainy seasons (Andrade, 2003). Plants mainly benefit from fog and dew channeled to soil surface through uptake by superficial plant roots (Batanouny, 2001). This fact explains *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.

It has been suggested that fog and dew amounts alone may not be adequate to support plant growth and only provide a means of assisting plants in maintaining a favourable water balance during the driest months of the year (Andrade, 2003). However the observed nearly 5-times greater amounts of precipitation contributed by fog and dew than rain in this study suggest otherwise. This study's observations were corroborated by measurements of $\delta^{18}\text{O}/\delta^{16}\text{O}$ and $\delta^2\text{H}/\text{H}$ isotope ratios which demonstrated unequivocally that fog and dew comprise a greater fraction of stem xylem water than rain in several succulent shrub species especially during the wet winter season. Indeed, the measured total precipitation amount of 111.2 mm contributed by fog and dew over the 8-month monitoring period was over 75% of the mean annual rainfall of 145 mm determined at a nearby Vredendal weather station over a 27-year period. These precipitation amounts exceeding the high percentages (up to 34%) of total hydrological input contributed by fog and dew reported for other ecosystems in tropical montane, desert and coastal regions (Dawson, 1998). Also, the nearly 9 time greater amounts of fog and dew intercepted by *A. pearsonii* than bare quartz gravel substrates suggest it may be a key species in augmenting the water requirements of other succulents on the quartz fields.

5.5. Acknowledgements

Mr S.G. Snyders is thanked for his technical support and the South African National Biodiversity Institute for provision of office and laboratory facilities. The study, a work package included within the BIOTA Southern Africa Project, was funded by the German Federal Ministry of Education and Research (Promotion number 01LC0624A2).

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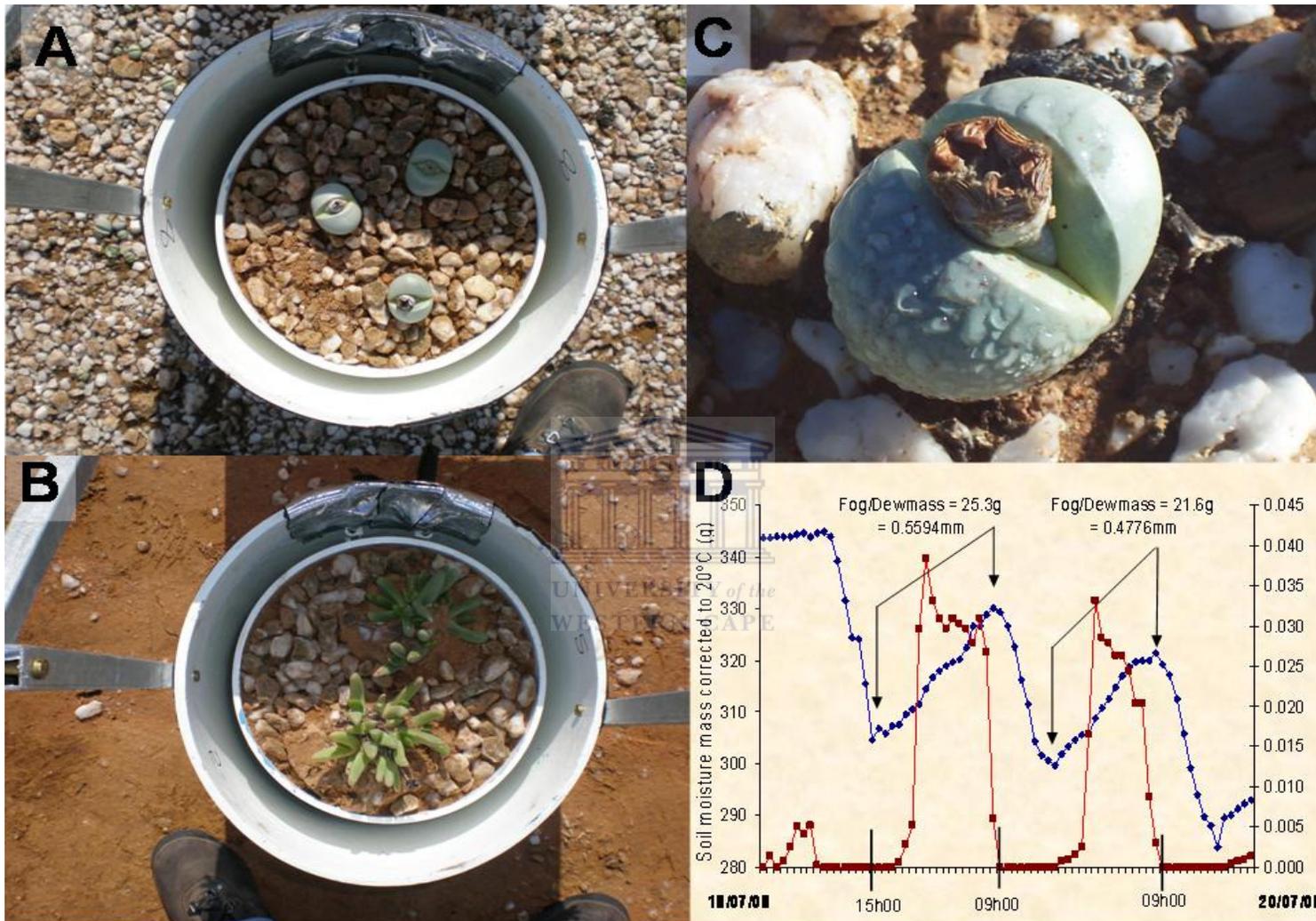


Figure 5.1. Microlysimeter design with the weighing pan containing *A. pearsonii* (A) and *C. spissum* (B). Insert is a photographic image of *A. pearsonii* plants at 0730 SAST (25th July 2008) following nocturnal dew showing high water repellence of its leaves(C). Inserted graph shows the calculation of fog/dew amounts from lysimeters (D). Right axis shows leaf wetness (mm).

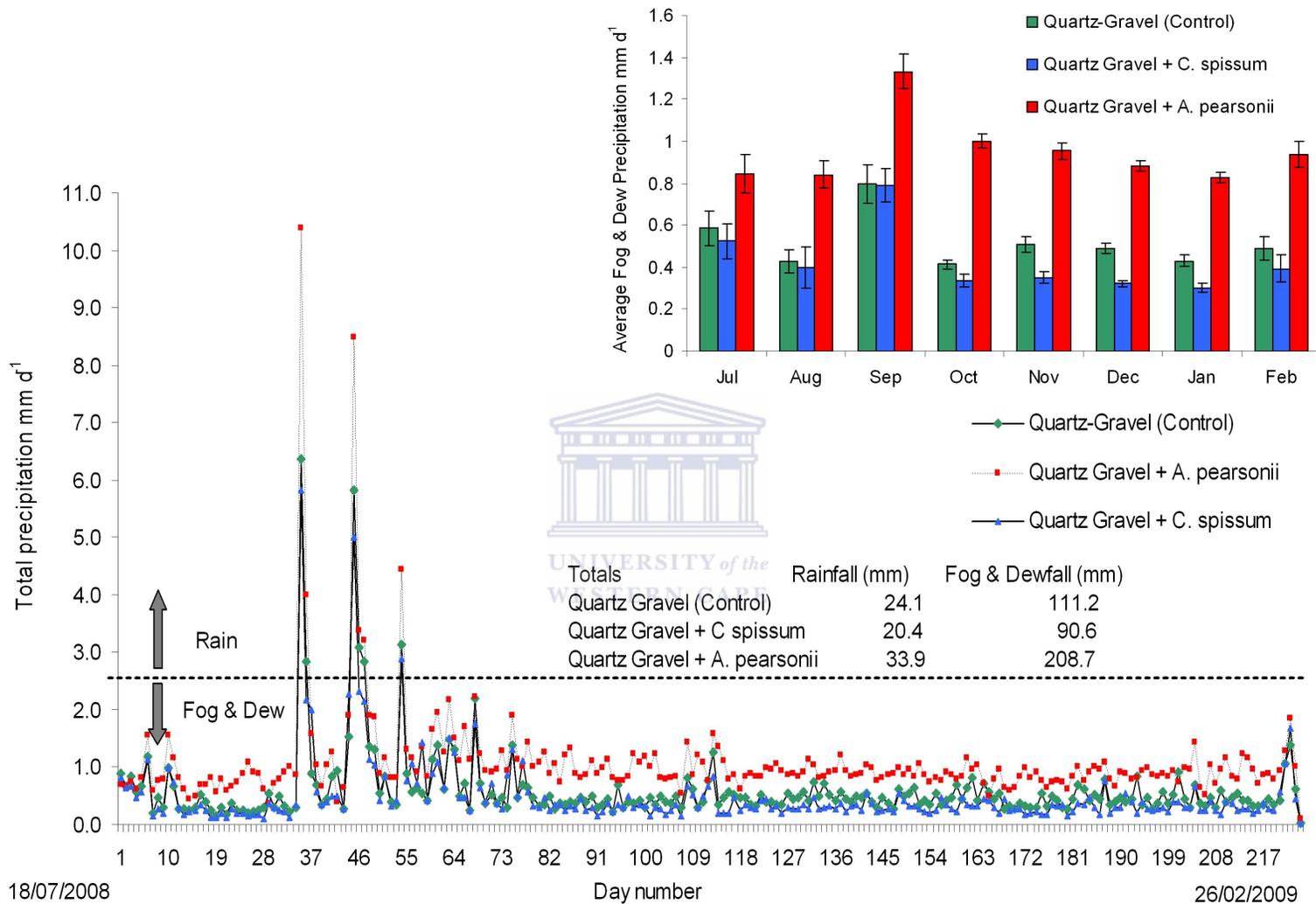


Figure 5.2. Graph of total precipitation measured by microlysimeters containing quartz substrate, quartz+*Agroderma pearsonii* and quartz + *Cephalophyllum spissum*. Insert is a line demarcating rain and fog & dew occasions. Inserted bar graph shows average fog & dew precipitation (mm day^{-1}) from July 2008 to Feb 2009, with error bars indicated.

Chapter 6

Conclusions and recommendations

6.1. Main conclusions

The outcomes of this study have confirmed that succulent karoo plant species of different life forms indeed intercept, absorb and channel significant amounts of fog and dew for their hydration, photosynthesis and growth. This was confirmed using stable water isotopes and stem diameter variation sensors in eight different succulent shrubs growing in ambient and fog excluded conditions and in two dwarf succulent species using weighing lysimeters. The main conclusions are as follows:

1. Fog and dew are essential sources of water for succulent shrubs, even more important than rain, and effect succulent foliar water contents and quantum yields of photochemistry.
2. Different isotope ratios in stem xylem water of evergreen and drought deciduous leaf succulents during summer result from different amounts of lighter isotopes lost by different amounts of water transpired.
3. Fog and dew moderate nocturnal water loss in succulents displaying CAM photosynthetic modes, these effects indistinct among species displaying C₃ photosynthetic modes.
4. *Agyroderma pearsonii* with less radiation absorbent and hydrophobic (water repellent) leaves intercept greater amounts of fog and dew than *Cephalophyllum. spissum*.
5. Fog and dew seemingly contribute as much, or even greater amounts of water than rain.

6.2. Recommendations

The recommendations arising from each of the main conclusions of the study are as follows:

1. Whilst these results are the first to be reported on reliance of succulent shrubs on fog and dew for their survival in South Africa, their implications are phenomenal. Climatic warming has been predicted to increase by 2 to 6°C by the year 2100 (Hulme, et al., 2000), a phenomenon that can raise average night-time temperatures, thereby reducing the availability of these moisture sources. Restoration efforts could capitalise on the importance of fog and dew as moisture sources in these arid environments. These moisture sources can be harnessed for supplementing moisture to plants in disturbed ecosystems. For example, in Nepal, Chile and other developing countries fog water has been harnessed using mesh grids for household use (Karkee, 2005;

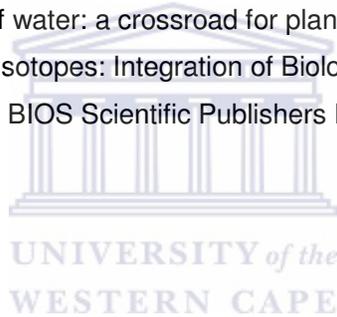
Schemenauer & Cereceda 1991; 1994), whilst passive condensers such as sea stones and roof surfaces have also been used for harvesting dew (Sharan, 2006; Mileta, et al., 2006). Moreover, fog harvesting along the west-coast of South Africa has already been considered feasible for household consumption purposes (Olivier, 2002; 2004) hence further efforts should develop harvesting techniques for enhancing available moisture in these semi-arid ecosystems.

2. The influence of vapour pressure deficit on isotopic signatures of xylem water was confirmed in this study. Since leaf-water isotope signal can be imparted to CO₂, O₂, and plant organic material (Yakir, 1998), future isotope studies should also consider using carbon isotopes in understanding fog and dew, in order to eliminate the need for the costly and time-consuming procedure of extracting xylem water from the stem (cryogenic extraction) for δ¹⁸O and δ²H assays.
3. Complementary studies on both night-time and daytime transpiration are required in order to fully understand the trends shown in stem diameter fluxes. Furthermore the absorption of fog and dew at cellular level requires further investigation. This has not been extensively studied in other species, except *Crassula* species, where epidermal hydathodes identified in 27 *Crassula* species in the Namib Desert were observed as responsible for fog and dew uptake that resulted in increasing stem and leaf thickness (Martin & von Willert, 2000).
4. Previous studies have linked the unparalleled radiation of species to winter rainfall regimes in the succulent Karoo (Klak, et al., 2004). In view of the much greater amounts of water contributed by fog and dew than rain, there is also a need to consider also the role of fog and dew in the radiation of succulent species.
5. The canopy properties that make succulent species efficient interceptors of fog and dew require further investigation as such species could potentially augment the water requirements of other succulents in restoration initiatives.

6.3. References

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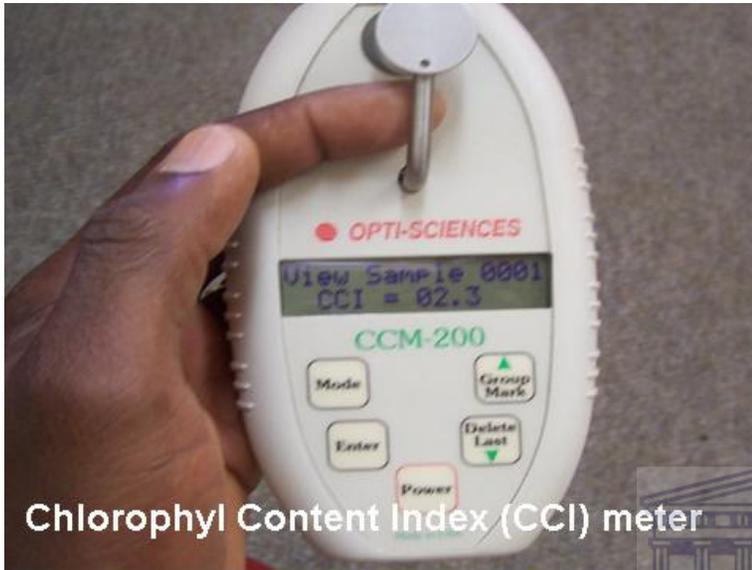
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6.4. Appendices to Chapter 3



Appendix 3.1. Succulent shrubs used in the study *Cephalophyllum framesii* (A), *Lycium cinereum* (B), *Monalaria pisiformis* (C), *Ruschia bolusiae* (D), *R. senaria* (E), *R. stricta* (F), *Tripteris sinuate* (G) and *Zygophyllum cordifolium* (H).



Chlorophyll Content Index (CCI) meter



Steady state fluorescence



Leaf samples for water content, malate, N & P assays



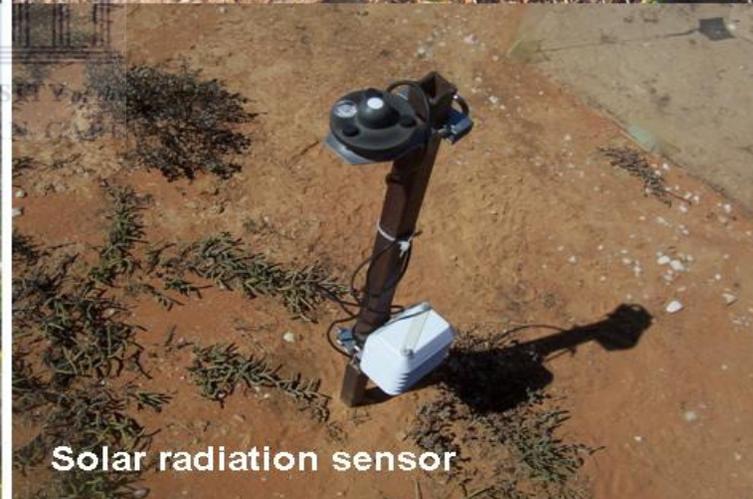
Stem sample collection xylem

Appendix 3.2. Measurement of chlorophyll content, PSII function, plant canopy interception and sampling of stems for isotope assays.



Appendix 3.3. Cryogenic extraction of xylem water and assays of $\delta^{18}\text{O}$ and $\delta^2\text{H}$ of xylem and meteoric water samples.

6.5. Appendices to Chapter 4



Appendix 4.1. Fog harvesters used for sampling (Type 2) and quantifying (Type 1) fog interception at study sites. Temperature, radiation, humidity and leaf wetness sensors.



Appendix 4.2. Stem diameter microvariation sensors interfaced with data loggers.