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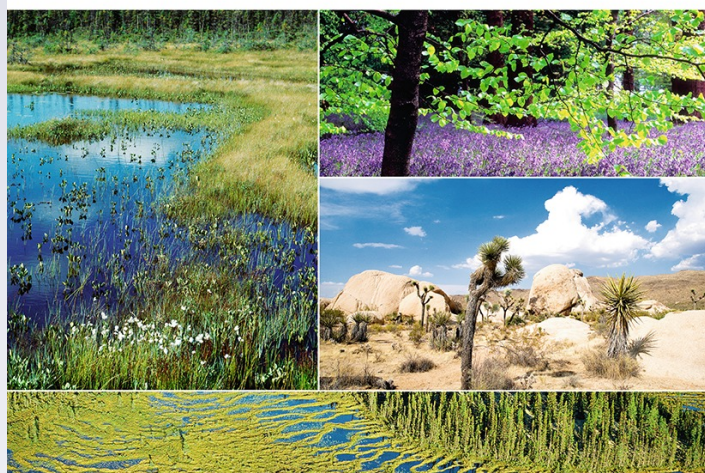
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Root niche partitioning between shallow rooted succulents in a South African semi desert: implications for diversity

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Abstract With a high percentage of endemics along the west coast of South Africa, especially in the family Aizoaceae, the region is considered one of the earth's biodiversity hot spots. It has been suggested that the diversity and radiation of the Aizoaceae are coincident with low but predictable rainfall and lack of competition between species. In this study we examine the relationship between water source and the efficiency of PSII photochemistry for representative Aizoaceae and non-Aizoaceae. We do this to determine the extent to which the different genera are adapted to the frequent, low volume, precipitation characteristic of the region and to ascertain the extent to which there is competition for water. Our water isotope results show that the Aizoaceae use shallow surface water while the non-Aizoaceae use a deeper water source. We are however not able to show the extent to which the Aizoaceae utilize fog or dew. Our chlorophyll fluorescence results show that there are no differences in efficiency of PSII photochemistry between the species in the wet season. The decline from wet to dry season for the Aizoaceae is, however, more dramatic than that of the non-Aizoaceae reflecting the differences in rooting depth between the different families. These results suggest that, during the dry season, there is no competition for resources between families but there is competition between species. We conclude that the adaptation to using shallow water, coupled with susceptibility to drought of adult short lived Aizoaceae may be a, mechanism for the diversification of this family.

Keywords δ^{18}O · δ^2H · Water source · Photosynthesis · Community structure

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Introduction

Namaqualand, on the west coast of South Africa, is a winter rainfall desert region receiving between 20 and 290 mm of rain annually (Milton et al. 1997). The Succulent Karoo vegetation that characterizes the region shows over-representation of families that are succulent, especially Aizoaceae and Crassulaceae (Desmet and Cowling 1999). Depending on rainfall, canopy heights vary from 50 to 75 cm (Desmet 2007). With approximately 40 % of the nearly 5,000 species endemic to the region the Succulent Karoo is considered one of the earth's biodiversity hot spots (Hilton-

Taylor 1996; Klak et al. 2004). Constituting approximately 85 % of the Aizoaceae, subfamily Ruschiodeae is by far the largest group of plants in the succulent Karoo with about 1,563 species in 101 genera. It has been suggested that the diversity and radiation of these short- to medium-lived (3–10 years) succulent shrubs are coincident with low winter rainfall and mild, fog-ameliorated summers (Cowling et al. 1994; Desmet 2007). The low rainfall is considered to be very reliable as the year on year coefficient of variation of monthly rainfall is very low (Cowling et al. 1999, 2005). Klak et al. (2004) suggest that climate and environmental factors alone may not explain the diversity of Aizoaceae, especially within Ruschiodeae. They suggest that several morphological innovations contributed toward the radiation including wide band tracheids (Landrum 2001), leaf shape and hygroscopic capsules (Klak et al. 2004). These may, however, not be the only adaptations that facilitated radiation of Aizaoceae.

A number of recent studies have shown that plants are able to intercept and utilise moisture from fog events (Corbin et al. 2005; Dawson 1998; Gabriel and Jauze 2008). These studies have also 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 (enriched), than rain condensing at higher levels in the atmosphere. These isotopic differences between different sources of precipitation makes it possible to determine the water source (fog, dew or rain) of a plant by examining isotope ratios of water extracted from suberized plant stems.

South westerly winds off the cold South Atlantic Ocean result in regular fog and heavy dew events primarily in summer. These events cover the entire region, moving inland from the coast to the foothills of the escarpment (Desmet 2007). Data collected along the west coast of South Africa between 1954 and 1986 show that, in this area, fog occurs on 84–140 days of the year. These data also show that these regular fog events may deposit considerable amounts of water with projected annual yields at Cape Columbine of around 2,080 Lm^{-2} of collecting surface per year (Olivier 2002). In the Namib Desert, several studies have shown that such fog events provide a predictable source of water for both plants and animals (Lange et al. 2007; Seely 1979). In the Succulent Karoo, plants that are able to use these water inputs such as
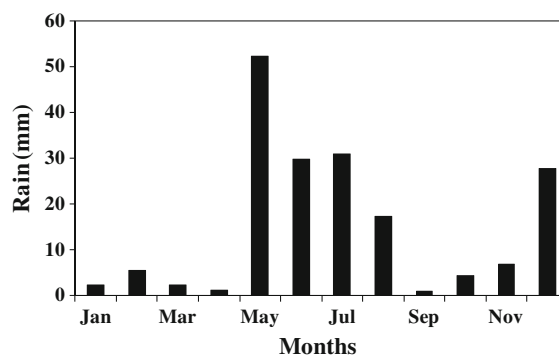

Fig. 1 Total monthly rainfall at our study site for the year of our study (June 2007–May 2008) showing both rainfall seasonality and regularity

some of the dwarf succulents (Matimati et al. 2012a), would likely have a significant productivity gain over those that are unable to utilise them. Several studies have demonstrated that the Aizoaceae have extremely shallow roots (Carrick 2003; February et al. 2011; Midgley and van der Heyden 1999). Given their diversity and abundance in the Succulent Karoo, it is possible that the Aizoaceae have adapted rooting depth not only to the low but reliable rainfall (Fig. 1), but also to taking up fog and ephemeral rain in summer.

Here we examine the relationship between water source and the efficiency of PSII photochemistry for representative, succulent, shrub, Aizoaceae and non-Aizoaceae. Our primary objectives are to determine the extent to which different genera in the Succulent Karoo are adapted to the frequent but low volume rainfall events characteristic of the region, and the extent to which the different groups can utilise water from fog. We do this through a determination of quantum yield efficiency (F_v/F_m), and water source for both Aizoaceae and non-Aizoaceae. Relative to the non-Aizoaceae, we expect the Aizoaceae to utilize ephemeral rainfall events which should manifest in an increase in the efficiency of PSII photochemistry.

Methods

Study area

The study site was located on the farm Quaggaskop in the Moedverloren region of the Knersvlakte approximately 22 km NW of Vanrhynsdorp in Namaqualand,

South Africa (S31.427363 E18.643497). Mean annual rainfall at the closest weather station, Vredendal, between 1957 and 1984 was 145 mm (Weather Bureau 1986). The mean monthly temperature is 18.9 °C, with the lowest temperature 11.3 °C in July and highest 25.3 °C in December. Rainfall, consisting predominantly of frontal systems from the South Atlantic to the west, falls primarily in the cooler months from June to August (winter), with occasional thundershowers during the hot dry season (summer) (Desmet 2007). Large parts of the Knersvlakte, are covered by quartz-gravel fields, an extra-zonal special habitat, with a globally unique flora comprising specialized dwarf succulents (canopy covers: 0.5–3.4 cm^2 $plant^{-1}$) (Schmiedel and Jürgens 1999). Inter-dispersed among the quartz-gravel fields are areas where the underlying quartz gravel is covered with shale, phyllite and limestone derived substrates where larger shrubby species up to 40 cm high with multiple leaves are more prevalent (canopy covers: 59.6–341.8 cm^2 $plant^{-1}$).

We investigate water use in six of these succulent shrub species, each with a different growth form. These include three Aizoaceae, the erect evergreen *Ruschia bolusiae* Schwantes and *Ruschia stricta* L. Bolus var. *turgida* L. Bolus, as well as the prostrate dwarf succulent *Cephalophyllum framesii* L. Bolus and three non-Aizoaceae, the partly drought deciduous microphyllous succulent *Lycium cinereum* Thunb. (Solanaceae) the mesophyllous drought deciduous *Tripteris sinuata* DC. (Asteraceae) and the prostrate dwarf succulent *Zygophyllum cordifolium* L. f. (Zygophyllaceae). Of these, the Aizoaceae species are predominantly using CAM photosynthesis while the non-Aizoaceae have mixed C_3–CAM photosynthesis (Matimati et al. 2012b).

Sampling and measurements were carried out at the end of each month for 1 year from the end of June 2007 to the end of May 2008.

Water source

Oxygen and hydrogen isotope ratios of water extracted from plants may be used to determine the water source of the plant (Dawson and Ehleringer 1991; February et al. 2007). The method is based on the understanding that the stable isotope ratio of the water in suberized woody tissue is not significantly different from its source (White et al. 1985). We collected soil and twig samples as well as potential source waters (rain, fog and dew) for stable isotope analysis. The twig samples (c. 10 mm Ø × 60 mm) of suberized wood were collected from six randomly selected individuals of each shrub species while the soil cores were taken directly under the canopy of each shrub. Soil samples were taken at depths of 5, 10 and 20 cm. Both twig and soil samples were collected directly into borosilicate tubes (Kimax-Kimble, Vineland, USA). These tubes were subsequently inserted onto a cryogenic vacuum extraction line to extract the xylem and soil water for isotope analysis.

One meter square sheets of plexiglass mounted at 45° angles with gutters installed at the lower ends (Muselli et al. 2002) were used to separately intercept rain and dew water which were channelled to an insulated bottle with a layer of liquid paraffin to minimise evaporation. Collections of rainwater were confined to sporadic daytime rain events and dew collections to overnight dew precipitation which was restricted to night time conditions of high humidity and low temperature. Fog water was collected using a harp-style collector based on a design by Hutley et al. (1997) and channelled through a tipping bucket rain gauge into an insulated bottle with a layer of liquid paraffin. The plexiglass rain/dew collector as well as the harp style fog collector were solely used for sampling water for isotope analysis, and was checked daily at 07 h and after a precipitation event. Rain, dew and fog samples were collected immediately after rain, dew and fog events and were stored in borosilicate tubes prior to mass spectrometry (Kimax-Kimble, Vineland, NJ, USA).

All water samples were analysed for $^{18}O/^{16}O$ ratios using the CO_2 equilibrium method of Socki et al. (1992) while $^2H/H$ ratios were obtained after the closed tube zinc reduction method of Coleman et al. (1982). Isotopic ratios of both $^2H/H$ and $^{18}O/^{16}O$ were then determined using a Finnigan Mat 252 mass spectrometer (Bremen, Germany) at the University of Cape Town. Our own internal standards were run to calibrate the measurements relative to standard mean ocean water (V-SMOW) and to correct for drift in the reference gas. Analytical uncertainty in measurement of δ was c. 2 ‰ for δ^2H and c. 0.2 ‰ for $\delta^{18}O$.

Rainfall

Rainfall amounts at the study site were measured with a tipping bucket rain gauge (Campbell Scientific Inc., USA).

Chlorophyll fluorescence

The determination of chlorophyll fluorescence emission is a useful means for quantifying the effects of stress on photosynthetic performance. Fluorescence, a measure of the efficiency of electron transfer, decreases under any stress that negatively affects the PSII reactions (Logan et al. 2007). We determined dark adapted PSII quantum efficiency by enclosing the entire shrub under a purpose built wire cage covered with a thick black cloth. Measurements of F_o and F_m were made following dark adaptation for 30 min to determine F_v/F_m. We did this on between 5 and 10 fully expanded apical leaves of 6 randomly selected individuals of each shrub species using a hand held modulated fluorometer (OSI-FL, Opti-Sciences Inc., Hudson, USA). To produce a maximal fluorescence signal we exposed each leaf to a 0.8 s light pulse of 15,000 μmol m^{-2} s^{-1}.

Statistical analyses

Since the experimental designs were not fully balanced due to unequal measurements, we applied a residual maximum likelihood (REML) variance components analysis (repeated measures mixed model) to test for significant differences in measured $\delta^{18}O$ and δ^2H values and PSII function between the different succulent species, dry (Oct–Mar) and wet (Apr–Sept) seasons and their interactions using the Wald χ^2 statistics generated by REML (GENSTAT Discovery Edition 3, VSNI Ltd, UK). Species were fitted in the fixed model and months in the random model. Differences exceeding twice the average standard error of differences were used to separate significantly different treatment means at $P \leq 0.05$. This is based on the assumption that for a normal distribution from REML estimates, the 5 % two-sided critical value is two.

Results

Water source

When there were multiple rainfall events in a month, the measured $\delta^{18}O$ and δ^2H values for each rain event were volume weighted. There is a linear relationship in δ^2H and $\delta^{18}O$ depletion in fresh water described by

the global meteoric water line (GMWL) with the equation $\delta^2H = 8\delta^{18}O + 10$ (Craig 1961). Evaporatively enriched water (shallow soil water) plots below the meteoric water line with a slope that is less than 8 and an intercept less than 10. We constructed a local meteoric water line (LMWL, $\delta^2H = 8.3\delta^{18}O + 5$) from our monthly measures of rainfall (Fig. 2). When plotted on the LMWL the volume-weighted values for both wet (April–Sept) and dry (Oct–Mar) season fog fell very close to the LMWL and was not significantly different from wet season rain (Fig. 2a). Wet season rain was not significantly different from wet season fog but was different ($P = 0.002$) from dry season fog (Fig. 2a). There is very little rain in the dry season (Oct–Mar; Fig. 1). These light rainfall events were enriched relative to all other water samples (wet season rain, wet season fog, dry season fog and dew (Fig. 2b).
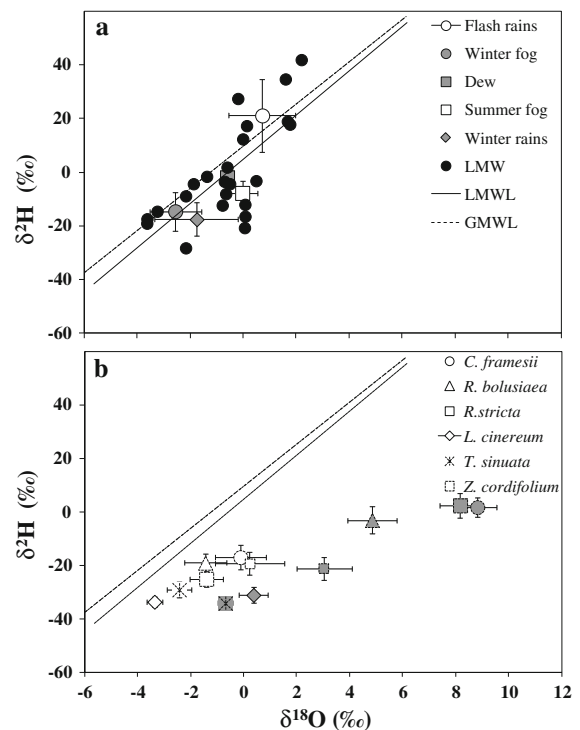

Fig. 2 a. δ^2H and $\delta^{18}O$ values for precipitation at our study site showing the local (LMWL, $\delta^2H = 8.3\delta^{18}O + 5$) as defined from local precipitation (*filled circle*) during the course of our study relative to the global (GMWL, $\delta^2H = 8\delta^{18}O + 10$) meteoric water line. Also shown are mean values with standard error for rain fog and dew. **b** δ^2H and $\delta^{18}O$ values for both Aizoaceae and non-Aizoaceae relative to both the LMWL and the GMWL. *Bars* are standard error and *points* are means. *Symbols* are dry season (*grey*) and wet season (*open*)

In the dry season plant water isotope ratios for the Aizoaceae, *C. framesii*, *R. stricta* and *R. bolusiae*, plotted away from and with a shallower slope than the amount-weighted LMWL. Dry season values for the non-Aizoaceae *T. sinuata*, *L. cinereum* and *Z. cordifolium* are not as conspicuously different as the Aizoaceae. In the wet season values for both the Aizoaceae and non-Aizoaceae are not significantly different from rain (Fig. 2b).

Although we did extract water from the soil profiles under each shrub to establish the depth at which the different species are sourcing water, the extremely dry soils resulted in analytical problems which made the data unreliable.

Chlorophyll fluorescence

We did determine Fv/Fm ratios at the end of each month (Suppl. Table 1), however, we report on differences between the Aizoceae and non-Aizaceae manifested in the wet (Apr–Sept) and dry (Oct–Mar) seasons (Fig. 3). There are no significant differences between species in mean wet season Fv/Fm ratios (0.75–0.77). There are however significant differences between wet and dry season for all species except the drought deciduous *T. sinuata* (Fig. 3). For the non-Aizoaceae these differences are less apparent than for the Aizoaceae. Mean dry season Fv/Fm ratios for the Aizoceae are between 0.50 and 0.61 while those of the non-Aizoaceae are much higher ranging between 0.71 and 0.77 (Fig. 3). While the two ruschia shrubs have similar values in the dry season the prostrate dwarf succulent *C. framesii* had significantly lower Fv/Fm ratios than the rest (Fig. 3).
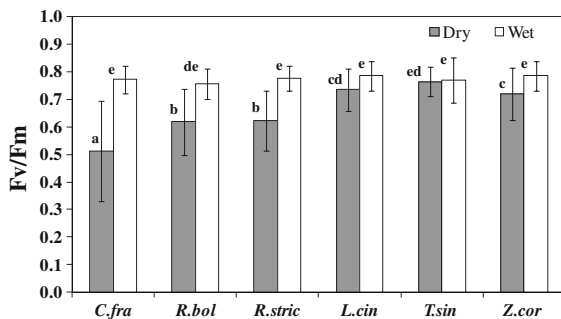

Fig. 3 Dry and wet season quantum yields of photochemistry at a steady state (Fv/Fm). *Bars* are standard error. *Values* not sharing the *same letters* indicate significant differences between species and season ($p < 0.05$)

Discussion

The isotopic ratio of water available to plants reflects the isotopic ratio of precipitation as affected by various evaporative processes. Free evaporative processes from shallow soils will result in plant water from these shallow soils plotting away from, and with a shallower slope than, the global or local meteoric water line. This relationship is extremely useful as the greater the distance along an evaporative line away from the rain the more shallow the soil water source (Dawson 1996; West et al. 2012). Cooler temperatures and regular replenishment of water in the surface soils in the wet season results in the plant water of both Aizoaceae and non-Aizoaceae reflecting isotope ratios very similar to that of the rain. In the dry season, however, the Aizoaceae xylem water reflects an isotopic enrichment typical for plants using surface soil water while the non-Aizoaceae values are consistent with deeper rooting (West et al. 2012).

Several studies have shown that the Aizoaceae are rooted in the top 5 cm of the soil (Carrick 2003; February et al. 2011; Midgley and van der Heyden 1999). Our results show that the shallow rooting of the Aizoaceae is associated with these plants using highly evaporated water from the surface layers in the hotter dry season. We are, however, unable to draw conclusions as to the nature of this water source as there are not sufficient differences in isotope ratio between the source waters rain, fog and dew. We may however speculate that the source of the highly fractionated water in the xylem of the Aizoaceae in the dry season is from either, light summer rain, fog or dew or a combination of the three.

It is generally accepted that photosynthesis is down-regulated as plant available water decreases with this response dependent on CO_2 availability in the mesophyll, as regulated by the stomata, rather than on leaf or stem water potential (Flexas and Medrano 2002). Our chlorophyll fluorescence results demonstrate that the efficiency of PSII photochemistry for the Aizoaceae is high in the wet season declining significantly as stomata close and CO_2 availability declines as water becomes less available in the dry season. In contrast, the decline in efficiency of PSII for the non-Aizoaceae while significant is not as pronounced as in the Aizoaceae. With much less fractionation of the xylem water, isotope ratios for the non-Aizoaceae suggest a deeper water source that allows these species

to maintain the efficiency of PSII photochemistry at a higher rate and for much longer. While all shrubs in Namaqualand are relatively shallow rooted (Esler et al. 1999) our results show that there are differences in rooting depth between the Aizoaceae and non-Aizoceae. These differences in rooting depth and water uptake indicate that there is no competition for resources between the Aizoaceae and non-Aizoceae when rainfall is limiting. When rainfall is high enough to wet the soil throughout the profile our results show no difference in water source between Aizoaceae and non-Aizoaceae. The Aizoaceae and non-Aizoaceae growing in this low rainfall environment avoid competition for limited resources through partitioning of rooting niches, with the non-Aizoaceae sourcing resources from deeper soil layers than the Aizoaceae allowing these species to remain less stressed than the Aizoaceae when rainfall declines (February et al. 2011; Walter 1971). Rather than competition for resources between families our results show that there is competition for resources between species of the same family as the different families in our study are rooted in the same soil depths and using the same water source.

The key feature of the rainfall in Namaqualand is its reliability when compared with other arid regions (Desmet 2007). While there may be a low coefficient of variation in the rainfall in Namaqualand the region is prone to local droughts, the most recent of which occurred in 2010 and the most severe in 1979 (Hoffman et al. 2009; Jurgens et al. 1999). Several studies have suggested that despite its leaf succulence the Aizoaceae are vulnerable to drought (Carrick 2003; Midgley and van der Heyden 1999; von Willert et al. 1985). In a review article Hoffman et al. (2009) have, however, indicated that many species within the Aizoaceae may not be susceptible to drought as greenhouse experiments have shown seedlings to survive with no water for as much as 160 days. Many of the Aizoaceae in Namaqualand are, however, relatively short lived and it is mature individuals of these relatively short lived succulents that are primarily susceptible to drought (Jurgens et al. 1999). Sensitivity of the short lived Aizoaceae to these droughts, possibly because of competition for resources within the family, are likely to have profound consequences on their metapopulation dynamics. The demographic and genetic properties of metapopulations experiencing periodic, severe, and patchy extirpations such as occurred in the 1979

(Jurgens et al. 1999) drought are likely to be highly conducive to evolutionary radiation and local speciation (Lande 1980, 1988; Levin 1995). Thus the adaptation to using shallow water because of competition for resources with non-Aizoaceae, coupled with stochastic, local, and lethal drought events for the short lived adult Aizoacea, may constitute another, completely unexplored, mechanism whereby the Aizoaceae have diversified so spectacularly in Namaqualand.

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