

An isotopic assessment of the water sourced by *Ischyrolepis sieberi* (Restionaceae) growing at high altitudes in the Cederberg: does fog play an important role?

Benjamin Wigley

Supervised by Dr E.C. February

For the module Ecophysiology
Submitted in partial fulfillment of the BSc Honours degree in Plant Ecology
University of Cape Town
October 2004

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

An isotopic assessment of the water sourced by *Ischyrolepis sieberi* (Restionaceae) growing at high altitudes in the Cederberg: does fog play an important role?

B.J. Wigley
Supervised by Dr E.C. February

Abstract

The main aim of this study was to determine if *Ischyrolepis sieberi*, a common restiod species found at high altitudes in the Cederberg captures fog to supplement its water needs. This was done by comparing the isotopic ratios of δD and $\delta^{18}O$ in captured fog, rainwater, and stream water and comparing these to the δD and $\delta^{18}O$ values found in the xylem water of *Ischyrolepis sieberi* plants growing at the study site. The δD values of the collected fog samples were enriched relative to rainwater, stream water, and xylem water from *I. sieberi*, however these differences were not significant. The $\delta^{18}O$ values of the *I. sieberi* xylem water were significantly (p < 0.01) more enriched than rain, stream, and fog water. The xylem water of *I. sieberi* was depleted in δD and enriched in $\delta^{18}O$ relative to all other water sources. The plants therefore did not appear to be utilizing fog during the three months of this study. The $\delta^{18}O$ values of *I. sieberi* were consistently 4-6% enriched compared to rainwater, suggesting that they are utilizing rainwater, which has undergone fractionation due to evaporation in the soil before being taken up by the plants. This study was run during the wet winter months. The δD and $\delta^{18}O$ values from previous data suggest that the *I. sieberi* plants do utilize fog during the dry summer months.

Introduction

The Cape Floristic Region is a highly distinctive phytogeographical unit, recognized as a floral kingdom of its own (Goldblatt 1978). The region which comprises an area of roughly 90 000 km² boasts the highest recorded species density for any temperate or tropical region in the world, with over 9000 species of which at least 69% are endemic (Cowling et al. 1989; Goldblatt and Manning 2000). One of the major attributes of this diversity is that fynbos plant species have a range of anatomical and morphological features, which allow the co-occurance of a number of growth forms with potentially different water usage patterns (Campbell and Werger 1988). It has been found that marked differences in patterns of water stress exist between different fynbos growth forms (Stock et al. 1992). The shallow-rooted restiods and ericoid shrubs exhibit greater water stress during the dry summer months than deeper-rooted proteiod shrubs. Within the fynbos biome, a distinct group of drought tolerant plants is recognized. This group includes mostly restiod and shallow-rooted understorey species, which are able to maintain high stomatal conductances, irrespective of water availability. These plants have been shown to have highly variable seasonal and daily xylem pressure potentials (Miller 1985; Stock et al. 1992). The shallow rooted restiod species make up one of the major families in fynbos and are extremely diverse in habitat (Cowling and Richardson 1995). This high diversity has been ascribed to different habitat and resource use (Haaksma and Linder 2000). The shallow fibrous roots of restiods suggest that their growth is restricted when water is depleted in shallow soil during the driest time of the year (Cowling and Richardson 1995). To supplement the low moisture available in surface soils, many shallow-rooted restiods make use of their architecture to trap dew and mist common to the habitats in which they are growing. The condensed droplets of water then run down the stalks to the base of the plant where it can be absorbed by their shallow roots (Cowling and Richardson 1995).

Ischyrolepis sieberi (Restionaceae) commonly occurs in the Cederberg at altitudes of between 900 and 1400 meters above sea level (Taylor 1996). Ischyrolepis sieberi is a shallow rooted species and is therefore unlikely to be relying on groundwater for its water needs. It is a widespread species occurring from the Richtersveld to Port Elizabeth (Haaksma and Linder 2000). It occurs mostly in the winter rainfall regions of the Western Cape, which is characterized by cool wet winters and hot dry summers. A potential water source available to shallow rooted plants such as Ischyrolepis sieberi growing in these areas is from moisture trapped from mist or clouds. The

importance of fog as a water source for plants has in fact been shown to be significant in many ecosystems around the world (Ingraham and Mathews 1988, 1990, 1995; Dawson 1998). In the Western Cape, Marloth (1904) was probably the first to demonstrate this when he captured substantial amounts of water on Table Mountain simply, by mounting bundles of reeds over the opening of a rain gauge. During misty weather, he caught considerably more water with this gauge, than with an identical one without mounted reeds. He suggested that captured cloud moisture plays an important role for the ecosystems found at altitudes high enough to intercept it, especially during the dry summer months. Another study at Pella in the Western Cape by Moll and Romoff (1983) concluded that *Thamnochortus punctatus*, a shallow-rooted member of the Restionaceae captured sufficient amounts of water from mist to maintain predawn water potentials at midday. This was only achieved in plants of an intermediate age, when their tussocked, funnel shaped habit was at a maximum, ensuring a sufficient surface area to capture mist. They also found that these plants were less stressed than deeper-rooted plants of similar age growing in the same area.

Fog may be particularly important to ecosystems in coastal regions, which receive little or no rainfall each year, or during particular periods when plant demand for water is high (Dawson 1998). A number of studies (Dawson 1998; Ingraham and Mathews 1995) have shown that fog plays an important role in the water relations of the plants growing in coastal redwood (*Sequoia sempervirens*) forests in California. In the New Zealand uplands, Ingraham and Mark (2000) suggested that the interception of fog by the foliage of the dominant tall snow tussock grasses makes a substantial contribution to the water yield from these uplands. Weathers (1999) claimed that although most previous studies demonstrated that occult precipitation could deliver water, nutrients, and pollutants to coastal and montane ecosystems, several ecological questions remained unanswered. For example, do plants actually use cloud or fog water and nutrients and if so, what are the mechanisms? This study thus aims to use stable δD and $\delta^{18}O$ isotopes in order to determine whether fog is utilized as a major water source by the shallow rooted restiod species; *Ischyrolepis sieberi* growing at high altitudes in the Cederberg.

Fog, being an early stage condensate from saturated air, relatively close to the earth's surface, has a higher proportion of the heavy deuterium and oxygen isotopes than rain which is a later stage condensate generally from higher levels in the atmosphere (Ingraham and Mark 2000).

These differences in the stable isotopic compositions of fog and rain have been observed to be consistent and predictable (Ingraham 1998). With this understanding of the isotopic differences between fog and rain, Ingraham and Matthews (1988) proposed that stable isotopes were the best tools available to trace fog water movement into plants and groundwater systems. The water used by plants can come from a number of sources, including soil water, runoff and groundwater. The δD and $\delta^{18}O$ of these waters can be significantly influenced by a number of processes including the type of precipitation, physical processes such as evaporation, the size and extent of the catchment basin contributing to the total source-water pool, the depth of the water table and finally the dissolution characteristics and velocity of water movement in subsurface strata into the groundwater (Dawson 1993). With the exception of salt-excluding species, no fractionation occurs during water uptake by plant roots (Wershaw *et al.* 1966; Zimmerman *et al.* 1966; White *et al.* 1985) so that root water, stem water, and xylem water that have not been subjected to evaporative or metabolic fractionation (Dawson 1993) will reflect the water sources used by any particular species (Dawson 1993). In this way, the analysis of δD in water allows one to trace where plants are obtaining their water (White 1988; Dawson and Ehleringer 1991; Dawson 1993).

The key question being addressed in this study is whether fog or mist is captured by *Ischyrolepis sieberi* to supplement its water needs. This was done by determining the stable hydrogen and oxygen isotope ratios of captured fog, rainwater, and streamwater from the study site and comparing these to the isotopic ratios of the xylem water of *Ischyrolepis sieberi* plants growing at the same site. Previous δD and $\delta^{18} O$ values sampled from the restios suggest that the species relies on rainwater for the majority of its water needs especially during the wet months. This rainwater however does appear to have undergone evaporative fractionation before being taken up by the plants. The primary objective of this study was to determine the extent to which fog is utilized by *Ischyrolepis sieberi* for its water needs. If fog is being used by the plants the δD and $\delta^{18} O$ values of the water extracted from the roots of *Ischyrolepis sieberi* are expected to correspond to the values of the fog, which is predicted to exhibit enrichment in both δD and $\delta^{18} O$ (Ingraham and Mark 2000). Root water is used as it has been shown that no fractionation occurs during water uptake by plants (Wershaw *et al.* 1966; Zimmerman *et al.* 1966; White *et al.* 1985).

Methods

Study site

All water and plant samples were collected from the Welbedacht study site (032 24.515 S 019 10.777 E) in the Cederberg Mountains, Western Cape Province, South Africa (Fig.1). The site is at an altitude of 1330m above sea level. The predominant vegetation type in the Cederberg is mountain fynbos, which is well known for its exceptionally rich flora and high degree of endemism (Hall 1981). The plant community at the study site falls into the *Stoebe aethiopica – Widdringtonia cedarbergensis* community type as defined by Taylor (1996). The structure of the community is defined as open woodland with mid-dense restiod understorey; or low to mid-high, mid-dense restiod shrubland. The predominant species at the site are *Widdringtonia cedarbergensis* and *Ischyrolepis sieberi*. The substrate consists of course sand, gravel and stones over bedrock, often with rock cover of over 50%. The average annual rainfall at the site is approximately 480mm (2000-2004).

Data collection

Rain and fog collectors were placed at the study site at the beginning of June 2004. Rain was collected in a 1 litre glass bottle with a funnel attached while fog was collected using a purpose built collector. The fog collector was designed to collect deposition only in the vertical plane. It consisted of a 500mm x 500mm metal frame to which was attached a fine nylon mesh screen providing a collecting surface of $0.25m^2$. A gutter made from pvc piping was placed beneath the screen to collect the droplets and divert the water into a 2.51 collecting bottle. The collector was erected 0.5m above the ground and was orientated to face downslope to intercept the prevailing wind. A tin roof was constructed over the collector to minimize the admixture of rain. Two replicate samples of collected rainwater, captured fog, and water from a nearby stream were collected in vacutainers at the end of June, July and August 2004. Due to the rocky nature of the study site, we were unable to obtain soil samples for water extraction. The vacutainers were filled to a maximum and sealed with parafilm to ensure that no evaporation occurred after collection. A layer of silicon oil was placed in the containers used for rain and fog collection to ensure that no evaporation occurred from collected water samples. Two samples of *Ischyrolepis sieberi* roots were collected at each collection; these samples were placed in Kimax tubes, sealed with parafilm

and frozen upon return from the field. Rainfall and temperature data were obtained from an automatic weather station installed at the site.

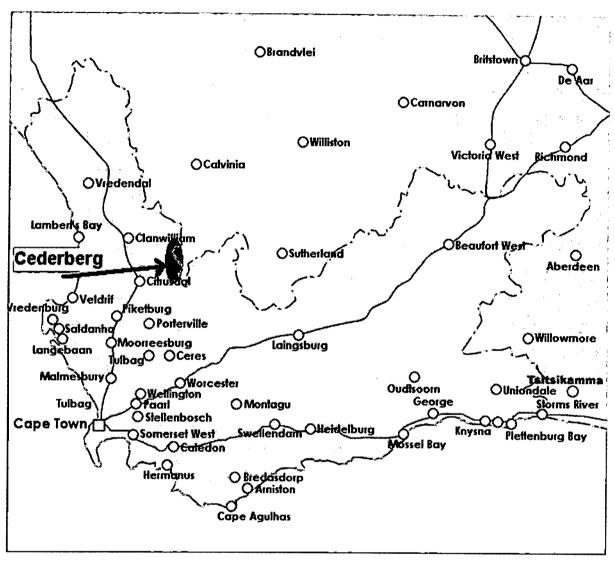


Fig.1. Map showing the location of the Cederberg in the Western Cape, South Africa.

Isotope sampling

Stable hydrogen and oxygen isotope analyses were performed on water collected from fog, rainfall, stream water and *Ischyrolepis sieberi* xylem water, which was extracted from root samples using cryogenic vacuum distillation (Dawson 1996). Oxygen isotopes were extracted using the CO₂ equilibrium method (Socki *et al.* 1992). This involved injecting 1.5 ml of the water sampled into 7 ml Vacutainers® prefilled with 500 mbars CO₂. The Vacutainers® were then placed in a

Results

The total rainfall (Fig.2) for the three months of the study was consistently below the long-term average. The total rainfall in August was nearly half of that from the previous two months, The amount of fog captured each month (Fig.3) increased slightly over the three months with the maximum (1500 mm)caught in August. The amounts of fog caught each month correspond with data provided by the South African Weather Service (SAWS) (Fig.3). These data show August to have had almost twice as many (15) fog days as June and July (9) in Cape Town. Fog is most frequent during the autumn and winter months (March-August) in Cape Town (Fig.4). The majority of annual rainfall at the site falls in the winter months (Fig.4), while the months preceding these experience the highest number of fog days.

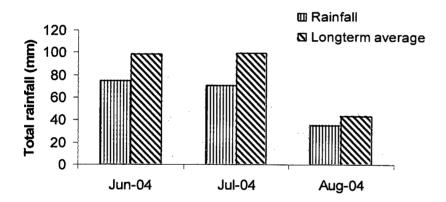


Fig.2. Total monthly rainfall for the three months of the study period, and the longterm average for June July and August at the study site.

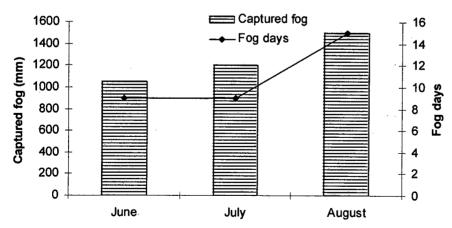


Fig.3. Total fog captured by the fog collector during each of the three months of the study period. The total number of fog days recorded in Cape Town by the SAWS during each month of the study have also been plotted.

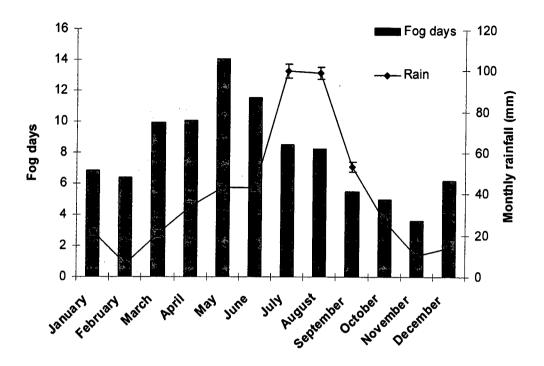


Fig.4. The mean number of fog days (1992-2004) experienced each month in Cape Town and the mean monthly rainfall (±SE;1999-2004) at the study site. Fog data was provided by the SAWS.

The δD and $\delta^{18}O$ values of each water source sampled each month (Fig.5) shows the $\delta^{18}O$ values of the fog to be slightly enriched relative to the rain and stream water. This enrichment was most pronounced in July when the fog was over 3% heavier than the rain and stream water. The $\delta^{18}O$ values of the xylem water extracted from *Ischyrolepis sieberi* were much more positive (4-6%) than all three water types during June and August; however during July they were slightly more negative (-6% $\delta^{18}O$) than the fog (-4% $\delta^{18}O$). The δD values showed a completely different pattern, whereby the fog values were enriched in deuterium (6-10%) relative to both the rain and stream water for all three months. The fog δD values also showed a steady increase over the three months from -32% δD to -18% δD . The δD values of *Ischyrolepis sieberi* were similar to the rain and stream water during June. The δD values of *Ischyrolepis sieberi* from July and August were more negative (8-20%) then the fog, rain and stream water.

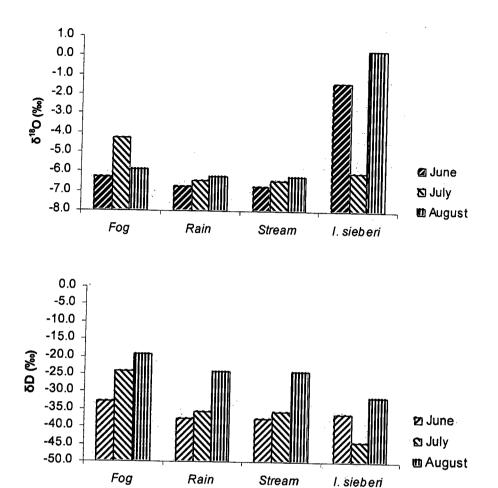


Fig.5. The δD and $\delta^{18}O$ values of the fog, rain, stream and xylem water sampled during June, July and August. Each bar is the average of two replicates sampled each month.

The local meteoric water line for the Cederberg formed the equation y = 7.7302x + 4.7387 (Fig.6). The δD and $\delta^{18}O$ values of the fog samples fell slightly above both the local and global meteoric water lines (Fig.6). The δD and $\delta^{18}O$ values of the *Ischyrolepis sieberi* plants sampled during this study fell below both the LMWL and GMWL.

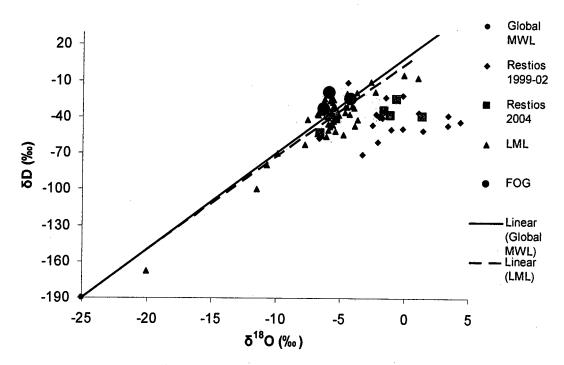


Fig.6. Fog and restio δD and $\delta^{18}O$ values. Large squares show restio values taken from this study, while diamonds show values taken from previous data. Circles show fog values for the three months of this study. The solid line shows the GMWL while the dashed line shows the LMWL being the trendline of all rain and stream δD and $\delta^{18}O$ values taken from the site.

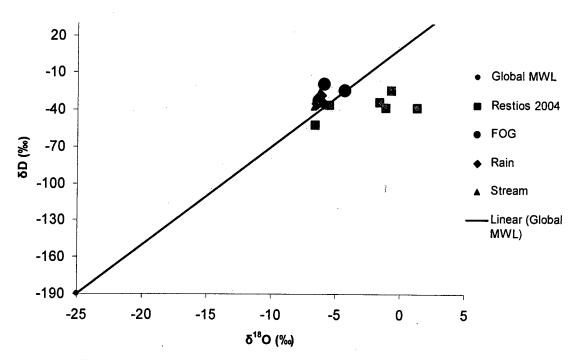


Fig.7. δD and $\delta^{18}O$ values for fog, rain, stream and *I. sieberi* xylem water samples from June-August 2004. The GMWL has been included for comparison.

The δD and $\delta^{18}O$ values of the fog samples from June and July fell very close to the GMWL, however the values from August showed substantial enrichment in δD relative to the previous two months (Fig.7). The LMWL calculated from all the δD and $\delta^{18}O$ values of meteoric water from the study site falls slightly below the GMWL. The *Ischyrolepis sieberi* δD and $\delta^{18}O$ values were consistently enriched in $\delta^{18}O$ but depleted in δD , relative to rain, stream and fog values. Analysis of variance (ANOVA) analyses of δD and $\delta^{18}O$ values from the four sampled water types (fog, rain, stream, and *Ischyrolepis sieberi* xylem water) showed no significant differences in δD values (Fig.8) between the four water types. ANOVA comparisons of $\delta^{18}O$ values showed significant (p < 0.01) enrichment in $\delta^{18}O$ of *Ischyrolepis sieberi* xylem water compared to fog, rain and stream water (Fig.9).

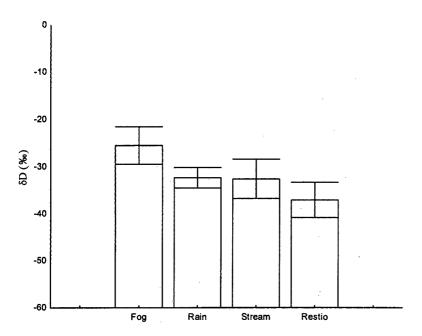


Fig.8. Mean δD values ($\pm SE$) for each water source sampled during the study period. There were no significant differences between any of the groups (ANOVA).

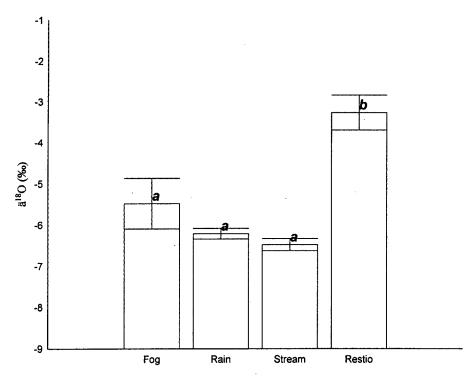


Fig.9. Mean δ^{18} O values (±SE) for the four water sources sampled in the three months of this study. There were no significant differences between (a), however differences between (a) and (b) were significant (ANOVA, Tukey HSD test, p < 0.01).

 δD (‰) The mean δD and $\delta^{18}O$ values for the xylem water of *Ischyrolepis sieberi* (Fig.10) shows a general trend of enrichment during the spring and summer months (between -0.5‰ and 0.5‰ in $\delta^{18}O$ and between -42‰ and -34‰ in δD), while the values are more negative during the autumn and winter months (approximately -2.5‰ in $\delta^{18}O$ and -52‰ in δD). The δD values during winter (June-August) were an exception in that they were enriched relative to the $\delta^{18}O$ values. The mean $\delta^{18}O$ and δD ratios of all *Ischyrolepis sieberi* samples were plotted against the corresponding rainfall from that season (Fig.11). The $\delta^{18}O$ values from the restios show a distinct enrichment (3-6‰) in all seasons, while the δD values can be seen to be very similar to the rainfall in all seasons.

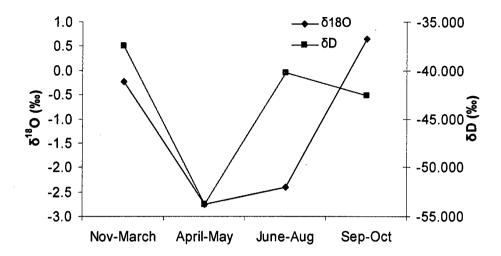
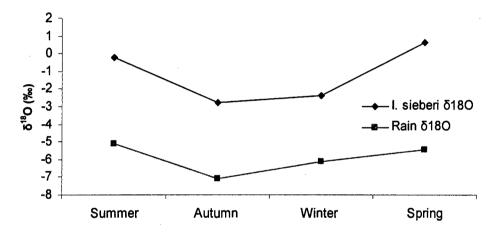


Fig. 10. Mean δD and $\delta^{18}O$ values of *lschyrolepis sieberi* xylem water sampled during the different seasons of the year.



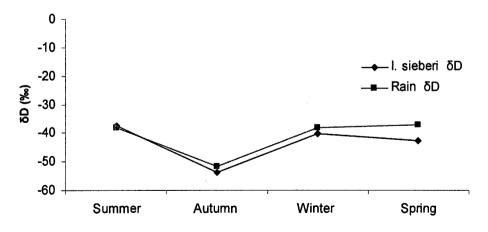


Fig.11. The mean δ^{18} O and δD values of *Ischyrolepis sieberi* and rainfall sampled in each season. Seasons were divided as summer being November to March, autumn being April and May, Winter being June to August and spring being September and October.

Discussion

The primary objective of this study is to determine if the shallow rooted restiod species, *Ischyrolepis sieberi*, growing at high altitudes in the Cederberg captures fog and to what extent this fog is utilized as a water source for the plants. In order to answer this we first need to determine if fog occurs at the site and if so, how frequently? The higher rainfall in June and July corresponds to more negative δD and $\delta^{18}O$ values for the fog samples from these two months. This is possibly because of higher cloud cover during these months, which would increase the amount of cloud moisture as apposed to coastal fog caught by the fog collector. The number of fog days measured in Cape Town shows that June and July experienced considerably less fog than August. The δD and $\delta^{18}O$ values of the fog samples from August were enriched in both deuterium and $\delta^{18}O$ compared to the previous two months, these values being closer to the expected values of coastal fog as found in other studies (Ingraham and Matthews 1990, 1995).

The higher volume of fog captured, higher number of fog days measured in Cape Town and lower amount of rainfall all suggest that the fog captured during August was predominantly coastal fog and therefore more enriched then the previous two months. The quantities of fog captured during this study were not as high as studies such as Marloth's (1904) who captured nearly 2000 mm of moisture in fifty-six days using a gauge fitted with reeds on Table Mountain and Dawson's (1998) who reported collecting at least 59mm per day in a collector half the size of this study. However, the results from this study do suggest that a substantial amount of fog or mist does occur at the study site (±50 ml/day/0.25 m²) suggesting that fog is a potential water source for the plants growing at the site.

A previous study by Moll and Romoff (1983) established that another shallow rooted restiod species, *Thamnochortus punctatus*, does capture fog to supplement its water needs. It is therefore very likely that *Ischyrolepis sieberi*, which has the same restiod architecture, is able to intercept fog or mist. If *Ischyrolepis sieberi* does use fog as a water source, the deuterium and oxygen ratios in their xylem water should be similar to those of the collected fog, which are expected to be enriched in the heavier deuterium and oxygen isotopes (Ingraham and Mark (2000).

Although the fog values were slightly enriched in both D and 18 O values each month, the magnitude of this difference was much lower than similar studies in other parts of the world (Ingraham and Matthews 1988, 1990,1995; Ingraham and Mark 2000). The measured δD and δ^{18} O values of coastal fog formed from a similar upwelling system to the West Coast in California by

Ingraham and Matthews (1995) were enriched relative to the values found in this study. The stable isotope compositions of the collected fog water from California ranged from -15.6 to -9 ‰ in δ D and -2.9 to -2‰ in δ^{18} O. The fog was also consistently more enriched then the rain, which ranged from -43 to -30‰ in δ D and from -7.6 to -5.8 2‰ in δ^{18} O. The isotope values from this study also showed much more variation from -6.3 to -4.3‰ in δ^{18} O and -32.9 to -19.4 ‰ in δ D compared to the Californian study. However, the values from the Californian study were from summer fog, while those of this study were from winter fog. This could partially explain the differences in isotopic ratios between the two studies.

Although the differences in δD and $\delta^{18}O$ values between fog and rainwater were not significant, the fog was more enriched in both isotopes compared to the rainwater. However, the δD values of the *Ischyrolepis sieberi* xylem water were more negative (10-15‰) than both rain and fog values. The $\delta^{18}O$ values of *I. sieberi* were significantly more enriched than rain, stream and fog water (2-3‰). The heavier deuterium and oxygen isotopes therefore appear to be fractionating in opposite directions within the xylem of the restios. The isotopic ratios of the *Ischyrolepis sieberi* xylem water therefore do not directly correspond to any of the available water sources. Because the plants were sampled from a rocky ledge on top of a big rocky outcrop, it was also highly unlikely that the plants had access to groundwater.

The δD and $\delta^{18}O$ values found in the xylem water of *I. sieberi* during this study suggest that the plants are utilizing rainwater, which has undergone some fractionation, most likely during evaporation in the shallow soil layer. The basis for evaporative enrichment in the heavier isotopes has been explained by Friedman *et al.* (1964). The vapor pressures of the different isotopic molecules of water are inversely proportional to their masses. Therefore, ${}^{1}H_{2}{}^{16}O$ has a significantly higher vapor pressure than ${}^{2}H_{2}{}^{18}O$. For this reason, water vapor formed by evaporation of liquid water is enriched in ${}^{16}O$ and ${}^{1}H$ while the remaining water is enriched in ${}^{18}O$ and Deuterium (Friedman *et al.* 1964). The comparisons of rainwater and *I. sieberi* water (Fig.12) shows the $\delta^{18}O$ values of the *I. sieberi* samples to be consistently 4-6‰ more enriched than rainwater. The δD values on the other hand are consistently very similar in both *I. sieberi* and the rainwater samples. This is supported by the ANOVA analyses, which showed no significant differences in δD between all water samples, however the $\delta^{18}O$ values of the *I. sieberi* samples were significantly enriched compared to fog, rain, and stream water.

When the *I. sieberi* water samples were divided into seasons and compared there appears to be a seasonal difference in both δD and $\delta^{18}O$ values of the xylem water. The trend shows enrichment in both δD and $\delta^{18}O$ during the dry months (September – March), the values then decrease during the winter months (April – August). The enrichment in isotopic ratios would correspond to periods when the plant would be most likely to be utilizing fog as a water source. During the winter months, the plants are unlikely to be limited by water and therefore would not need to utilize fog.

Conclusion

The results of this study show that fog does occur at the study site, however it is unclear if this fog constitutes coastal fog or moisture from low clouds. The composition of the collected fog is most likely to be a mixture of the two occult precipitation types. The δD and $\delta^{18}O$ values of the collected fog were enriched relative to both rainwater and stream water. However, the magnitude of this enrichment was low compared to areas such as California, which experiences similar coastal fog. The similar isotopic ratios found in the collected fog and rainwater could either be because of contamination by rainwater or due to a higher degree of cloud moisture than coastal fog being captured by the fog collector. The isotopic ratios of the water extracted from I. sieberi roots did not correspond to the ratios of fog, rain, or stream water sampled during this study. The $\delta^{18}\text{O}$ values of I. sieberi were consistently 4-6% enriched compared to rainwater, suggesting that they are utilizing rainwater, which has undergone fractionation due to evaporation in the soil before being taken up by the plants. The δD values of *I. sieberi* were similar to fog, rain and stream water samples throughout the study. The results of this study therefore suggest that I. sieberi did not utilize fog water during the three winter months of this study. However, the δD and $\delta^{18}O$ ratios of *I. sieberi* sampled during the dry season are more enriched than the wet season suggesting that fog could play a more important role as a water source for the plants during the dry season. This study would need to be continued throughout the dry season in order to determine if fog plays a more important role in the water relations of *I. sieberi* during the dry summer months.

Acknowledgements

I thank Ed February for his help with conceptualizing and implementing the study. Thanks to Matthew Britton for his help in building and erecting the fog collector and collection of samples. Thanks to Cape Nature Conservation for allowing the study to be performed in the Cederberg Wilderness Area. Thanks to the South African Weather Service for their provision of fog data.

References

- Cambell B.M. and Werger M.J.A. 1988. Plant form in the mountains of the Cape, South Africa. Vegetatio 43: 43-47.
- Coleman M.L., Shepard T.J., Durham J.J., Rouse J.E. and Moore G.R. 1982. Reduction of water with zinc for hydrogen isotope analysis. Analytical Chemistry 54: 993-995.
- Cowling R.M., Russel G., Hoffman M.T. and Hilton-Taylor C. 1989. Patterns of plant species diversity in sourthern Africa. In Huntley B.J. (ed). Biotic Diversity in Southern Africa. Concepts and Conservation. Oxford University Press, Cape Town.
- Cowling R.M and Richardson D. 1995. Fynbos South Africa's Unique Floral Kingdom. Institute for Plant Conservation, Cape Town.
- Dansgaard W. 1964. Stable isotopes in precipitation. Tellus XVI 4: 436-468.
- Dawson T.E. 1993. Water sources of plants as determined from xylem-water isotopic composition: perspectives on plant competition, distribution, and water relations. In Ehleringer J.R., Hall A.E. and Farquhar G.D. (eds). Stable Isotopes and Plant Carbon-Water Relations.

 Academic Press, Inc. San Diego.
- Dawson T.E. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117: 476-485.
- Dugan J.P., Borthwick J., Harmon R.S., Gagnier M.A., Glahn J.E., Kinsel E.P., Macleod S., Viglino J.A. and Hess J.W. 1985. Guanidine hydrochloride method for determination of water oxygen isotope ratios and the oxygen-18 fractionation factor between carbon dioxide and water at 25°C. Analytical Chemistry 57: 1734-1736.
- Ehleringer J.R., Phillips S.L., Schuster W.S.F. and Sandquist D.R. 1991. Differential utilization of summer rains by desert plants. Oecologia 88: 430-434.
- Friedman I., Redfield A.C., Schoen A. and Harris J. 1964. The variation of deuterium content of natural waters in the hydrological cycle. Reviews of Geophysiology 2: 177-224.

- Goldblatt P. 1978. An analysis of the flora of Sorthern Africa: its characteristics, relationships, and origins. Annals of the Missouri Botanical Garden 65: 369-436.
- Goldblatt P. and Manning J. 2000. Cape Plants: A conspectus of the Cape Flora of South Africa.

 National Botanical Institute and Missouri Botanical Garden, Cape Town.
- Gonfiantini R. and Longinelli A. 1962. Oxygen isotope compositions of fog and rains from the North Atlantic. Experientia 18: 222-223.
- Hall A.V. 1981. Fynbos handle with care. SAPPEX Newsletter 31.
- Haaksma E.D. and Linder H.P. 2000. Restios of the Fynbos. Botanical Society of South Africa, Cape Town.
- Ingraham N.L. 1998. Isotopic variations in precipitation. In Kendell C. and McDonald J.L. (eds). Isotopic Tracers in Catchment Hydrology pp.87-118. Elsevier, Amsterdam.
- Ingraham N.L. and Matthews R.A. 1988. Fog drip as a source of groundwater recharge in Northern Kenya. Water Resources Research 24(8): 1406-1410.
- Ingraham N.L. and Matthews R.A. 1990. a stable isotope study of fog: the Point Reyes Peninsula, California, U.S.A. Chemical Geology 80:281-290.
- Ingraham N.L. and Matthews R.A. 1995. The importance of fog-drip water to vegetation: Point Reyes Peninsula, California. Journal of Hydrology 164: 269-285.
- Ingraham N.L. and Mark A.F. 2000. Isotopic assessment of the hydrologic importance of fog deposition on tall snow tussock grass on southern New Zealand uplands. Austral Ecology 25: 402-408.
- Marloth R. 1904. Results of experiments on Table Mountain for ascertaining the amount of moisture deposited from the south east clouds. Transactions of the South African Philosophical Society 14: 403.
- Miller J.M. 1985. Plant water relations along a rainfall gradient, between the succulent karoo and mesic mountain fynbos, in the Cederberg Mountains near Clanwilliam, South Africa. MSc thesis, University of Cape Town.
- Moll E.J. and Romoff N. 1983. Evidence of mist trapping by *Thamnochortus punctatus* at Pella in the southwestern Cape Province. South African Journal of Science 79:432.
- Redwine J.C. and Howell J.R. 2002. Geochemical methods for distinguishing surface water from groundwater in the Knox Aquifer System. Environmental Geology 42: 485-491.

- Socki R.A., Karlsson H.R. and Gibson E.K. 1992. Extraction technique for the determination of oxygen-18 in water using pre-evacuated glass vials. Analytical Chemistry 64: 829-831.
- Stock W.D., van der Heyden F. and Lewis O.A.M. 1992. Plant structure and function. In Cowling (ed). The Ecology of Fynbos, Nutrients, Fire and Diversity. Oxford University Press, Cape Town.
- Taylor H.C. 1996. Cederberg vegetation and flora. National Botanical Institute, Pretoria.
- Weathers K.C. 1999. The importance of cloud and fog in the maintenance of ecosystems. Trends in Ecology and Evolution 14(6): 214-215.