# SOIL DRYING CYCLES IN THE SUCCULENT KAROO:
# DIFFERENT ROOTING SYSTEMS AND WATER UPTAKE

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# ABSTRACT

In the semi-arid Succulent Karoo water is one of the most limiting resources, and plants that survive in the area require competitive water-use strategies suited to long periods of drought. Over the years much emphasis has been put on mechanisms that allow for the competitive success of water-use strategies, and root structure features as an important attribute. This study investigated soil drying cycles in the semi-arid Succulent Karoo. It measured the rates at which soil water was depleted at two different depths in five different microhabitats, and investigated whether these are related to different rooting systems. Three prevalent plant species in the region were used, namely *Leipoldtia schultzei* of the Mesembryanthemaceae, *Tripteris sinuata* of the Asteraceae, and *Galenia africana* of the Aizoaceae, all of which have their roots in the upper 20cm of soil. However, *Leipoldtia's* roots are concentrated in the top 5cm of soil, while the other two species root mainly at depths between 10 and 20cm. This vertical separation of roots provided the opportunity to relate soil water depletion at two different depths (0-10cm and 10-20cm) to the different rooting strategies, and explore what this means in terms of compatibility between close neighbours and seedling establishment under adult plants. The shallow-rooting *Leipoldtia* showed the highest rates of soil moisture depletion in both the shallow and deeper soil zones, and is therefore a strong competitor for water and probably an undesireable neighbour. Soils at both depths below *Tripteris* plants maintained the highest moisture content over the 2-week period of sampling, suggesting it to be favourable site for seedling establishment. *Galenia* showed intermediate soil-drying effects in the upper 0-10cm, but high rates of moisture depletion at 10-20cm below the surface, suggesting that it may be a suitable neighbour for shallow-rooting species but not for other deeper-rooting species. Additionally, the two sampling methods - electronic probe readings and gravimetric analysis - were examined. The two methods correlated fairly well to each other ($R^2 = 0.759 \pm 0.002$), although the probe readings were consistently higher and showed greater variation (probe SD = 2.8 as opposed to gravimetric SD = 1.2)

## INTRODUCTION

A common feature of plant communities in arid and semi-arid areas is that they are structured by competition (Yeaton 1990), indicated both by patterns of spacing as well as differentiation in rooting depth (Cody 1986). In the study by Cody (1986) on spacing patterns in Mojave Desert plant communities, species are shown to have either 'preferred' neighbours or 'avoided' neighbours. The hypothesized mechanism of differential compatibility of root systems and specificity of germination sites is regarded to be of importance in the maintenance of diversity of desert shrubs. Other studies in the Namib desert (Yeaton 1990) and the Sonoran semi-desert (Nobel 1997) support the hypothesis that vertical separation of root systems should facilitate co-existence of different species in semi-deserts. In

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context of the three shrubs in my study - *Leipoldtia schultzei, Tripteris sinuata* and *Galenia africana* - a closer look at their rooting systems and successional life histories led to tentative predictions of ~~on~~ their respective water use strategies and compatibilities for co-existence.

The competition among co-existing species in semi-arid areas such as the Succulent Karoo is likely to be largely for water. At the study site near Paulshoek, Northern Cape, water is supplied in small amounts. According to long-term rainfall data for the nearby town of Springbok, rainfall incidents of <10 mm account for 81% of the rainfall events and 42% of the total rainfall over the last century. Apparently well-suited to fairly superficial percolation of water, the bulk of root biomass in the Strandveld is ~~are~~ concentrated in the upper 30cm of soil (Esler et al. 2002), while this study deals with plants whose roots occur in the upper 20cm of soil. *Leipoldtia* has its roots in the top 10cm of soil and qualifies as being 'shallow-rooted', while *Tripteris* and *Galenia,* are 'deeper-rooted' species, having the bulk of their root masses in the 10-20 cm zone (Carrick 2001). Bare areas in the study site were also sampled, in order to examine drying cycles in soils not immediately underneath plants. These so-called gaps contained shallow roots from nearby mesembs, but were not shaded nor affected in any other way by the immediate presence of plants. A final treatment was root-trenched gaps. These provided sites whose soil moisture was not subjected to any influence from plants, thereby acting as controls to assess to what extent the soils were dried by physical processes such as evaporation and drainage.

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No, some plants have roots to 30cm

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*Leipoldtia schultzei* is a late-successional, shallow-rooted succulent that frequently occurs in the area, and especially in the least degraded communities. As is typical of mesembs, its roots are concentrated in the top 5cm of soil, forming a dense web in this soil layer and with very few roots extending below 10cm (Carrick 2001). Mesembs are understood to dominate over the other shrubs in the area as a result of the combination of shallower roots together with their active growth during winter, which is when most of the rain falls (Esler et al. 1999). Mesembs frequently co-exist with deeper-rooted shrubs, and predominantly with asteraceous species such as *Tripteris*. Given that it is the top soil layer which is most regularly percolated by the small rainfall events (<10 mm), typical in the Succulent Karoo, plants with shallow roots are most likely to benefit greatest in such an area. Furthermore, we may predict that roots in the top 5 cm are likely to take up most of the water provided by small showers, such that neighbouring plants with deeper roots do not receive much of the moisture, unless the events are larger or occur in close succession. This idea has been supported by experiments by Sala et al. (1989), that indicated that it is possible for shallow-rooted grasses to reduce availability of resources to deeper-rooted shrubs in semi-arid systems. In ~~contradiction to this,~~ converse Carrick (2001) found that the impact of shallow-rooted species such as *Leipoldtia* on a deeper-rooted species, *Hirpicium alienatum,* "appears negligible", and that there is "only weak and restricted evidence for competition" between the species. A possible explanation that rules out any significant competitive effect of mesemb roots for water is that very shallow infiltration of water is lost fairly rapidly by evaporation, even in the absence of mesembs. Nonetheless, at the outset of this study, we predicted that the presence of mesemb roots depletes water from the shallow soil faster than if the roots are absent, and that microhabitats with active shallow roots but without shade from

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better to state reasons than quote from conclusions above-soil plant structures, have the highest rates of water depletion. Such findings would have implications for seedling establishment below mesembs, since possibly the greatest potential competition for underground resources occurs soon after germination, and it is at this stage that rooting systems of deeper-rooted shrubs overlap vertically with those of the mesembs.

*Tripteris sinuata* and *Galenia africana* are non-succulent shrubs whose roots grow noticeably deeper than those of the Mesembryanthemaceae, and clearly fall into a different functional group. Since they are non-succulent, they are limited in their ability to store water, and thus need access to larger and more permanent pools of water than the mesembs. Such pools are only available at greater soil depths, where they are not depleted as rapidly by evaporation as those closer to the surface (Carrick 2001). Both *Tripteris* and *Galenia* have similar rooting depths; however, they show different successional life histories. *Galenia* - an early successional species - is the only shrub to occur in large numbers in the most degraded areas (Carrick 2001). This may imply that it is well adapted to establishing and growing in microhabitats too hostile for other species, but also that it may be outcompeted for limiting resources when growing close to other plants. *Tripteris*, on the other hand, is a late successional species, which may indicate a greater ability to compete for limiting resources. In this study it was therefore expected that the deeper soil region beneath *Tripteris* would show more rapid drying than that under *Galenia*.

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Measuring soil water content in association with the different plant types contributes to our understanding of the roles played by the relevant species in utilising and depleting this limiting resource.

distinct
functional groups

Since two different methods for measuring the soil moisture were used, it provided an opportunity to compare the two methods. A number of different techniques can be used, as described in detail by Rundel and Jarrell ( in Pearcy et.al. 1991) and Rawlins (in Kozlowski 1976). The two used in this study are gravimetric analysis and direct measurement with an electronic probe.

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Gravimetric water content is the mass of water in a unit mass of dry soil (Pearcy et.al. 1991). Water content is gauged from core samples of soil, which requires many samples obtained at each depth - a labour intensive procedure which causes considerable disturbance to the soil (Pearcy et.al. 1991; Kramer and Boyer 1995). It is however a popular method because it is both simple and reliable, and has been used by numerous researchers (e.g.Carrick 2001; and Vasek and Lund 1980).

why?

The probe is an easy-to-use portable instrument whose four metal rods are simply pushed into the soil, and the reading taken. It measures volumetric soil moisture content by converting changes in the apparent dielectric constant into a DC voltage, which is virtually proportional to soil moisture content. It is a portable, user-friendly device, but requires accurate installation prior to being used. Its accuracy can be affected by variations in soil density and composition, stones close to the rods, roots, and holes caused by soil organisms (User Manual 1999, Delta-T Devices Ltd, Cambridge).

## METHODS

### *Study site*

The study site is situated close to the Paulshoek village, and is typical of moderately browsed shrubland, defined by Acocks (1988) as Namaqualand broken veld. Eight plants of each of the three species (*Leipoldtia, Galenia* and *Tripteris*) were chosen and labeled; the replicates for each species chosen to be of similar size. Next, sixteen gaps were chosen, of which eight were randomly assigned to be root-trenched. The gaps consisted of areas approximately 1m$^2$ in size, which had shallow-rooted mesembs around the periphery. The eight untrenched gaps are referred to as 'rooted gaps' since they contained active roots from the surrounding mesembs. The 'open gaps' were trenched with a shovel around the edges to a depth of 20cm, so as to cut off any roots from nearby plants and thereby provide a plot devoid of any active roots. Thus the five microhabitats we used in the study were, the upper 20cm (divided into two 10cm zones) underneath each of *Leipoldtia* (LS), *Galenia* (GA) and *Tripteris* (TS), as well as the upper 20cm of open gaps (OG) and rooted gaps (RG).

### *Soil water measurements*

The first day of sampling occurred eleven days after the last rainfall event of 20mm. Within the twelve days prior to this, two substantial rainfall events of 20mm and 17mm had already wet the ground considerably, and we assume that after the last rain the soil had reached field capacity. The open gaps were root-trenched one day prior to sampling, in other words ten days after the last rainfall event. The soil at the study site has been classified as sandy-loam ~~across the upper 20cm~~ (Carrick 2001).

why assume why not check?

Two methods were used to measure soil moisture, and both used in analyses. Sampling was done as close as possible to the base of the plants, below the canopies. The first measure was made with the probe ('ThetaProbe' soil moisture sensor type ML2x; set to Soil type 1 and field capacity of 0.38m$^3$m$^{-3}$), which gave an instant reading for volumetric water content. Then a hollow stainless steel tube (45mm diameter; 3mm walls) was hammered into the same patch of soil, and a 10cm core removed. The soil was thoroughly mixed and a subsample immediately placed in a paper bag and sealed in a second plastic bag to prevent loss of moisture to the air. The same was repeated for the subsequent 10 to 20cm zone. The entire procedure was carried out for eight replicates of each of the five microhabitats, for a total of five days at three-day intervals. Since core sampling disturbs the soil, we took samples from different sides around each plant on subsequent days to avoid sampling a patch that had been affected by earlier coring. The first days' work was done on the South side, then moving to East, West, North, and finally North-West on the following days. Samples were weighed the same evening to get initial wet mass. On completion of all the fieldwork, the samples were oven-dried in their paper bags at 70°C over 2½ days and re-weighed to get dry mass. Masses of the paper and plastic bags were subtracted from the initial wet samples, and paper bag masses from the dried ones.

### *Analyses*

Gravimetric water content was calculated as (wet mass – dry mass) / dry mass x 100, expressed in percent. Mean soil water content for each microhabitat and for both gravimetric and probe readings were plotted for the consecutive sampling days, ~~using Microsoft~~ Excel. The eight replicates for each treatment were also plotted to examine variation among the replicates.

The probe readings were plotted against the gravimetric results to assess how closely they match each other. This was done for 1) all measurements together, across both depths, all days, and all microhabitats; 2) all 0-10cm readings; 3) all 10-20cm readings; and 4) separately for each microhabitat but considering both depths together. why not for each microhabitat at each depth since this is the basic unit of comparison?

An analysis of co-variance (ANCOVA) was run using the SAS system for Windows (version 8.02; SAS Institute Inc. 2001, USA) to analyse for variation between rates of soil-drying observed in the different microhabitats.

Since the two possible factors causing change in soil moisture were time (number of days after rain) and microhabitat, the ANCOVA initially contained the time x microhabitat interaction to ascertain whether water content in the various microhabitats changed *differently* over time. Since this was not significant in any case, and since the rate at which soil moisture was depleted over time was linear, a simple ANCOVA was performed for each microhabitat at each depth. This ANCOVA functions essentially as a comparison of linear regressions, thereby comparing soil-drying rates in the microhabitats.

## RESULTS

Appendix 1 gives all the soil moisture data as measured with (a) the probe and (b) gravimetrically.

Table 1. Codes used for the microhabitats sampled.

| Code | Microhabitat |
|---|---|
| LS | underneath *Leipoldtia schultzei* |
| TS | underneath *Tripteris sinuata* |
| GA | underneath *Galenia africana* |
| OG | Open gap (root-trenched; no active roots) |
| RG | Rooted gap (contains active roots) |

Figures 1(a) – (d) show mean soil water contents in each microhabitat. Comparisons of the graphs reveal that there is greater variation among the microhabitats in the 0-10cm zone than at 10-20cm. In the 0-10cm zone zone, TS and OG show highest soil moisture, while LS shows the lowest. Corresponding results are indicated by comparisons of least squares means, given in Table 2.1. In the deeper zone less

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variation is apparent, with TS showing the wettest soil and GA the driest. However the overall range only covers about 1%, while in the 0-10cm region the wettest microhabitat contains 2.5% more water than the driest one.

So this refers to probe measures in table 2

No 1(c) 1(d)

The gravimetric measurements from the core samples show similar trends to the probe readings (Figures 1.3 and 1.4). In the shallow zone OG and TS lie closely on the wetter end while LS is clearly the driest. Once again this is supported by the least squares means figures ~~in~~ Table 2.3. In the 10-20cm zone the gravimetric measures also show less variation between microhabitats, with a range of 0.2% compared with a range of about 1% for the 0-10cm figures measures. TS once again shows the highest moisture content, and LS the lowest (Table 2.4).

Table 2.1 Least squares means for (a) probe 0-10cm, (b) gravimetric 0-10cm, ~~(c) probe~~ 10-20cm, and (d) gravimetric 10-20cm readings. The values are percentages; probe readings are volumetric.

| (a) Probe 0-10cm | |
|---|---|
| Microhabitat | LSM |
| LS | 6.30 |
| TS | 8.47 |
| GA | 7.06 |
| OG | 8.78 |
| RG | 7.90 |
| (b) Gravimetric 0-10cm | |
| LS | 4.01 |
| TS | 4.97 |
| GA | 4.58 |
| OG | 4.76 |
| RG | 4.62 |
| (c) Probe 10-20cm | |
| LS | 9.64 |
| TS | 10.34 |
| GA | 9.30 |
| OG | 10.21 |
| RG | 10.23 |
| (d) Gravimetric 10-20cm | |
| LS | 5.03 |
| TS | 5.21 |
| GA | 5.01 |
| OG | 5.27 |
| RG | 5.18 |

Separate tests of the two sources of variation (time and microhabitat) with an analysis of covariance (ANCOVA) show that both time (at intervals of three days, i.e. categorical data) and type of microhabitat contribute significantly to changes in soil moisture levels for both sampling methods and at both depths, except for the 10-20cm gravimetric measures. The 10-20cm probe readings are only barely significant. Tests for the interaction between the two sources show that there is no interaction (Table 3), in other words that they co-vary in their soil-drying effects. From Table 3 it is also evident that microhabitat is a significant cause of variation in soil moisture for the probe 0-10 and 10-20cm readings, and the gravimetric 0-10cm readings, but not for the gravimetric 10-20cm values.

Repetition

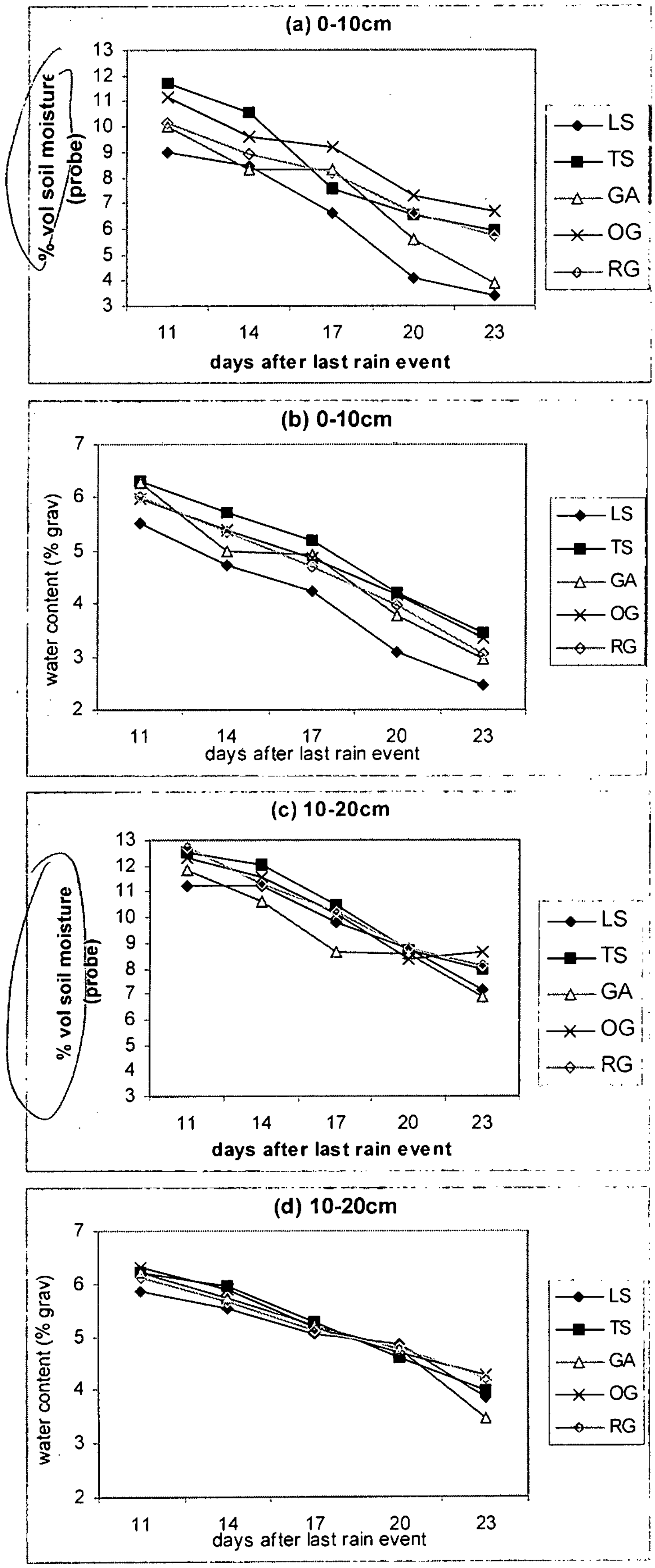

Figure 1. Mean soil moistures in the various microhabitats, at 0-10cm for (a) the probe and (b) gravimetric; and at 10-20cm for (c) the probe and (d) gravimetric.

Table 3. ANCOVA results showing levels of significance of the two sources causing variation in soil moisture at the two depths as measured with the probe and gravimetrically, as well as significance of the interaction of the two sources. M = measure used; DF = degrees of freedom; SS = sum of squares; mcrhbt = microhabitat; P0-10 = probe at 0-10cm; P10-20 = probe at 10-20cm; G0-10 = gravimetric sample at 0-10cm; G10-20 = gravimetric sample at 10-20cm.

| M | Source | DF | Type I SS | Mean Square | F value | P |
|---|---|---|---|---|---|---|
| P0-10 | mcrhbt | 4 | 166.35 | 41.59 | 18.10 | <.0001 |
| | time | 1 | 748.84 | 748.84 | 325.86 | <.0001 |
| | mcrhbt*time | 4 | 16.01 | 4.00 | 1.77 | 0.1367 |
| P10-20 | mcrhbt | 4 | 32.63 | 8.16 | 2.43 | 0.0492 |
| | time | 1 | 527.16 | 527.16 | 156.90 | <.0001 |
| | mcrhbt*time | 4 | 2.46 | 0.615 | 0.18 | 0.9486 |
| G0-10 | mcrhbt | 4 | 20.67 | 5.17 | 13.25 | <.0001 |
| | time | 1 | 215.56 | 215.56 | 552.94 | <.0001 |
| | mcrhbt*time | 4 | 0.97 | 0.242 | 0.62 | 0.6502 |
| G10-20 | mcrhbt | 4 | 1.51 | 0.38 | 0.94 | 0.4437 |
| | time | 1 | 116.92 | 116.92 | 290.28 | <.0001 |
| | mcrhbt*time | 4 | 1.86 | 0.47 | 1.16 | 0.3298 |

To closer examine the differences caused by microhabitat as given by the ANCOVA above, post-hoc pair-wise comparisons of the least squares means were made, ~~presented in~~ (Table 4). These tests compare each microhabitat separately with every other microhabitat, revealing how they relate to each other w.r.t. soil-drying rates. Probe 0-10cm values show that LS and GA differ significantly from all the other microhabitats, while TS, OG and RG do not differ. Gravimetric 0-10cm values indicate only LS to be different to all the others, and TS and GA, and RG and TS to differ from each other. At 10-20cm, only the probe readings for GA stand out -they differ from OG, RG and TS, but not from LS. Even though a post-hoc analysis was not necessary for the gravimetric 10-20cm microhabitats (since the ANCOVA indicated that they did not show significant variation), it was run, and reaffirmed that all treatments were similar.

OG & RG do differ!

from

Table 4. Pair-wise comparisons of least squares means show which microhabitats differ significantly to each other (significance level: P <= 0.05), as measured by the probe at (a) 0-10cm, and (b) 10-20cm; and (c) gravimetrically at 0-10cm. Bold print indicates a significant difference. As is evident from the ANCOVA results in Table 3, the gravimetric 10-20cm values are all similar ~~(GLM-procedure, SAS system)~~.

| (a) Probe 0-10cm | | | | | |
|---|---|---|---|---|---|
| | GA | LS | OG | RG | TS |
| GA | | **0.0266** | **<.0001** | **0.0143** | **<.0001** |
| LS | **0.0266** | | **<.0001** | **<.0001** | **<.0001** |
| OG | **<.0001** | **<.0001** | | **0.0097** | 0.3501 |
| RG | **0.0143** | **<.0001** | **0.0097** | | 0.0957 |
| TS | **<.0001** | **<.0001** | 0.3501 | 0.0957 | |
| | | | | | |
| (b) Probe 10-20cm | | | | | |
| | GA | LS | OG | RG | TS |
| GA | | 0.4147 | **0.0280** | **0.0242** | **0.0124** |
| LS | 0.4147 | | 0.1641 | 0.1465 | 0.0893 |
| OG | **0.0280** | 0.1641 | | 0.9514 | 0.7561 |
| RG | **0.0240** | 0.1465 | 0.9514 | | 0.8028 |
| TS | **0.0124** | 0.0893 | 0.7561 | 0.8028 | |
| | | | | | |
| (c) Gravimetric 0-10cm | | | | | |
| | GA | LS | OG | RG | TS |
| GA | | **<.0001** | 0.2148 | 0.7858 | **0.0059** |
| LS | **<.0001** | | **<.0001** | **<.0001** | **<.0001** |
| OG | 0.2148 | **<.0001** | | 0.3321 | 0.1252 |
| RG | 0.7858 | **<.0001** | 0.3321 | | **0.0128** |
| TS | **0.0059** | **<.0001** | 0.1252 | **0.0128** | |

Results obtained by the two methods were compared (Fig. 2).

~~Comparisons of the results obtained with the two methods were inspected.~~ Figure 2 shows the regression for all probe vs all gravimetric measures. $R^2$ values (for all the above regressions) indicate a fairly sound correlation between the two methods (mean = 0.759 ± 0.0194; SE = 0.0064), with a slope mean of 0.372 ± 0.0239 (SE = 0.0084). Comparison of the two methods shows that the probe gave more variable readings that gravimetric analysis, as can be seen from the standard deviations: probe SD = 2.77 vs gravimetric SD = 1.16 (Table 5). The probe readings on average gave double the values of those obtained gravimetrically; apparent in Tables 3 and 5.

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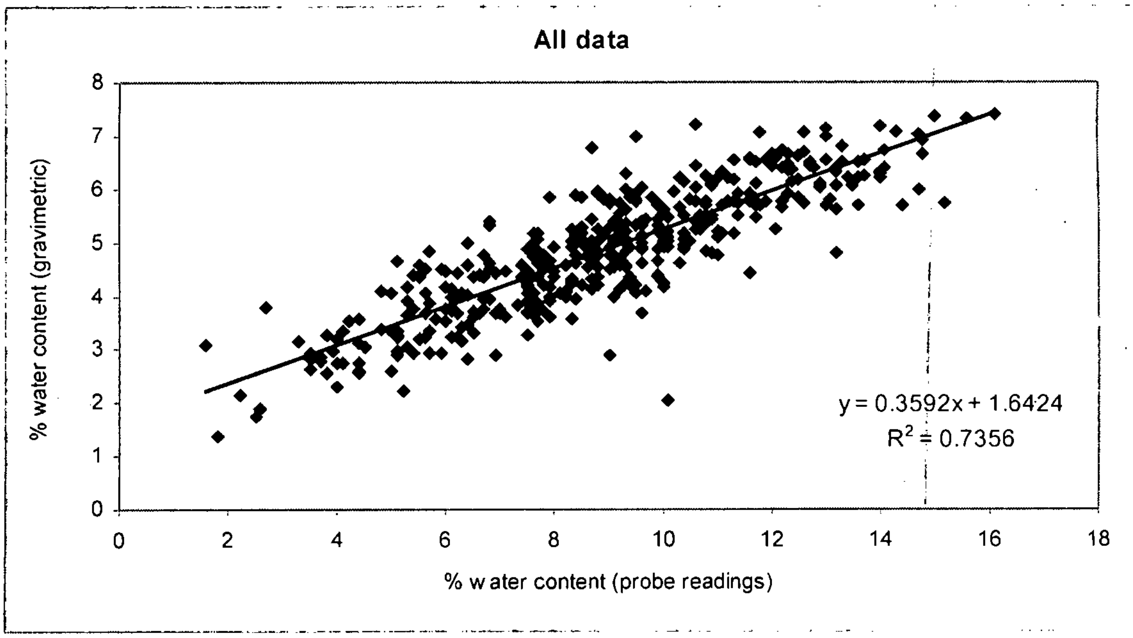

Figure 2. Gravimetric vs probe readings, plotting all data points from the entire study.

Table 5. Descriptive statistics comparing the two methods used to measure soil moisture. N = 410; SD = standard deviation; SE = standard error (STATISTICA).

| Method | Mean | Min | Max | SD | SE |
|---|---|---|---|---|---|
| Probe | 8.97 | 1.60 | 16.1 | 2.77 | 0.14 |
| Gravimetric | 4.86 | 1.36 | 7.40 | 1.16 | 0.06 |

## DISCUSSION

### *Methods*

Methods of measuring soil water concentration

Although the two methods used correlate fairly well with each other, the probe readings are generally higher and more variable than the gravimetric measures. This may be due to inaccurate specification of the soil type. Possibly the core samples dried out marginally during the mixing and bagging process, although this seems unlikely to cause a noticeable discrepancy. During the field work we noticed that the probe gave fairly fluctuating results when inserted into patches of soil only a few cm apart. Further variation occurred when rocky ground was sampled. Both procedures however showed similar trends when comparing rates of soil drying in the different microhabitats. Nonetheless, due to the greater variation shown with the probe and to simplify the discussion below, I have used the results obtained gravimetrically.

### *Results*

In the shallow zone both the effects of time and the microhabitat play important roles in drying the soil, while deeper down the drying is less affected by the microhabitat, but still varies over time. This is a broad observation and requires a closer look at how the specific microhabitats respond before comparisons or deductions can be made about water use strategies. The variation over time is expected and inevitable in this semi-arid system, given that fairly high temperatures (ranges from about 18° C to 32°C during the day) and windy conditions which were prevalent during the course of the study.

*(a) 0-10cm zone:*

In th 0-10cm zone the microhabitats beneath different shrub species deplete soil moisture at different rates. This indicates that the root systems are related to different water use strategies. The shallow-rooted *Leipoldtia* showed the highest rate of soil drying, an expected outcome when considering its rooting strategy compared to the two deeper-rooted species. The dense concentration of mesemb roots in the upper regions of ground give theses plants prolific access to shallow water stores; a mechanism suggested to be of competitive advantage to mesembs after small rainfall events (Carrick 2001) and in dry years not for mesemb (Nobel 1989). It was however expected that the rooted gaps (RG) also subjected to shallow roots but without any shading from canopies show highest rates of moisture depletion. Instead, the rooted gaps remained wetter than the soil beneath *Leipoldtia,* and were similar to the open gaps and the deeper-rooted *Galenia* soils. A possible explanation may be that the concentration of roots in these gaps was not as dense as immediately underneath the *Leipoldtia* plants and therefore did not take up as much water. It also may indicate that the shade provided by *Leipoldtia* canopies is negligible and therefore did not shelter what, soil? significantly from evaporation - a reasonable proposition given the small, scrawny appearance of these shrubs.

Similar high levels of moisture were recorded in the shallow regions under *Tripteris* plants and in the open gaps (OG), while *Galenia* shrubs showed lower levels than *Tripteris*, but nonetheless higher than *Leipoldtia*. Both deeper-rooted species, *Tripteris* and *Galenia* are not likely to deplete the upper soil regions of water at a high rate. The wetter conditions under *Tripteris* may be a consequence of its relatively dense and large shade-providing canopy. In contrast, the *Galenia* shrubs were slender and scrawny, and did not provide much shade. Nobel (1989) reported significant reductions in temperatures of soils shaded by desert plants compared to unshaded soil, giving reason to believe that evaporative water loss may play a considerable role. Since the open gaps were subject exclusively to the effects of evaporation, the fact that they displayed high water contents similar to the rooted gaps makes it ambiguous as to what the relative effects of evaporation and uptake by shallow roots are. We would expect the rooted gaps to be significantly drier than the open gaps, being exposed to both ~~the~~ drying factors (i.e. root uptake and evaporation). It is worth noting ~~here~~ that the probe results *do* show the shallow rooted gaps to be drier than the open gaps, even though the gravimetric results suggest the observed difference between these two microhabitats to be clearly insignificant (P = 0.3321).

*(b) 10-20cm zone:*

Differences in soil drying rates are less clear in the deeper zone. None of the observed differences measured gravimetrically are significant. It is surprising that no distinct variation is shown between the two deep-rooting species and *Leipoldtia*; it was expected that *Tripteris* and *Galenia* would extract more water from the deeper zone compared to *Leipoldtia*, since their roots are concentrated here. Some differences are apparent from the probe readings which are not indicated by the gravimetric values: *Galenia* shows the driest soil and differs from all other microhabitats except from *Leipoldtia*. *Tripteris* is on the wetter end of the scale, but only differs from *Galenia*. These results oppose the predictions made at the start of this study, and may suggest a number of possibilities {**Fairly extensive drying of the deeper zone underneath *Leipoldtia* may indicate that this mesemb is causing hydraulic lift, a transfer of subsoil water to topsoil during the night. Wan et.al. (1993) found hydraulic lift to exist with *Gutierrezia sarothrae,* a North American desert species with a shallow root system. Given also that mesembs have the ability to switch rapidly from CAM to C3 photosynthesis when water is available, Ref? it seems reasonable to infer that *Leipoldtia* may well be transpiring at rates high enough to cause hydraulic lift, thereby reducing soil moisture in the deeper zones. Further studies on relative transpiration rates may prove useful in explaining the trends seen in this study.

? New para?

so shallow soil is wetter?

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The hypothesis that *Tripteris* dries the deeper levels faster than *Galenia* due to being a better competitor for water is opposed by the results obtained. Instead, the results suggest *Galenia* to be the better competitor for water resources, which suggests that a different limiting resource or factor is responsible for its decline in late successional systems.

It should be considered that we have compared soil drying cycles of species of different sizes. The *Leipoldtia* shrubs were smallest in size - only 30 to 40 cm tall with diameters between 30 and 70 cm - while *Tripteris* plants were generally double that size, and *Galenia* plants were taller (from 50 to 70 cm) but generally with smaller diameters (measured on site). Also, leaf cover among the plants varied from about 20% to 85% (visual estimates). Both size and leaf cover may play roles in rates of soil water depletion, since both would influence area of shading as well as transpiration rates. Further studies relating factors such as transpiration rates, leaf cover, and even rooting volume to the results of this study would be useful in better understanding water use strategies of the various species.

Another factor that may influence water-holding capacity is the organic fraction of the soil, which may vary below different species and between soil in gaps vs under plants. Carrick (2001) found a higher organic fraction underneath *Ruschia robusta* shrubs (mesembs similar to *Leipoldtia*) than under *Galenia* shrubs.

### Conclusion

The role different desert plants play in depleting soil water stores is not conclusive. Root structure, plant size and photosynthetic strategy are just three of the possible factors affecting uptake of water. Plants surviving in arid and semi-arid environments must function in ways that maximize efficiency of water use - both in terms of individual adaptations and with respect to co-existence within communities. If those existing as close neighbours do not have complementary water-use strategies, we may infer that the benefits of co-existing - such as protection from herbivory (Cody 1993), and reduced soil surface temperatures and higher nitrogen levels (Franco & Nobel 1989) - override the cost of competition for water. According to this study *Tripteris* shrubs are favourable neighbours and provide a good site for seedling establishment. In both the shallow and deep soil zones, water content was highest under this species. *Leipoldtia* appears to provide the least favourable site for seedling growth, as it depletes the soil of moisture both in the shallow and deeper regions. This is contrary to the findings of Carrick (2001), at the same site, where competition between the shallow-rooted *Leipoldtia* and a deeper-rooted asteraceous shrub was found to be insubstantial. In my study *Leipoldtia* not only depleted soil moisture in the shallow zone, but also dried soil at a faster rate than the asteraceous shrub in the deeper zone, indicating that *Leipoldtia* can inhibit the access to soil moisture for deeper-rooting shrubs. This casts doubt on the argument by Cody(1986) that vertical separation of root systems should facilitate co-existence of species. good

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Appendix 1. Raw data

(a) Probe data

| 0-10cm | | 11days | 14 days | 17 days | 20 days | 23days | 10-20cm | | 11days | 14 days | 17 days | 20 days | 23 days |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LS | 1 | 11.7 | 6.2 | 7.3 | 4.4 | 4 | LS | 1 | 8.0 | 9.4 | 9.3 | 8.3 | 7.6 |
| | 2 | 7.9 | 9.1 | 7.8 | 6.1 | 5 | | 2 | 13.0 | 15.2 | 9.3 | 10.1 | 7.9 |
| | 3 | 8.8 | 7.9 | 5.8 | 3.5 | 1.8 | | 3 | 13 | 11.4 | 10.5 | 9.5 | 6.1 |
| | 4 | 8.9 | 10 | 4.2 | 4.1 | 3.5 | | 4 | 12.4 | 10.9 | 11.3 | 10.6 | 9.1 |
| | 5 | 9.4 | 7.5 | 7.6 | 3.7 | 3.5 | | 5 | 11.3 | 11.4 | 10.4 | 8 | 7.9 |
| | 6 | 10.6 | 9.3 | 7 | 1.6 | 3.7 | | 6 | 12.3 | 11.1 | 9.6 | 8.4 | 7.1 |
| | 7 | 8.5 | 9.9 | 6.3 | 4 | 3.8 | | 7 | 9.7 | 9.3 | 8.5 | 7.5 | 6 |
| | 8 | 6.1 | 7.6 | 6.7 | 5.1 | 2.2 | | 8 | 10.4 | 11 | 9.4 | 7.9 | 5.5 |
| **mean** | | **9.0** | **8.4** | **6.6** | **4.1** | **3.4** | **mean** | | **11.3** | **11.2** | **9.8** | **8.8** | **7.2** |
| **Std Error** | | 0.6 | 0.5 | 0.4 | 0.5 | 0.4 | **Std Error** | | 0.6 | 0.6 | 0.3 | 0.4 | 0.4 |
| TS | 1 | 14.8 | 7.6 | 5 | 7.8 | 6.4 | TS | 1 | 8.6 | 8.7 | 6.4 | 6.4 | 5.7 |
| | 2 | 13.6 | 13.2 | 8.3 | 9.9 | 8.3 | | 2 | 14.3 | 14.1 | 10.8 | 10.9 | 9.2 |
| | 3 | 10.2 | 9.2 | 7.8 | 4.8 | 5.1 | | 3 | 11.7 | 10.3 | 9.2 | 8.5 | 6.3 |
| | 4 | 11.6 | 11.6 | 8.5 | 5.5 | 7.3 | | 4 | 13.7 | 12.3 | 10.1 | 10.4 | 9.7 |
| | 5 | 12.9 | 13.2 | 7.5 | 5.6 | 5.8 | | 5 | 16.1 | 13.4 | 11.9 | 9.9 | 9.5 |
| | 6 | 12 | 10.8 | 7.5 | 7.6 | 5.6 | | 6 | 12.3 | 12 | 11.3 | 8.5 | 8.3 |
| | 7 | 8.8 | 12.2 | 7.1 | 5.9 | 5 | | 7 | 12.7 | 14.4 | 13.6 | 9.1 | 8.8 |
| | 8 | 9.6 | 6.8 | 9 | 5.3 | 3.9 | | 8 | 10.8 | 11 | 10.7 | 6 | 6 |
| **mean** | | **11.7** | **10.6** | **7.6** | **6.6** | **5.9** | **mean** | | **12.5** | **12.0** | **10.5** | **8.7** | **7.9** |
| **Std Error** | | 0.7 | 0.9 | 0.4 | 0.6 | 0.5 | **Std Error** | | 0.8 | 0.7 | 0.7 | 0.6 | 0.6 |
| GA | 1 | 9.3 | 5.7 | 6.8 | 3.8 | 2.6 | GA | 1 | 5.5 | 6.5 | 4.8 | 4.2 | 4.1 |
| | 2 | 8.7 | 10.4 | 9.4 | 8.3 | 5.6 | | 2 | 12.8 | 12.7 | 8.5 | 11 | 8.2 |
| | 3 | 9.2 | 9.6 | 5.2 | 4.4 | 2.5 | | 3 | 11.6 | 10.8 | 5.1 | 6.5 | 5.7 |
| | 4 | 9.8 | 9.1 | 7.9 | 5.3 | 2.7 | | 4 | 13.3 | 11.3 | 10.1 | 9.2 | 5.9 |
| | 5 | 12.6 | 11.7 | 9 | 7 | 4.4 | | 5 | 14.7 | 14.8 | 14 | 10.5 | 7.7 |
| | 6 | 9 | 6.8 | 9 | 7.1 | 5 | | 6 | 13.3 | 9.6 | 10 | 8.7 | 9 |
| | 7 | 9.5 | 6.7 | 5.9 | 3.3 | 4 | | 7 | 12.4 | 7.7 | 8.4 | 7.7 | 6.7 |
| | 8 | 11.8 | 6.4 | 7.1 | 5.3 | 4.5 | | 8 | 11.1 | 11.4 | 8.3 | 10.9 | 7.5 |
| **mean** | | **10.0** | **8.3** | **7.5** | **5.6** | **3.9** | **mean** | | **11.8** | **10.6** | **8.7** | **8.6** | **6.9** |
| **Std Error** | | 0.5 | 0.8 | 0.5 | 0.6 | 0.4 | **Std Error** | | 1.0 | 0.9 | 1.0 | 0.8 | 0.6 |
| OG | 1 | 9.6 | 8.4 | 7 | 5.4 | 6.1 | OG | 1 | 7.6 | 10 | 8.8 | 6.2 | 8.1 |
| | 2 | 11.9 | 9.5 | 10 | 9 | 6.9 | | 2 | 15.6 | 11 | 13 | 10.1 | 10.3 |
| | 3 | 12.5 | 9.9 | 10.9 | 7.4 | 7.5 | | 3 | 13.7 | 12.7 | 8.8 | 9.2 | 10 |
| | 4 | 12 | 8.8 | 8.3 | 6.6 | 6.9 | | 4 | 12.2 | 11.6 | 9.3 | 5.5 | 7.5 |
| | 5 | 8.2 | 7.8 | 9 | 7 | 7.5 | | 5 | 12.5 | 10.7 | 10 | 9.6 | 8.7 |
| | 6 | 13 | 12.6 | 11.4 | 8.2 | 6.2 | | 6 | 12.9 | 14 | 10.3 | 9.4 | 8.2 |
| | 7 | 12.3 | 12.1 | 9.6 | 8 | 6.8 | | 7 | 12.2 | 13.6 | 11.1 | 9.6 | 9.6 |
| | 8 | 10 | 7.7 | 7.2 | 6.7 | 5.4 | | 8 | 11.7 | 9 | 9.9 | 7.4 | 6.9 |
| **mean** | | **11.2** | **9.6** | **9.2** | **7.3** | **6.7** | **mean** | | **12.3** | **11.6** | **10.2** | **8.4** | **8.7** |
| **Std Error** | | 0.6 | 0.7 | 0.6 | 0.4 | 0.3 | **Std Error** | | 0.8 | 0.6 | 0.5 | 0.6 | 0.4 |
| RG | 1 | 12.4 | 7.7 | 8 | 6 | 6.3 | RG | 1 | 13.2 | 9.2 | 8.5 | 8.6 | 7.8 |
| | 2 | 7.6 | 8.3 | 6.5 | 5.1 | 5.1 | | 2 | 9.6 | 8.8 | 9.6 | 7.5 | 7.6 |
| | 3 | 10.8 | 8.7 | 9.1 | 8.8 | 6.3 | | 3 | 13.5 | 11.7 | 11 | 10.1 | 8.8 |
| | 4 | 9.3 | 8.7 | 7.9 | 5.6 | 5.2 | | 4 | 12.5 | 11.8 | 10 | 7.7 | 7.5 |
| | 5 | 11.2 | 8.6 | 8.3 | 6.1 | 6.5 | | 5 | 15.0 | 14 | 14.7 | 10.6 | 9.9 |
| | 6 | 10.6 | 9.5 | 7.4 | 5.1 | 4.4 | | 6 | 14.1 | 10.7 | 9 | 7.7 | 6.5 |
| | 7 | 10.6 | 10.9 | 7.7 | 7.5 | 5.3 | | 7 | 14.0 | 13.1 | 10.6 | 9 | 7.5 |
| | 8 | 8.5 | 8.9 | 10.2 | 8.6 | 6.6 | | 8 | 10.1 | 11.2 | 8.4 | 9.1 | 9.3 |
| **mean** | | **10.1** | **8.9** | **8.1** | **6.6** | **5.7** | **mean** | | **12.8** | **11.3** | **10.2** | **8.8** | **8.1** |
| **Std Error** | | 0.5 | 0.3 | 0.4 | 0.5 | 0.3 | **Std Error** | | 0.7 | 0.6 | 0.7 | 0.4 | 0.4 |

**(b) Gravimetric data**

| 0-10cm | 11days | 14 days | 17 days | 20 days | 23 days | 10-20cm | 11days | 14 days | 17 days | 20 days | 23 days |
|---|---|---|---|---|---|---|---|---|---|---|---|
| LS 1 | 6.50 | 3.70 | 4.45 | 2.74 | 2.31 | LS 1 | 4.90 | 4.92 | 5.19 | 4.28 | 3.65 |
| 2 | 5.83 | 4.56 | 4.53 | 3.99 | 2.62 | 2 | 6.56 | 5.74 | 4.99 | 5.19 | 3.98 |
| 3 | 5.95 | 4.65 | 3.89 | 2.63 | 1.36 | 3 | 7.00 | 5.93 | 5.80 | 6.99 | 4.12 |
| 4 | 5.12 | 5.53 | 4.18 | 3.33 | 2.83 | 4 | 6.14 | 6.09 | 5.18 | 5.38 | 3.99 |
| 5 | 5.82 | 4.86 | 3.86 | 2.80 | 2.93 | 5 | 5.76 | 5.50 | 4.95 | 4.35 | 3.62 |
| 6 | 6.02 | 5.04 | 4.24 | 3.10 | 2.85 | 6 | 5.90 | 5.69 | 5.00 | 4.61 | 4.45 |
| 7 | 5.07 | 5.69 | 4.65 | 3.19 | 2.56 | 7 | 5.44 | 5.69 | 4.98 | 3.90 | 3.77 |
| 8 | 3.80 | 3.92 | 4.05 | 2.96 | 2.16 | 8 | 5.16 | 4.78 | 4.37 | 4.16 | 3.20 |
| **mean** | **5.51** | **4.74** | **4.23** | **3.09** | **2.45** | **mean** | **5.86** | **5.54** | **5.06** | **4.86** | **3.85** |
| **Std Error** | **0.30** | **0.25** | **0.10** | **0.15** | **0.18** | **Std Error** | **0.25** | **0.16** | **0.14** | **0.35** | **0.13** |
| TS 1 | 6.66 | 4.98 | 3.87 | 3.73 | 2.82 | TS 1 | 4.73 | 4.66 | 4.01 | 3.46 | 2.96 |
| 2 | 6.50 | 6.32 | 4.81 | 4.86 | 3.57 | 2 | 7.07 | 6.73 | 4.82 | 5.41 | 4.12 |
| 3 | 5.94 | 5.22 | 4.59 | 3.38 | 3.25 | 3 | 5.72 | 5.67 | 4.69 | 4.19 | 4.05 |
| 4 | 6.57 | 6.60 | 5.93 | 4.40 | 3.82 | 4 | 6.26 | 6.49 | 5.47 | 4.86 | 4.10 |
| 5 | 6.11 | 6.06 | 5.62 | 4.50 | 3.56 | 5 | 7.40 | 6.23 | 5.78 | 4.39 | 4.04 |
| 6 | 6.65 | 6.25 | 5.77 | 4.74 | 4.07 | 6 | 6.65 | 6.45 | 6.56 | 5.27 | 4.22 |
| 7 | 5.91 | 5.77 | 5.66 | 4.50 | 3.36 | 7 | 6.49 | 6.30 | 5.70 | 5.02 | 4.78 |
| 8 | 6.04 | 4.62 | 5.30 | 3.64 | 2.99 | 8 | 5.36 | 5.21 | 5.25 | 4.18 | 3.54 |
| **mean** | **6.30** | **5.73** | **5.19** | **4.22** | **3.43** | **mean** | **6.21** | **5.97** | **5.29** | **4.60** | **3.98** |
| **Std Error** | **0.12** | **0.25** | **0.25** | **0.20** | **0.15** | **Std Error** | **0.32** | **0.25** | **0.28** | **0.23** | **0.19** |
| GA 1 | 5.98 | 3.86 | 4.84 | 3.28 | 1.88 | GA 1 | 4.56 | 4.36 | 4.08 | 3.53 | 2.75 |
| 2 | 6.78 | 6.15 | 5.51 | 5.26 | 3.69 | 2 | 6.41 | 6.51 | 5.17 | 5.20 | 3.99 |
| 3 | 5.71 | 5.40 | 3.69 | 3.11 | 1.74 | 3 | 5.81 | 5.70 | 4.64 | 3.73 | 3.35 |
| 4 | 5.84 | 5.41 | 4.75 | 4.18 | 3.81 | 4 | 6.83 | 6.18 | 5.02 | 5.35 | 2.94 |
| 5 | 7.06 | 5.69 | 5.47 | 3.69 | 2.59 | 5 | 7.02 | 6.94 | 6.28 | 5.01 | 3.54 |
| 6 | 5.81 | 4.52 | 5.39 | 3.63 | 4.06 | 6 | 6.52 | 5.34 | 5.62 | 4.88 | 2.92 |
| 7 | 5.92 | 4.37 | 4.78 | 3.17 | 2.74 | 7 | 6.35 | 5.05 | 5.86 | 4.82 | 3.77 |
| 8 | 7.08 | 4.59 | 4.99 | 3.91 | 3.06 | 8 | 6.31 | 5.74 | 5.04 | 5.50 | 4.48 |
| **mean** | **6.27** | **5.00** | **4.93** | **3.78** | **2.95** | **mean** | **6.23** | **5.73** | **5.21** | **4.75** | **3.47** |
| **Std Error** | **0.22** | **0.24** | **0.23** | **0.26** | **0.29** | **Std Error** | **0.14** | **0.23** | **0.20** | **0.21** | **0.20** |
| OG 1 | 5.13 | 4.77 | 3.96 | 3.75 | 3.24 | OG 1 | 5.19 | 5.11 | 4.35 | 4.03 | 4.06 |
| 2 | 6.57 | 5.76 | 5.32 | 4.75 | 3.67 | 2 | 7.34 | 6.20 | 5.70 | 5.04 | 4.61 |
| 3 | 6.63 | 5.73 | 5.42 | 4.36 | 3.70 | 3 | 6.56 | 6.44 | 5.27 | 5.35 | 4.23 |
| 4 | 6.52 | 4.83 | 4.53 | 4.37 | 2.91 | 4 | 6.75 | 5.75 | 4.58 | 4.34 | 4.04 |
| 5 | 4.56 | 4.52 | 4.76 | 3.75 | 3.26 | 5 | 6.17 | 5.42 | 4.91 | 5.10 | 4.13 |
| 6 | 7.16 | 6.68 | 5.74 | 4.05 | 3.25 | 6 | 6.02 | 6.22 | 6.20 | 4.21 | 4.10 |
| 7 | 6.36 | 6.57 | 5.26 | 4.45 | 3.94 | 7 | 6.40 | 6.20 | 5.19 | 4.92 | 4.63 |
| 8 | 5.01 | 4.36 | 3.86 | 3.95 | 2.93 | 8 | 6.10 | 5.74 | 5.20 | 4.57 | 4.44 |
| **mean** | **5.99** | **5.40** | **4.86** | **4.18** | **3.36** | **mean** | **6.32** | **5.88** | **5.18** | **4.70** | **4.28** |
| **Std Error** | **0.33** | **0.32** | **0.25** | **0.13** | **0.13** | **Std Error** | **0.22** | **0.16** | **0.21** | **0.17** | **0.09** |
| RG 1 | 6.38 | 5.16 | 4.61 | 4.47 | 3.43 | RG 1 | 6.40 | 5.54 | 5.01 | 4.89 | 4.21 |
| 2 | 4.92 | 4.90 | 4.33 | 3.26 | 2.89 | 2 | 4.87 | 5.02 | 5.10 | 4.28 | 3.81 |
| 3 | 5.51 | 5.42 | 5.04 | 5.01 | 3.18 | 3 | 6.05 | 5.76 | 5.11 | 5.10 | 4.22 |
| 4 | 5.62 | 4.75 | 4.33 | 3.22 | 2.24 | 4 | 5.84 | 5.70 | 4.92 | 3.88 | 3.73 |
| 5 | 6.23 | 4.92 | 4.55 | 3.71 | 3.32 | 5 | 7.35 | 6.34 | 5.99 | 5.77 | 5.31 |
| 6 | 6.44 | 5.80 | 4.19 | 3.33 | 2.55 | 6 | 6.38 | 5.50 | 4.51 | 4.35 | 3.61 |
| 7 | 7.22 | 6.08 | 4.81 | 4.16 | 3.03 | 7 | 7.17 | 5.81 | 5.23 | 4.90 | 4.21 |
| 8 | 5.83 | 5.85 | 5.80 | 4.75 | 3.67 | 8 | 4.90 | 5.77 | 5.15 | 5.05 | 4.53 |
| **mean** | **6.02** | **5.36** | **4.71** | **3.99** | **3.04** | **mean** | **6.12** | **5.68** | **5.13** | **4.78** | **4.20** |
| **Std Error** | **0.25** | **0.18** | **0.18** | **0.25** | **0.17** | **Std Error** | **0.32** | **0.13** | **0.15** | **0.21** | **0.19** |