

DIURNAL AND SEASONAL CHANGES IN WATER POTENTIAL OF
SELECTED SPECIES IN THREE VEGETATION TYPES IN SOUTH-
WESTERN CAPE/

Francois van der Heyden

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ABSTRACT

Pre-dawn, midday and post-dusk water potentials of selected species in Sand Plain Lowland Fynbos, West Coast Renosterveld and West Coast Strandveld communities were measured during winter and summer. Seasonal variation in osmotic potential of certain species were also determined. Differences in magnitude of seasonal and diurnal variation of water potential between species within the same vegetation type is related to rooting habit. Seasonal variation in soil moisture content could not account for differences in water and osmotic potentials between comparable species representative of the three vegetation types. Total soil phosphorous content was also considered as a possible environmental determinant of ecological attributes in these communities.

Results from this investigation and nutrient data indicate that the vegetation types segregate along gradients of soil phosphorous content and moisture.

1. INTRODUCTION

Mediterranean climate regions are noted for marked seasonality in rainfall (summer drought) (Miller & Hajek, 1981) and for being nutrient poor (Kruger et al., 1983). The vegetation of these areas shows some degree of similarity which has primarily been attributed to environmental factors (Cody & Mooney, 1978). Recent studies reveal divergences in vegetation ecology which may be related for example to nutrient status which has been suggested to account for the distribution of heathlands in mediterranean South Africa (Boucher & Moll, 1981).

In this study the importance of moisture in determining community ecology in a lowland heathland and two lowland shrublands in mediterranean South Africa was investigated. Seasonal and diurnal variation in water potential was determined as it is considered to give an indication of the behaviour of plants in response to soil moisture availability. In addition the osmotic potential of selected species was determined during winter and summer since this provides an index of the degree of osmotic adjustment to water deficits (Cheung et al., 1975).

Knowledge of the plant water relations in fynbos is poor, especially in relation to ecological attributes. Miller et al. (1983) measured water pressure potentials and leaf conductances for a comparative study with the chaparral in California. Miller et al. (1984) related plant-water relations to plant growth form in coastal and Mountain Fynbos.

Shoot water potentials of certain species appear to be influenced primarily by rooting depth (Sommerville, 1983). Poole and Miller (1975) found pressure potentials to be closely correlated with rooting habit in mediterranean California. In the mediterranean region of central Chile, aspect as well as rooting depths were found to influence plant-water relations (Giliberto & Estay, 1978).

To allow for assessment of the relative importance of soil moisture availability in determining structure and form in South African communities, the present study was conducted on three representative vegetation types. Four species for observation were selected in such a way to provide a basis for comparison at the growth-form, family and the species level.

2. METHODS

Species were selected from Sand Plain Lowland Fynbos(SPLF), West Coast Renosterveld(RV) and West Coast Strandveld(SV). For characteristics of these vegetation types refer to Moll et al.(1984). The SPLF site was at Pella, a study area for the CSIR Fynbos Biome Project. The SV study area was near Melkbosstrand and the RV site on unused farmland adjacent to the Pella study area. Measurements were made on four species in each study area(Table 1.).

The monthly total rainfall data for SPLF and RV are graphically illustrated in fig.2 (obtained from CSIR weather station at the Pella site) and for the SV study site in fig.3. Rainfall data for SV was recorded at Atlantis weather station(obtained from D.F.Malan Weather Bureau). Temperatures and Relative Humidities prevalent at the time observations were made are presented in the Appendix. Location of sampling sites and weather stations are illustrated in fig.1.

Soil Moisture Content was determined for all three sites during summer and winter. At midday, samples were taken at 10 cm below the surface and kept in air tight containers. Samples were weighed(fresh weight), then oven dried at 70°C for 72 hours and then reweighed. Soil moisture content is expressed as a percentage of the fresh weight.

Water Potential of each species was determined at pre-dawn, noon and post-dusk during summer and winter. Measurements involved the pressure chamber technique(Scholander et al.,1965) using a pressure bomb with a 40 bar pressure limit. Occasionally the maximum pressure was exceeded and

thus could not be measured accurately. Vegetative shoots were used in the measurement of all species except for the members of the Restionaceae and for Ehrharta villosa for which the flowering culms were used. The excised shoot or culm being placed in the pressure bomb (cut end in view), the pressure was applied. Water potential was recorded as the pressure at which the cut end slickens.

Osmotic Potential of selected species (Table 1) was determined using a modified pressure chamber technique. A fully hydrated excised shoot or culm was placed in the pressure chamber. Pressure was increased incrementally and the volume of sap expressed at each pressure recorded. The shoot or culm was allowed to equilibrate at the new pressure before the procedure was repeated. The log of the pressure was then plotted against the cumulative volume for each pair of readings. When the lower linear portion (A in fig.4) of the resulting curve is extended, it crosses at a value on the log pressure axis equal to the original osmotic potential (Cheung et al., 1975).

Table 1. Species investigated at the three study sites.

Sand Plain Lowland Fynbos	West Coast Strandveld	West Coast Renosterveld
<u>Lencospermum parille*</u>	<u>Euclea racemosa*</u>	<u>Euclea racemosa*</u>
<u>Phyllica cephalantha</u>	<u>Olea exasperata</u>	<u>Rhus angustifolia</u>
<u>Thamnochortus punctatus</u>	<u>Ehrharta villosa*</u>	<u>Calopsis vimineus*</u>
<u>Cannomois parviflora*</u>	<u>Thamnochortus spicigerus</u>	<u>Elytropappus rhinocerotis</u>

* Species used in determination of osmotic potentials

Species nomenclature follows Bond & Goldblatt (1984).

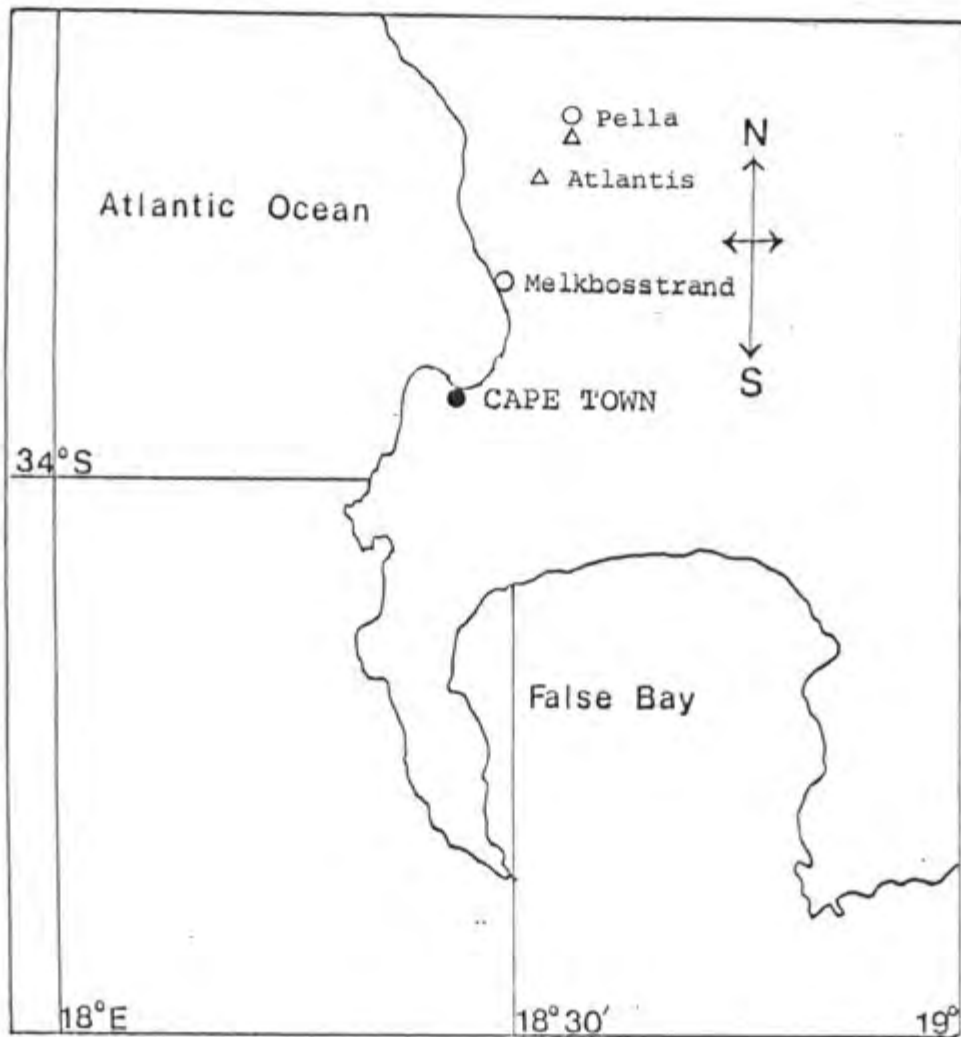


Fig.1 Map showing location of sampling sites and weather stations.

- Sampling sites
- △ Weather stations

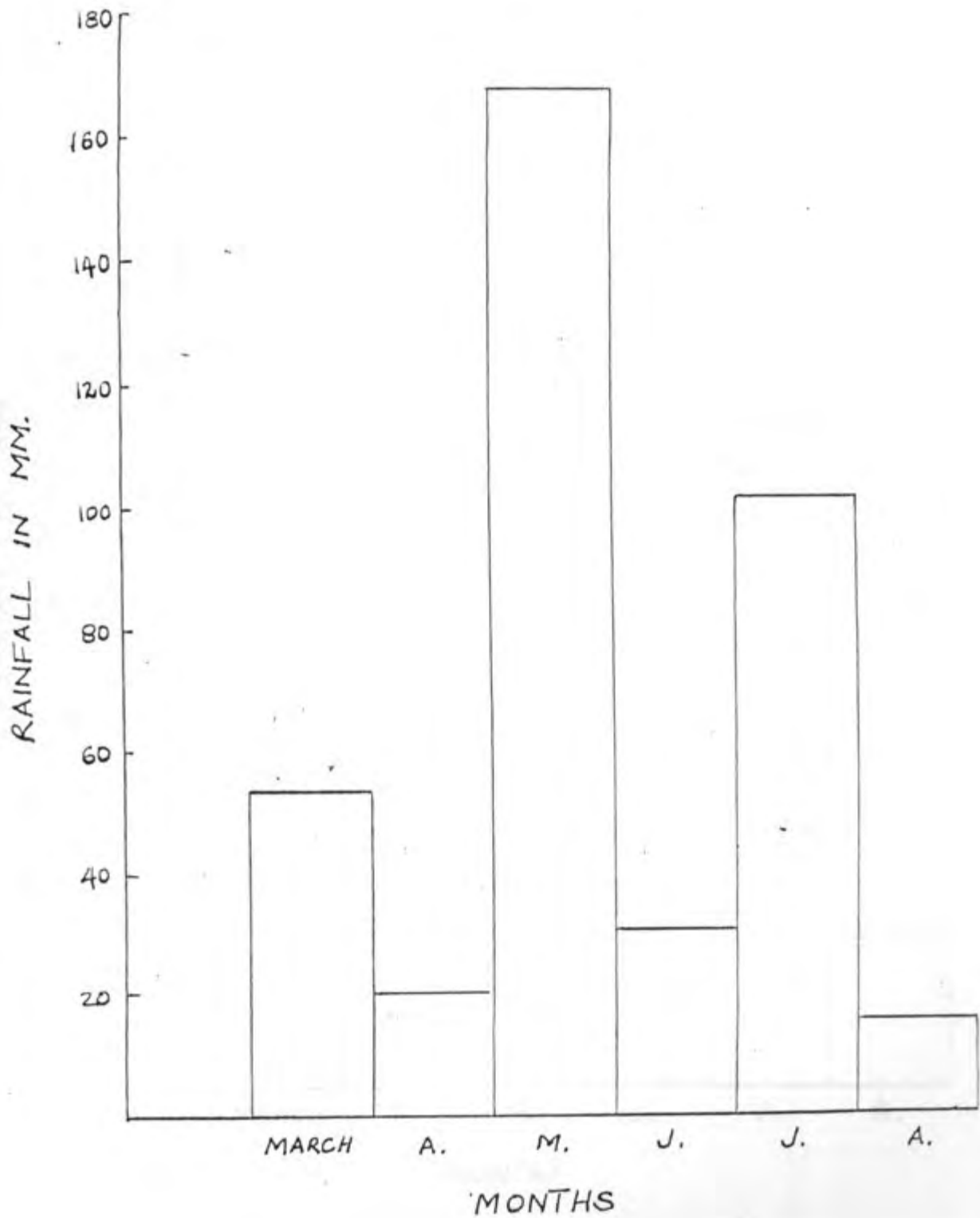


Figure 2. Monthly rainfall at the Pella study area.

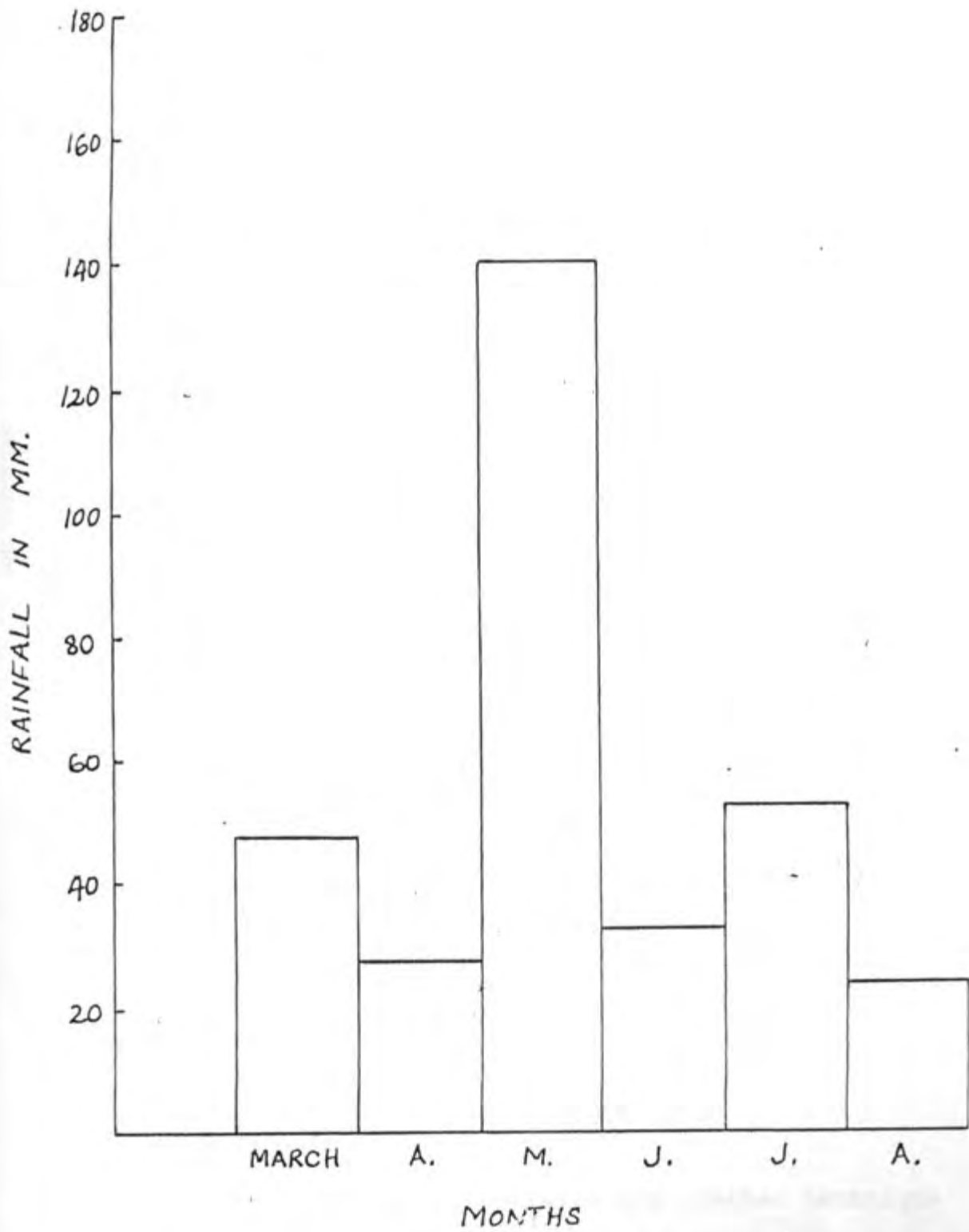


Figure 3. Monthly rainfall at the Atlantis Weather Station.

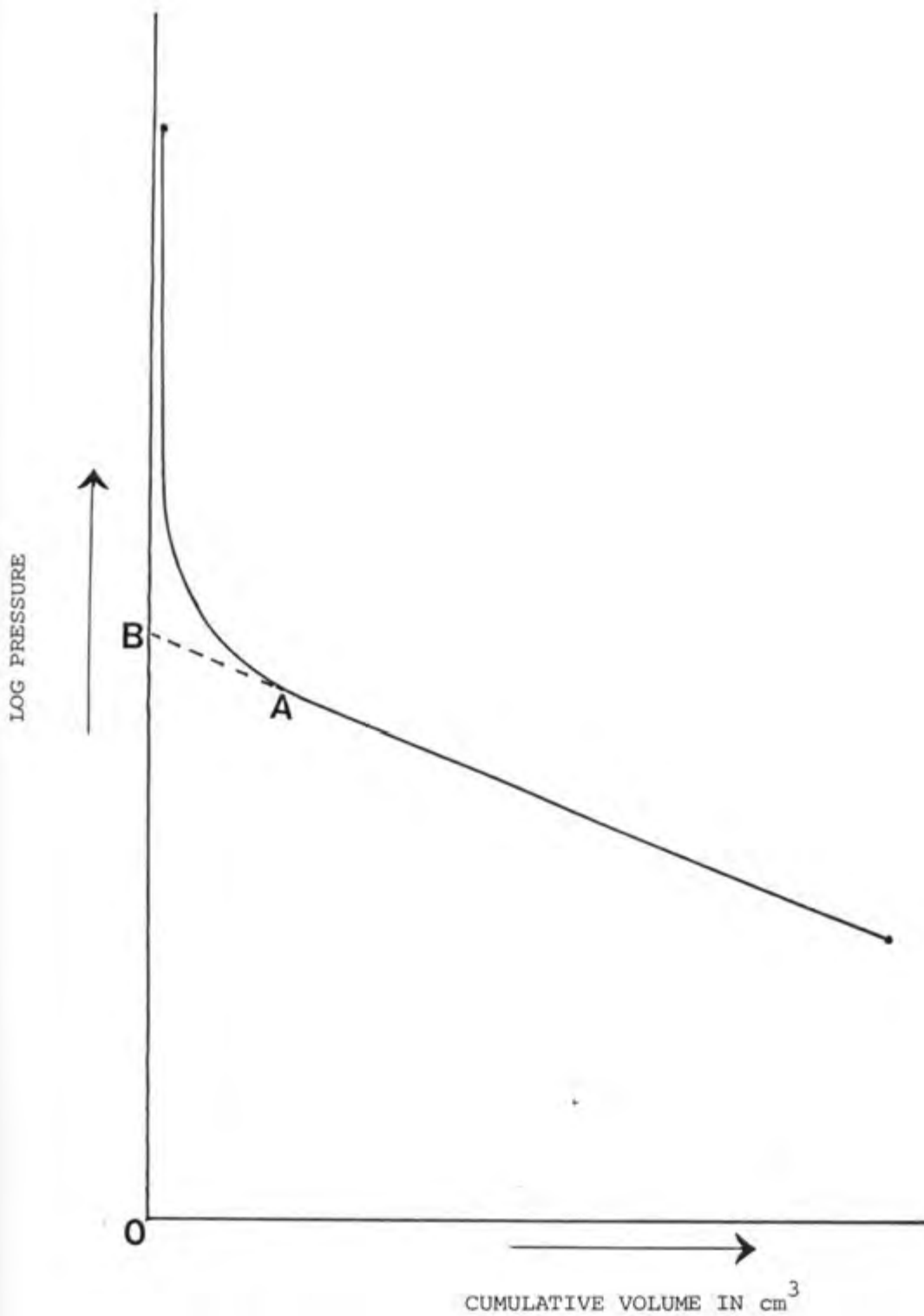


Figure 4. Illustrating the pressure chamber technique
as a method for determination of osmotic potential.

(adapted from Chueng et al., 1975)

point B: osmotic potential

(refer to methods section for
explanation)

3. RESULTS

3.1 Soil Moisture Content

The soil moisture data (Figure 5 & Table 2) illustrate the drying-out of all three soils during summer and their rehydration during the winter months. The decrease in total soil moisture during summer was more marked in the SPLF soils than in either the RV and SV soils.

3.2 Water Potential

The water potentials recorded were the lowest at midday during winter and summer. Higher potentials were displayed at pre-dawn and post-dusk. The seasonal course of water potentials indicated that the daily potentials recorded were lower during the summer months than in winter. Potentials differed dramatically between species (Tables 3(a), 3(b) and 3(c); Figures 6, 7 and 8).

Species studied at Sand Plain Lowland Fynbos: In Leucospermum parile, water potentials were relatively low with very little difference between the values obtained for the summer and winter months. There was a slight decrease in midday potentials followed by an increase after sunset. The water potentials for Phyllica cephalantha followed a similar diurnal pattern but the values obtained were always lower than those obtained for L. parile. In addition, the seasonal variation in potentials were more pronounced than for L. parile. I. punctatus displayed lower water potentials during summer and winter. The midday and post-dusk potentials were higher than -40 bars.

Cannomolis parviflora displayed generally moderate potentials during winter and summer (-5 to -18 bars). There was no significant seasonal variation in midday water potential.

Species studied in West Coast Renosterveld: Summer water potentials recorded for Euclea racemosa were moderate but lower than values obtained for a comparable broad-leaf sclerophyllous shrub in SPLF (L. parile). The deciduous shrub, Rhus angustifolia exhibited relatively low water potentials during summer and winter.

Elytropappus rhinocerotis showed wide variation in values recorded during summer (-13 to -31 bars) and winter (-2 to -14 bars). The potentials recorded for Calopsis vimineus were the highest of all the species studied in RV and also exhibited the widest variation from summer to winter (-6 to -40 bars; midday).

Species studied at West Coast Strandveld: Euclea racemosa in this vegetation type consistently revealed lower potentials than E. racemosa studied in RV. Pre-dawn, midday and post-dusk water potentials were lower and diurnal as well as seasonal variation were of larger magnitude. Olea exasperata generally exhibited much lower water potentials during summer (lower than -40 bars at midday). Similar diurnal and seasonal trends were found in Thamnochortus spicigerus. Ehrharta villosa showed relatively moderate water potentials during summer (-14 to -28 bars) and winter (-4 to -15 bars).

3.3 Osmotic Potentials

The osmotic potentials recorded showed wide variation within and overlaps between the different vegetation types as well as significant differences between the values obtained for summer and winter. Of all the species studied, L. parile, displayed the highest osmotic potential for summer (-3,73 bars) and for winter (-1,9 bars). Euclea racemosa showed statistically significant differences in values obtained for RV (-7,4 bars) and SV (-6,4 bars). Similar osmotic potentials were recorded for this species in RV and SV during winter. There were no significant differences in osmotic potential among members of the Restionaceae and Ehrharta villosa during summer or winter.

Table 2. Soil moisture content (in %) in SPLF, SV and RV soils.

	Summer	Winter
SPLF	0,4 ± 0,03	5,89 ± 0,65
RV	3,2 ± 0,5	15,77 ± 2,76
SV	0,7 ± 0,07	3,59 ± 0,25

Values are expressed as mean ± SEM.

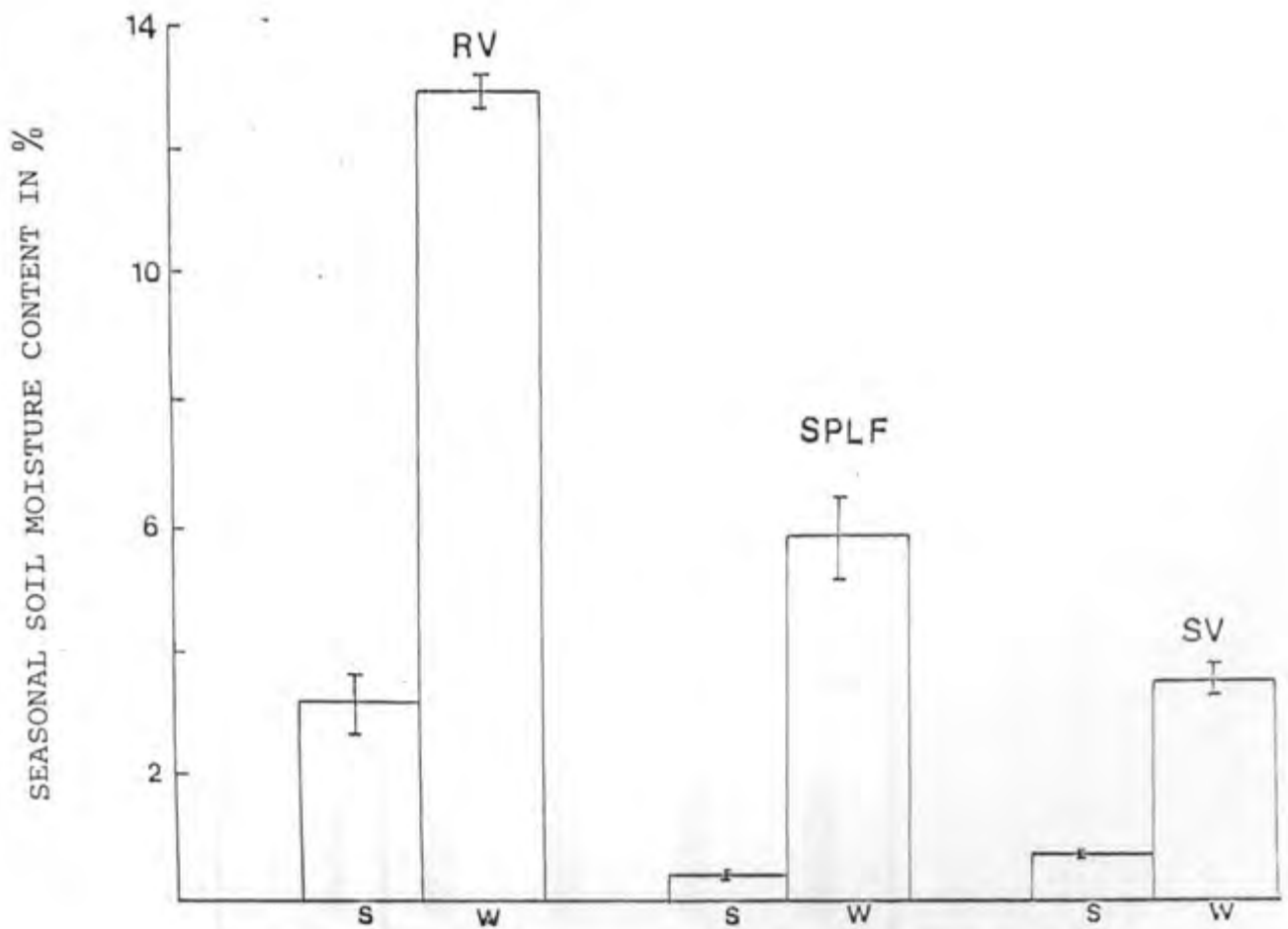


Figure 5. Seasonal soil Moisture Content of SPLF, SV and RV.

S: Summer

W: Winter

Table 3(a): Seasonal pre-dawn, midday and post-dusk water potentials (in bars) of SPLF species.

Values are expressed as mean \pm SEM.

Species	Summer			Winter		
	pre-dawn	midday	post-dusk	pre-dawn	midday	post-dusk
<u>L. parile</u>	-7,93 \pm 0,27	-9,4 \pm 0,76	-5,58 \pm 0,70	-2,68 \pm 0,05	-9,74 \pm 0,82	-1,13 \pm 0,05
<u>P. cephalantha</u>	-7,35 \pm 0,79	-25,08 \pm 0,21	-12,45 \pm 0,28	-2,00 \pm 0,07	-9,20 \pm 1,74	-2,00 \pm 0,09
<u>I. punctatus</u>	-33,95 \pm 0,74	< -40	< -40	-8,73 \pm 0,43	-21,75 \pm 1,89	-7,80 \pm 2,14
<u>C. parvifbra</u>	-11,70 \pm 2,51	-18,68 \pm 1,56	-17,20 \pm 0,72	-5,55 \pm 0,45	-18,62 \pm 0,94	-2,58 \pm 0,09

Table 3(b): Seasonal pre-dawn, midday and post-dusk water potentials (in bars) of RV species.

Values are expressed as mean \pm SEM.

Species	Summer			Winter		
	pre-dawn	midday	post-dusk	pre-dawn	midday	post-dusk
<u>E. racemosa</u>	-10,86 \pm 0,89	-19,32 \pm 0,59	-15,38 \pm 0,14	-4,65 \pm 0,05	-5,63 \pm 0,08	-4,03 \pm 0,21
<u>R. angustifolia</u>	45,06 \pm 0,03	-6,94 \pm 0,25	-4,68 \pm 0,25	-1,70 \pm 0,11	-4,60 \pm 0,16	-1,52 \pm 0,04
<u>C. vimineus</u>	-36,52 \pm 0,93	<-40	-39,86 \pm 0,59	-5,24 \pm 0,125	-6,60 \pm 0,158	-4,63 \pm 0,16
<u>E. rhinocerotis</u>	-13,24 \pm 0,67	-31,72 \pm 0,86	-22,24 \pm 0,15	-2,91 \pm 0,04	-4,20 \pm 0,08	-2,53 \pm 1,03

Table 3(c): Seasonal pre-dawn, midday and post-dusk water potentials (in bars) of SV species.

Values are expressed as mean \pm SEM.

Species	Summer			Winter		
	pre-dawn	midday	post-dusk	pre-dawn	midday	post-dusk
<u>E. racemosa</u>	-18,95 \pm 0,477	< -40	-27,90 \pm 0,89	-11,95 \pm 1,25	-21,58 \pm 1,16	-15,84 \pm 0,42
<u>O. exasperata</u>	-12,88 \pm 1,14	< -40	< -40	-4,85 \pm 0,29	-13,23 \pm 1,13	-10,58 \pm 0,58
<u>T. spicigerus</u>	-12,83 \pm 1,18	< -40	< -40	-3,5 \pm 0,08	-8,75 \pm 0,10	-5,34 \pm 0,47
<u>E. villosa</u>	-14,25 \pm 1,05	-28,7 \pm 3,35	-19,24 \pm 1,15	-4,85 \pm 0,22	-15,48 \pm 0,11	-10,0 \pm 0,31

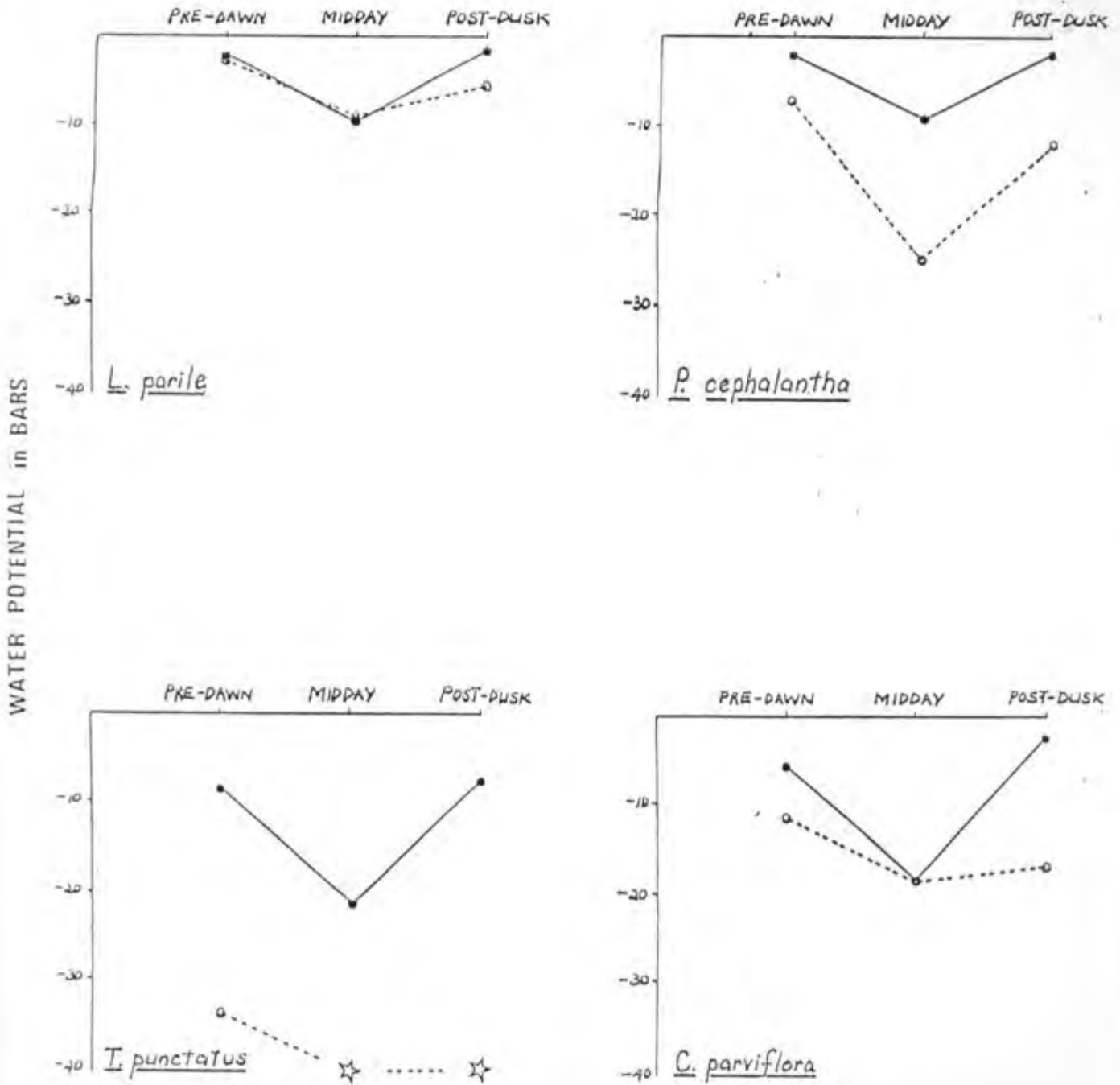


Fig.6: Mean pre-dawn, midday and post-dusk water potentials of selected species in SPLF during summer(o---o) and winter(●—●).

☆ -40 bars pressure gauge limit.

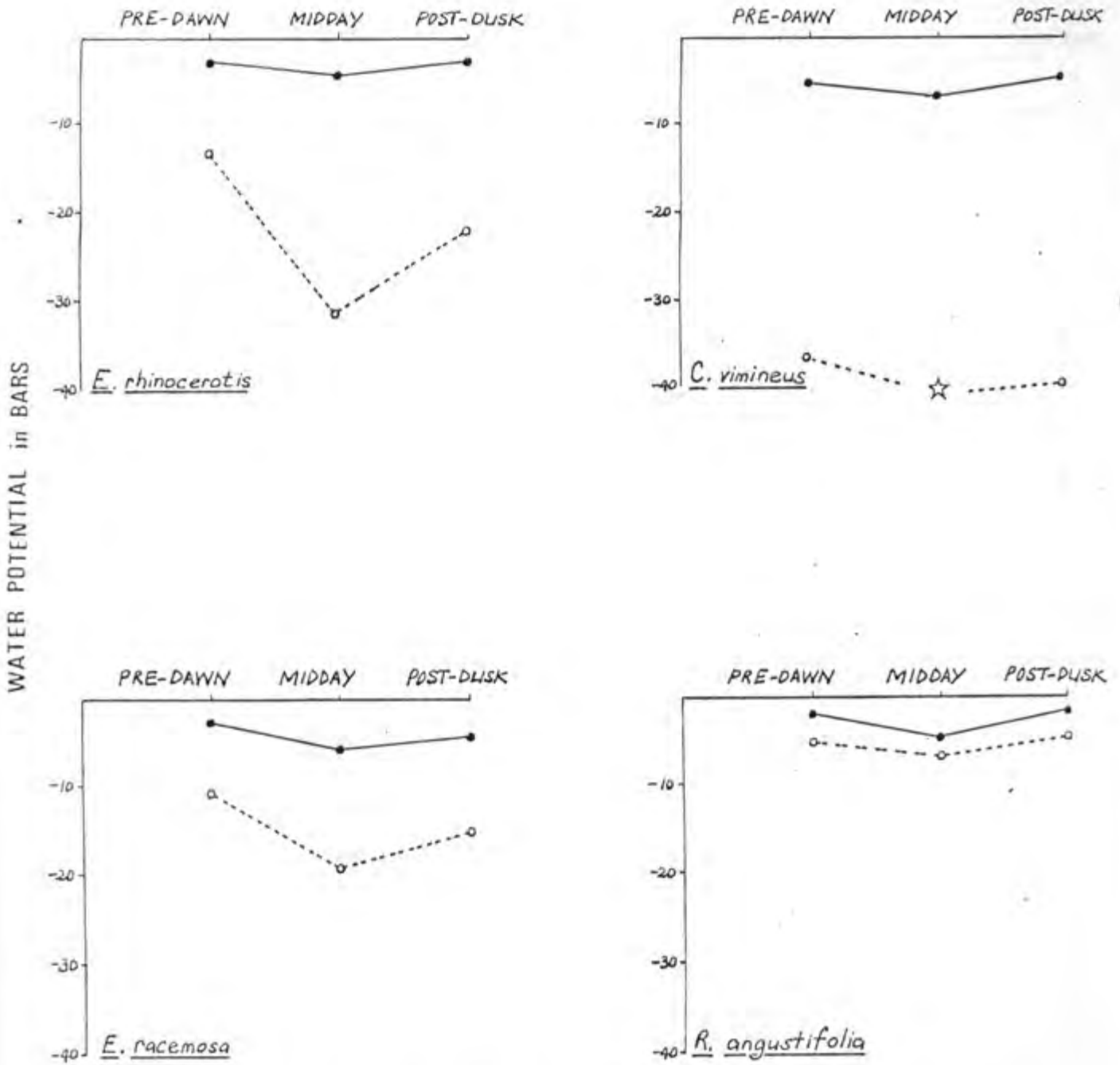


Fig.7: Mean pre-dawn, midday and post-dusk water potentials of selected species in RV during summer(o---o) and winter(●—●).

☆ -40 bars pressure gauge limit.

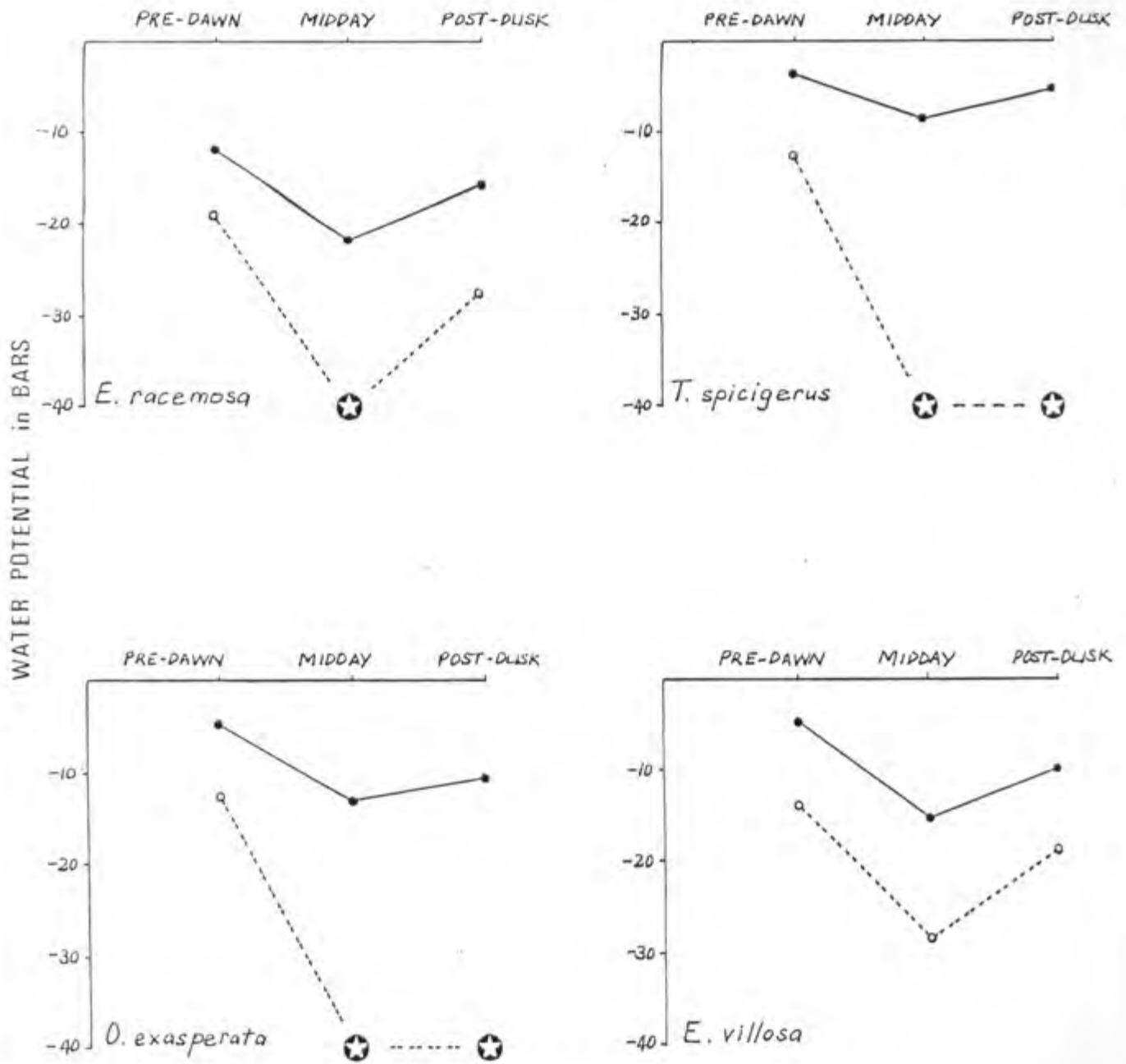


Fig.8: Mean pre-dawn, midday and post-dusk water potentials of selected species in SV during summer(o---o) and winter(●—●).

☆ -40 bars pressure gauge limit.

Table 4: Seasonal osmotic potentials of selected species in SPLF, SV and RV. Values are expressed in bars (mean \pm SEM).

Vegetation Type	Species	Summer	Winter
SPLF	<u>Leucospermum parile</u>	-3,73 \pm 0,12	-1,9 \pm 0,15
	<u>Cannomois parviflora</u>	-12,9 \pm 0,84	-7,68 \pm 0,18
RV	<u>Euclea racemosa</u>	-7,4 \pm 0,62	-4,5 \pm 0,11
	<u>Calopsis vimineus</u>	-12 \pm 1,25	-7,23 \pm 0,52
SV	<u>Euclea racemosa</u>	-6,4 \pm 0,46	-4,4 \pm 0,06
	<u>Ehrharta villosa</u>	-10,93 \pm 0,125	-10,8 \pm 0,49

4. DISCUSSION

The results indicate that soil moisture becomes more scarce during summer (fig.5), especially in soil from SPLF. However, in following the trends of water potentials (fig. 6-8) greater stresses are observed in species from RV and SV. These observations can therefore not readily be related to moisture content per volume of soil.

Diurnal and seasonal variations of water potential were previously reported for species in other mediterranean vegetation types. Poole & Miller (1975) showed that differences in magnitude of seasonal water potential variations in selected chaparral species depended on aspect and distance from the coast. Studies by Griffin (1973) and Krause & Kummerow (1977) also indicate seasonal alteration in plant water relations for chaparral species. Recently it has been shown that fynbos species also follow the same seasonal and diurnal patterns in terms of water potential (Miller et al., 1983; Miller et al., 1984). Species studied in this investigation exhibited similar trends. These results are coincident with those of other observers (Sommerville, 1983; Miller et al., 1983; Miller et al., 1984) working with the same species but not necessarily in the same areas.

It appears as if increased water availability during winter generates two distinctive patterns of response in terms of water potentials.

Broad-leaf sclerophyllous shrubs of RV (E. racemosa) and SV (E. racemosa and Q. exasperata) display dramatic increases in water potential. On the other hand a comparative deep-rooted shrub species in SPLF (L. parile) exhibits little seasonal variation in water potential. The ability of L. parile to maintain a relatively constant water potential throughout the year can perhaps be attributed to its deep rooting habit (Sommerville, 1983). Observations agree with those for many other mediterranean species (Giliberto & Estay, 1978; Poole & Miller, 1975) in that deeper rooted species exhibit higher water potentials than the shallow rooted species during periods of water stress.

All the non-restioid elements studied showed less seasonal variation in water potential in SPLF than in either RV and SV. The only species which could be considered as an exception is R. angustifolia. The unique response (high water potential during summer) could perhaps be attributed to strong xeromorphic characteristics such as its deciduous nature and pubescent leaves. The low water potentials of some members of the Restionaceae reflect different rooting depths (Sommerville, 1983). Restioids appear to use water rapidly when it is abundant and conserve water during the drier months (Miller et al., 1984).

The shrubs studied in SPLF appears to tolerate summer water deficits by maintaining higher water potentials throughout the year. The data for comperable species in RV and SV suggest a lesser degree of summer drought tolerance; species studied showed much lower water potentials. Differences in magnitude of water potentials

are also apparent between species studied in RV and SV. E. racemosa for example underwent larger seasonal changes in water potentials at SV (fig. 8). In addition, the daily pre-dawn, midday and post-dusk water potentials as well as the variation thereof were of a larger magnitude than the values recorded for E. racemosa in RV (fig. 7).

In general the water potential data for the species studied in the different vegetation types suggest differences between vegetation types in species' toleration of water deficits during summer. Species studied in SPLF showed little or no water stress, RV species a relatively higher degree of water stress and species in SV displayed the greatest degree of stress.

Differences in osmotic potential for shallow-rooted and deep-rooted species were reported for Chilean shrubs (Poole & Miller, 1978). Along a gradient of decreasing relative water content, shallow-rooted species exhibited a rapid decrease in osmotic potential while deep-rooted species showed a relatively constant decrease. No differences were found between the species of contrasting rooting habit at 100% turgidity. In this investigation, however, (1) statistically different osmotic potential were found between summer and winter for all species studied (2) deep-rooted species exhibited much higher osmotic potentials than shallow-rooted species. Unfortunately these observations cannot be directly compared with values obtained for species in other mediterranean regions because of different methods employed. Poole & Miller (1978) used the freezing point (cryoscopic) method.

Osmotic potential data obtained during this investigation lend support to the trend of decreasing water use efficiency from SPLF to RV to SV. Of the deep-root species, the osmotic potential of L. parile (SPLF) was the highest during summer (-3 bars). E. racemosa collected for both RV and SV showed the lowest osmotic potential during summer indicating that this species more readily employed osmotic regulation in coping with water deficits.

Differences in seasonal foliage area between the vegetation types are also apparent. No quantitative foliage area indices are available in a comparable form for all three vegetation types and comparisons are based on suggestions by E.J. Moll (pers. comm.) and personal observations of seasonal patterns in this regard. The high annual component of SV and RV after the first rains results in a dramatic increase of foliage projective cover (FPC) of the understorey during winter. An increase in FPC of the overstorey of SV and RV during winter could be attributed to the strong deciduous character of certain species in these communities. In contrast, the FPC of SPLF remained relatively constant throughout the year.

If increasing foliage area is related to higher water losses as suggested by Poole et al., (1981) then SV and RV appear to differ from SPLF in seasonal water utilization patterns. A relatively constant FPC in SPLF suggests little or no stress during periods of water deficits. SV and RV, on the other hand, appear to experience some form of stress in that these communities reach

a maximum foliage area only when water is readily available. These apparently different patterns of water conservation is an extension of the suggestion expressed earlier that the dynamics of SPLF communities are influenced to a lesser degree by moisture than is the case for RV or SV.

On the basis of soil moisture content data, one would expect species from SPLF to exhibit a relatively higher degree of moisture stress than species in SV or RV. SPLF species, on the contrary, appear to have a superior ability to cope with the moisture régime unlike SV or RV species. It therefore appears unlikely that community attributes in these vegetation types are determined by moisture alone.

Differences in community ecology of mediterranean-type communities have been linked with differences in the soil nutrient status of these communities (Specht et al., 1983). Recently, quantitative comparable data have become available in the form of total soil phosphorous content for these communities. Soils of RV and SV communities were found to have 169 and 422 ug P g^{-1} dry mass respectively (Witkowski et al., 1984). The total soil phosphorous content for soils supporting SPLF communities was estimated at 33 to 38 ug g^{-1} dry mass (Mitchell et al., 1984). These studies suggest the following gradient in terms of soil phosphorous content:

SV > RV > SPLF.

In Australia, phosphorous is assumed to have selected for sclerophylly (Beadle, 1966). Nutrient deficiencies and seasonal variation of moisture availability was suggested to explain some aspects of community structure in mediterranean-type ecosystems (Specht et al., 1983). Observations made during this investigation suggest a close relationship between the degree of moisture stress and the distribution of SV, RV and SPLF communities. Studies quoted here indicate that these communities are also distributed along a soil phosphorous content gradient. It is my contention that nutrients, especially phosphorous, and moisture have a strong interplay in segregation of SV, RV and SPLF communities. Phosphorous limitations appear to ^{be} of over-riding importance in determining ecological attributes of SPLF communities. A high degree of moisture stress could be considered as of superior importance in SV communities and RV could be thought of as having an arbitrary central position in terms of control by moisture and phosphorous limitations.

5. CONCLUSION

The diurnal courses and seasonality patterns in water relations of the species investigated were found to be similar for species for species of mediterranean regions in Chile(Gilberto & Estay,1978) and California(Poole & Miller,1978). Species differences could be related to rooting depths. Patterns of water utilization, however, must be viewed in the context of various physiological characteristics before a total understanding is reached in this regard.

Although observed differences in soil moisture content were not reflected in the water use patterns of the species investigated, soil moisture is recognized as a determinant of community ecology of the vegetation types studied. Further, it is suggested that differences in soil phosphorous content is also associated with vegetation form. The validity of these suggestions depends on quantitative evidence that the observed water relation patterns could be extrapolated to the entire community. Sampling also needs to be at more frequent intervals to adequately illustrate differences in this regard. In addition, direct comparable measurements on soil nutrient supply power and plant uptake ability are needed to clearly define the role of phosphorous as a determinant of vegetation form.

The methods used for measuring water potentials and osmotic potentials appear to be sufficiently sensitive to illustrate seasonal and diurnal variation within any one species as well as differences between species. It should be remembered, however, that the results only

show relative differences. It is possible that the pressure chamber technique is an overestimation of the true magnitude of the xylem sap tensions.

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APPENDIX

Relative Humidity and Temperature at the time water potentials were recorded.

		17.1	80
		23.8	90
		23.4	80
04/05/81	18:00	23.7	87

Temp.: Temperature in °C

R.H.: Relative Humidity in %

Vegetation Type	Date	Time	Temp.	R.H.
SPLF	05/03/84	06h15	16,2	70
	"	12h00	28,1	50
	"	18h45	20,8	70
RV	04/03/84	06h15	13,9	90
	"	12h00	25,0	55
	"	18h45	19,4	80
SV	06/03/84	06h15	18,7	80
	"	12h00	25,6	60
	"	18h45	22,5	75
SPLF	04/08/84	07h00	7,2	92
	"	12h00	16,4	70
	03/08/84	19h00	15,2	80
RV	05/08/84	07h00	12,0	90
	"	12h00	14,4	80
	04/08/84	19h00	13,7	87

Vegetation Type	Date	Time	Temp.	R.H.
SV	06/08/84	07h00	12,0	91
	"	12h00	15,5	85
	"	19h00	13,4	88