

# Water stress as a factor influencing the distribution of the ericoid shrub *Philippia evansii* in the Natal Drakensberg mountains, South Africa

C.S. Everson and C.M. Breen

Department of Botany, University of Natal, Pietermaritzburg

Xylem pressure potential ( $\Psi_p$ ) was measured in *Philippia evansii* plants growing on a cool, south aspect and a warm, valley bottom site. There were no significant differences in the minimum  $\Psi_p$  values (min  $\Psi_p$ ) between sites during the day despite differences in the water vapour pressure deficit (VPD). It is deduced that *P. evansii* plants are sensitive to water loss with  $\Psi_p$  values stabilizing at ca -1100 kPa by the control of transpirational flux. In spite of the higher VPD measured at the warmer site, pre-dawn values of  $\Psi_p$  (base  $\Psi_p$ ) were more negative at the cool site. Since plants were experiencing water stress on the cool southern slopes at night, it appears that conditions on the northern slopes would be too dry for colonization by *P. evansii* plants. It is concluded that the indirect effects of radiation on the water balance are important factors controlling the distribution of *P. evansii*.

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Die xileëmdrukpotensiaal ( $\Psi_p$ ) van *Philippia evansii* plante, wat op die koel suidelike glooiings en die warm valleibodems groei, is bepaal. Daar was geen noemenswaardige verskille in die minimum  $\Psi_p$ -waarde (min  $\Psi_p$ ) tussen groeiplekke gedurende die dag nie ten spyte van verskille in die dampdruktekorte. Dit is afgelei dat *P. evansii*-plante sensitief is vir waterverlies en dat transpirasie hul  $\Psi_p$ -waarde op ongeveer -1100 kPa stabiliseer. Ten spyte van die hoër dampdruktekort (VPD) wat by die warmer toetsgebied geheers het, was die  $\Psi_p$ -waarde wat voor dagbreek verkry is en wat as verwysingswaarde gebruik is, laer by die koeler toetsgebied as by die warmer toetsgebied. Aangesien plante op die koeler suidelike glooiings gedurende die nag waterspanning ondervind het, wil dit voorkom asof toestande teen die noordelike glooiings te droog sal wees vir koloniserings deur *P. evansii* plante. Daar is tot die gevolgtrekking gekom dat die indirekte invloed van uitstraling op die waterbalans 'n belangrike faktor is wat die verspreiding van *P. evansii* beheer.

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C.S. Everson\*

Present address: Cathedral Peak Forestry Research Station, Private Bag X1, Winterton, Natal, 3340 Republic of South Africa

C.M. Breen

Department of Botany, University of Natal, P.O. Box 375, Pietermaritzburg, 3200 Republic of South Africa

\*To whom correspondence should be addressed

## Introduction

*Philippia evansii* N.E. Br. is a woody pioneer invading grasslands protected from fire (Killick (1963). It occurs in the sub-alpine belt (1 829–2 865 m) of the Natal Drakensberg mountains (Granger 1976). Invasion is largely restricted to slopes having a south or south-east aspect. Since these aspects intercept least radiant energy in the southern hemisphere, Granger & Schulze (1977) hypothesized that they constituted a more mesic environment than other aspects with similar slopes, and thus provided favourable sites for colonization by *P. evansii*.

This study investigated the seasonal and diurnal changes in xylem pressure potential,  $\Psi_p$ , of *P. evansii* growing at two sites; a valley bottom site intercepting high radiant energy, and a site on a steep south facing slope. Although it was not possible to study plants on north facing slopes, since none occurred on those sites, we postulated that if the plants on the south facing slopes exhibited low water potentials, then the lower water balance associated with north facing slopes might be sufficient to exclude *P. evansii*, thus supporting the hypothesis of Granger & Schulze (1977). If the south aspect plants did not show low water potentials then although not conclusive, Granger & Schulze's hypothesis would be less attractive.

## The study area

This study was carried out at Cathedral Peak State Forest (29°00'S, 29°15'E, Figure 1). *P. evansii* was uncommon in

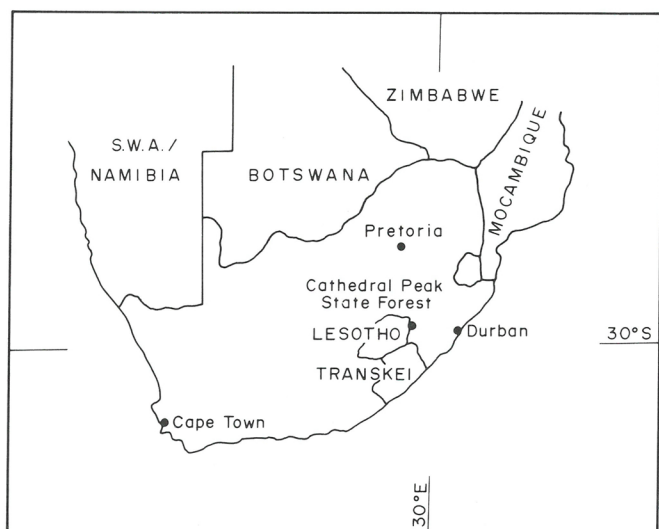
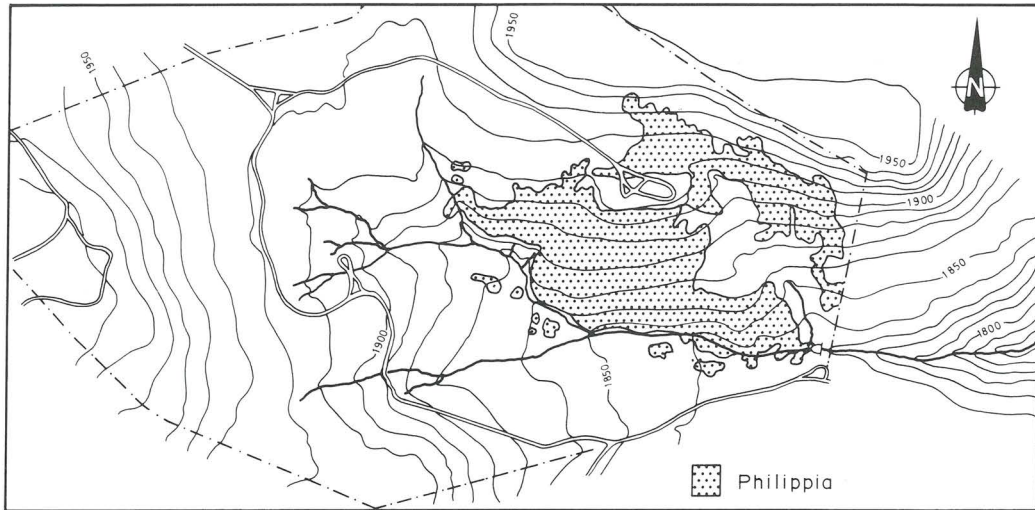


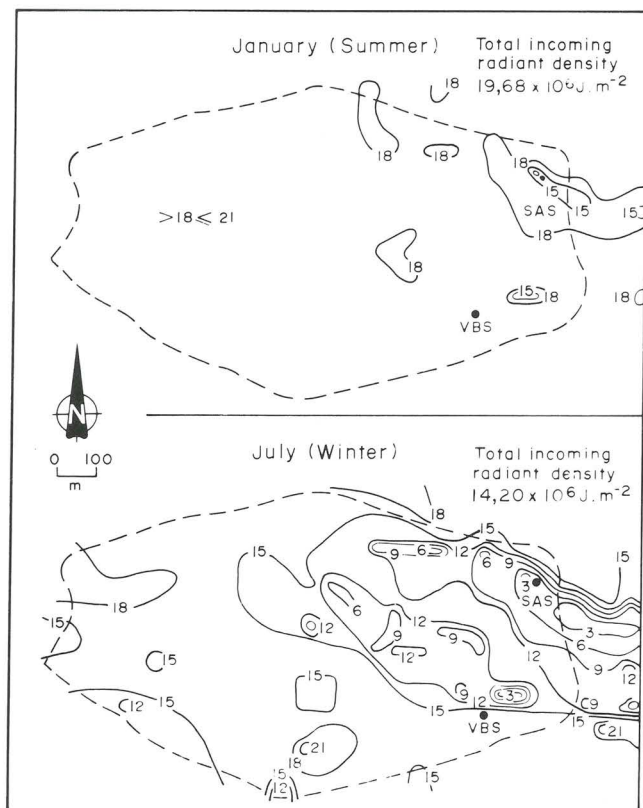
Figure 1 The locality of Cathedral Peak State Forest in South Africa.



**Figure 2** Contour map of Catchment IX showing that *Philippia* dominated communities are largely confined to south aspect sites (after Granger 1976). In 1952 *Philippia* occurred only as isolated plants along the stream (Killick 1963).

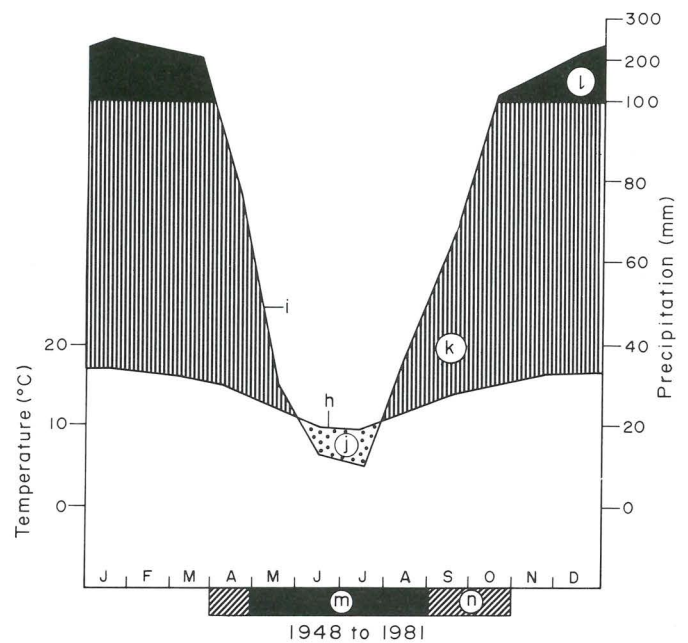
one small catchment (Catchment IX) until the catchment was protected from fire (Granger 1976). The last fire occurred in 1964, and since then *P. evansii* has advanced from the valley bottom up the slopes with a southerly aspect (Figure 2). These slopes intercept slightly less radiant energy than the valley bottom and north aspect slopes during summer, and 28% less during the winter (Figure 3). In summer the difference is further reduced by the prevalence of cloudy conditions. Summers

are wet and humid whilst winters are cold and dry (Figure 4). Maximum between site differences in radiant flux density thus occur during the dry winter and early spring when soil water availability is expected to be lowest and water demand highest. Aspect is thus expected to exert the greatest influence on  $\Psi_p$  at this time.



**Figure 3** Maps showing the daily distribution of incoming radiation density ( $\times 10^6 \text{ J m}^{-2}$ ) in Catchment IX in summer (January) and winter (July). High solar altitudes in summer increase the total incoming radiation but reduce the influence of slope and aspect on radiation interception. Greatest between site differences occur on cloudless winter days. Total net incoming radiation in summer is lower than expected because of the prevailing cloudy conditions (after Granger 1976). VBS – valley bottom site; SAS – south aspect site.

- a Cathedral Peak
- b 1 817m
- c 22-33
- d 13,9°C
- e 1 380mm
- f 5,0°C
- g -2,3°C



**Figure 4** A climatic diagram representing a period of 33 years (1948–1981), for the central meteorological station at Cathedral Peak. The symbols and figures on the diagram have the following meaning: a. station; b. height above sea level; c. number of observation years (first figure for temperature, second for precipitation); d. mean annual temperature; e. mean annual precipitation; f. mean daily minimum temperature of the coldest month; g. lowest absolute minimum temperature recorded; h. monthly mean temperatures; i. monthly precipitation; j. drought period; k. humid period; l. mean monthly precipitation exceeding 100 mm with scale reduced to 1/10; m. months with mean daily grass minimum less than 0 °C; n. months with absolute grass minimum less than 0 °C (after Walter 1979).

## Materials and Methods

Plant water potential was measured using the pressure chamber method of Scholander *et al.* (1965). We did not calibrate the pressure chamber values against leaf water potential (Boyer 1967; Ritchie & Hinckley 1975) and the values are therefore 'relative' indicators of xylem pressure potential ( $\Psi_p$ ). Estimates of  $\Psi_p$  were carried out on site, and measurements were obtained within two minutes after excision of the shoot from the plant. To prevent phloem exudate from obscuring the end point, the phloem and bark were stripped back a short distance from the cut surface. Only 1–2 mm of stem was allowed to extend beyond the chamber. Once the shoot was sealed in the pressure chamber, the pressure was increased at a rate of *ca* 70 kPa s<sup>-1</sup> until the end point was reached. Ten samples were required to give a standard error within 10% of the mean.

Diurnal variation in  $\Psi_p$  was estimated eight times between April 1976 and August 1977. Mean  $\Psi_p$  estimates taken at approximately three-hourly intervals during the day were used to estimate total daily  $\Psi_p$  ( $\Sigma\Psi_p$ ) and net daily  $\Psi_p$  (net  $\Psi_p$ ) using the following equations:

(a) total daily  $\Psi_p$ :

$$\Sigma\Psi_p = \Sigma \frac{(\Psi_{p1} + \Psi_{p2})}{2} (t_2 - t_1) + \frac{(\Psi_{p2} + \Psi_{p3})}{2} (t_3 - t_2) + \frac{(\Psi_{pn-1} + \Psi_{pn})}{2} (t_n - t_{n-1})$$

where  $\Psi_p$  = mean xylem pressure potential at *t* hours.

(b)  $\Sigma$ base  $\Psi_p$ :

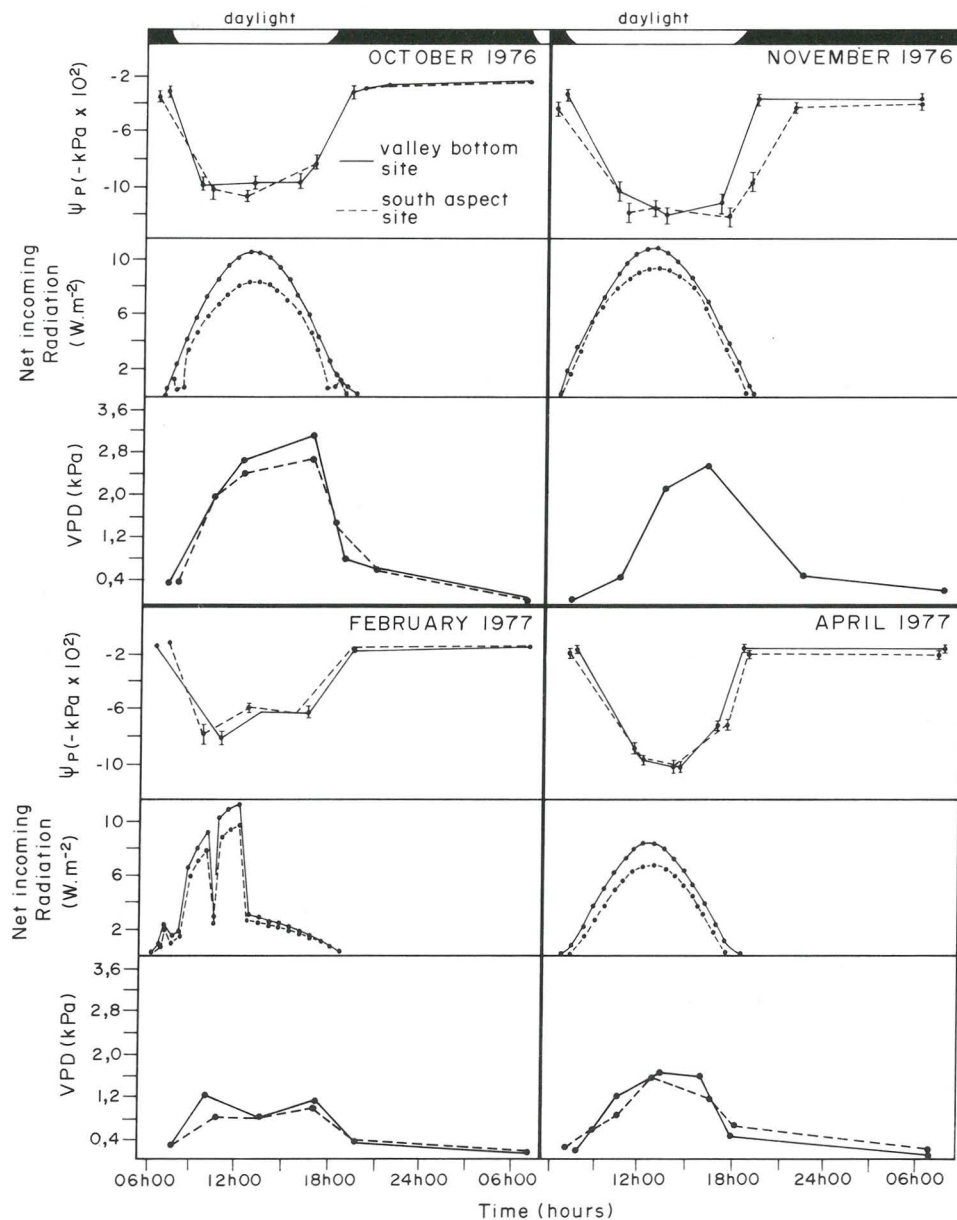
$$\Sigma \text{base } \Psi_p = (\text{base } \Psi_p) (t_n - t_1)$$

where base  $\Psi_p$  = mean reading at *t* hours.

(c) net daily  $\Psi_p$ :

$$\text{net } \Psi_p = \Sigma\Psi_p - \Sigma \text{base } \Psi_p \text{ (after Haas \& Dodd 1972).}$$

Net incoming radiation was not measured directly, but was predicted for each site and occasion by the input of measured two-hourly sunshine duration intervals into the radiation model for the Cathedral Peak area (Schulze 1974). Rainfall in Catch-



**Figure 5** Summer: Diurnal march of xylem pressure potential ( $-kPa$ ), net incoming radiation ( $W m^{-2}$ ) and vapour pressure deficit ( $kPa$ ) at the study sites. Vertical lines represent the 95% confidence limits.

ment IX was measured continuously by two Casella\* recording gauges and weekly totals were obtained from a Snowdon\* gauge. Atmospheric temperature and relative humidity were measured with a Casella wet and dry-bulb whirling hygrometer\*. Water vapour pressure deficit (VPD) was determined from the estimates of air temperature and atmospheric relative humidity (Schulze 1974). Soil moisture was measured gravimetrically (Gardner 1965) from two depths, 0–249 mm and 250–500 mm. Moisture content was expressed as a percentage of the dry weight after oven drying at 105 °C for 48 hours.

**Results**

**Radiation interception**

In summer the valley bottom site (VBS) intercepted 28% more radiant energy than the south aspect site (SAS), but in winter the difference increased to 56% because the SAS was shaded for longer in the morning and afternoon and received a lower maximum radiation (Figures 5 & 6).

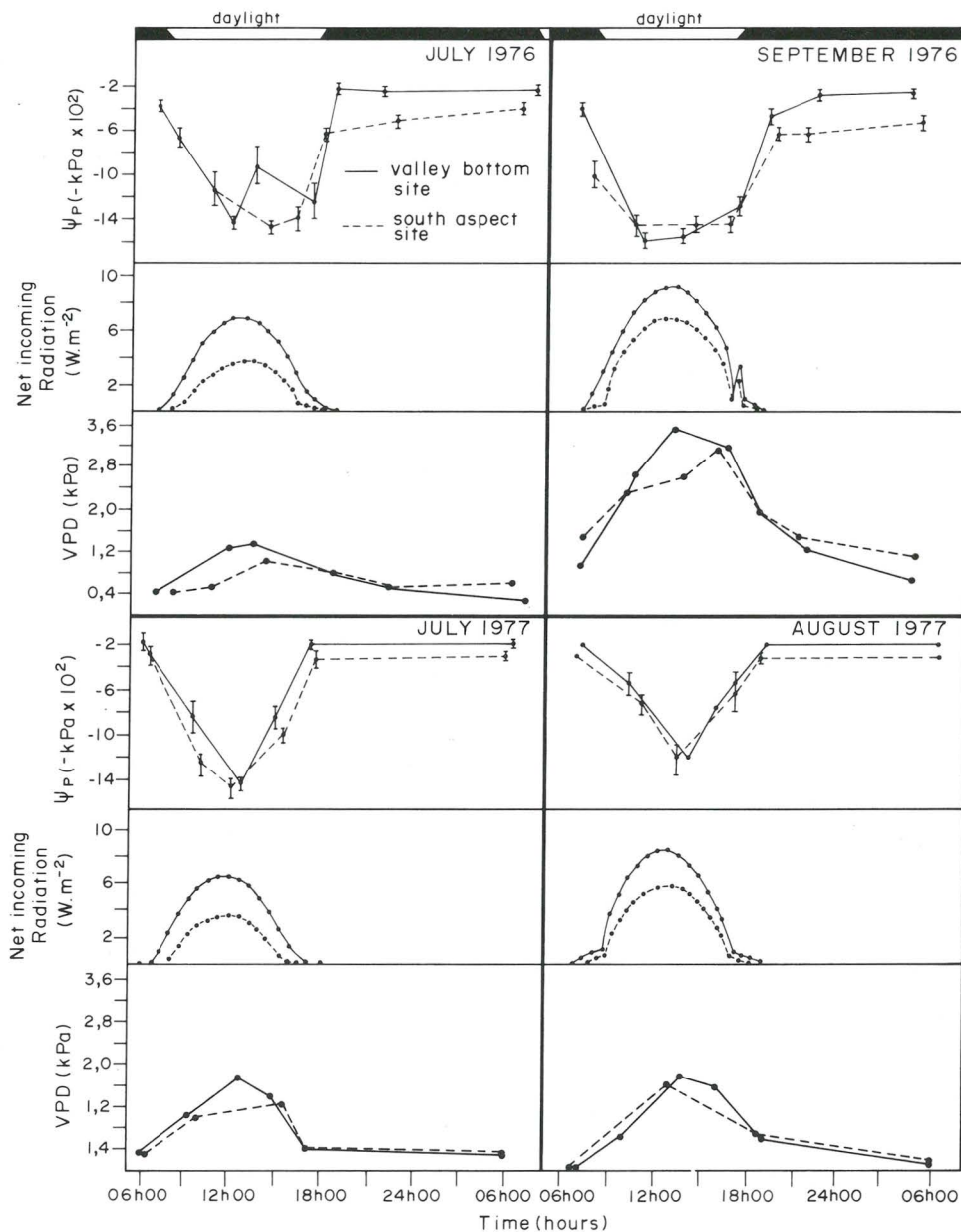
\*Trade names and company names are included for the benefit of the reader and are not endorsed by the authors.

**Precipitation**

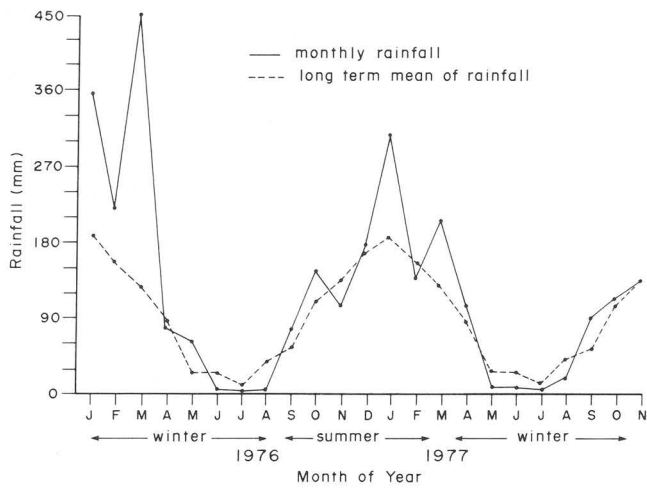
Rainfall distribution showed marked seasonality, being low in winter and high in summer. During this study winters were drier and summers wetter than usual (Figure 7). Over a 92-day winter period (late May to the end of August) in 1976 only 2,2 mm of precipitation were recorded and over 113 days in autumn and winter (late April to late August) of 1977, 10 mm of rain were measured. These long dry periods coincided with the greatest differences of radiation interception between sites.

**Vapour pressure deficit**

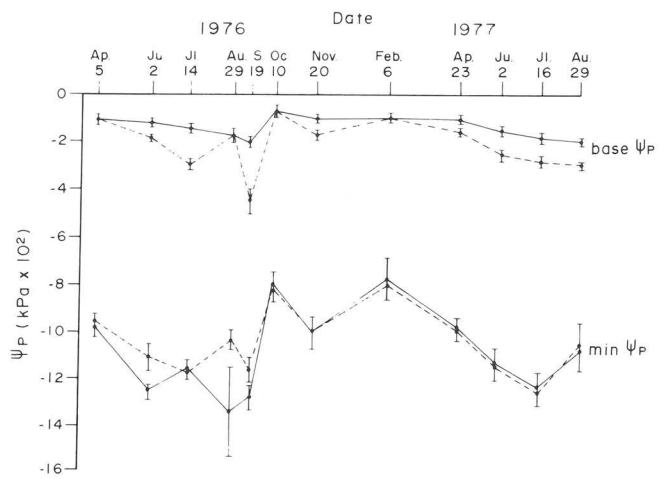
Diurnal estimates of VPD exhibited increases towards mid-day, declining in the afternoon and remaining low at night (Figures 5 & 6). When compared with the SAS, the VBS experienced greater deficits during the day and smaller deficits at night when cold moist air accumulated in the valley. When the total daily VPD is compared seasonally (Figure 8), it is evident that during 1976 the VBS generally experienced greater total VPD than the SAS. During 1977 the sites were similar. There is no conclusive evidence that the differences were more



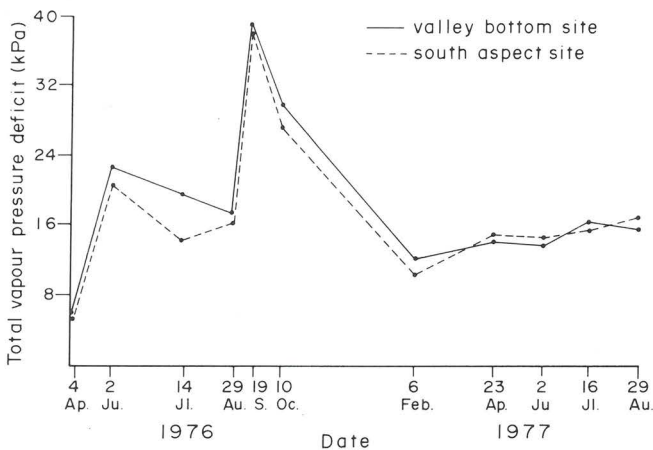
**Figure 6** Winter: Diurnal march of xylem pressure potential ( $-kPa$ ), net incoming radiation ( $W m^{-2}$ ) and vapour pressure deficit ( $kPa$ ) at the study sites. Vertical lines represent the 95% confidence limits.



**Figure 7** Monthly rainfall in Catchment IX during the study period (1976 and 1977). Plotted on the same axes are the long term means of monthly rainfall (base period 8 years). Long term data after Granger (1976).



**Figure 9** Mean pre-dawn (base  $\Psi_p$ ) and daily maximum water stress (min  $\Psi_p$ ) during 1976 and 1977. Vertical lines represent the 95% confidence limits.



**Figure 8** Total vapour pressure deficit ( $\Sigma VPD$ ) calculated from the diurnal estimates of VPD measured periodically throughout 1976 and 1977. Note that  $\Sigma VPD$  was much lower in 1977 than in 1976, indicating less atmospheric stress. Site differences in VPD were greater in 1976 than in 1977.

pronounced during the dry period. This is to be expected since air turbulence would tend to reduce between-site differences.

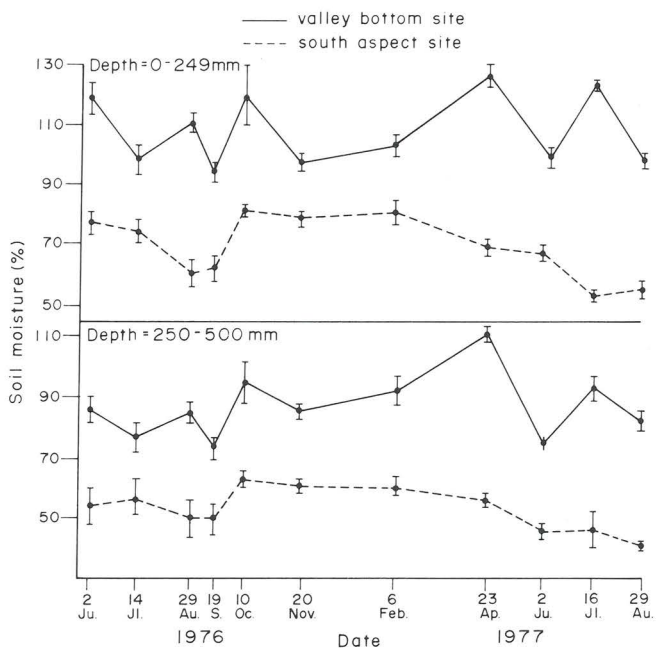
**Xylem pressure potential**

The diurnal pattern of  $\Psi_p$  during the summer period (October to February) is depicted in Figure 5. In February 1977, at the end of the wet summer,  $\Psi_p$  declined from  $-100$  kPa at 07h00 to  $-900$  kPa at 10h30 after which there was no significant change until 12h30 when it began to increase. By 16h00  $\Psi_p$  was  $-650$  kPa, and the base  $\Psi_p$  of  $-100$  kPa was reached by 18h00. Sites were not significantly different. The pattern was similar in April with favourable water status being rapidly reinstated in the late afternoon. Clearly, soil moisture was in adequate supply. It was not until July in both years (Figure 6) that there was evidence of greater stress in the SAS plants. It became apparent with a significant decrease in base  $\Psi_p$ , indicating that the plants at the SAS were experiencing difficulty in replacing water loss by uptake from the soil. This pattern became more pronounced in August and September when at 06h00 the difference in base  $\Psi_p$  between sites could be as much as 200 kPa, despite the fact that base  $\Psi_p$  at the VBS had decreased from  $-100$  kPa in February (summer) to  $-200$  kPa in September (Figure 9). Towards the end of the dry period,

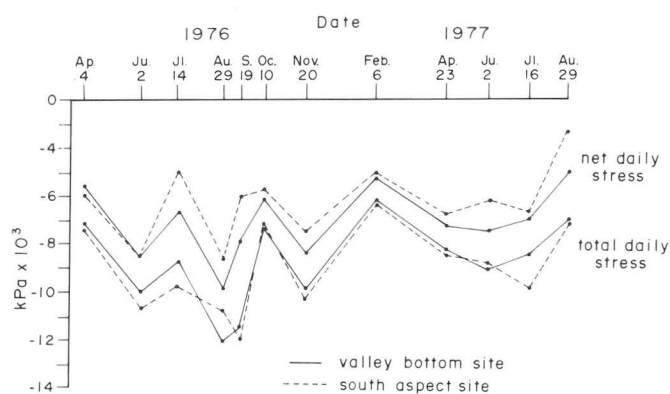
the plants in the valley bottom were also experiencing enhanced stress.

Despite the apparent shortage of soil moisture, min  $\Psi_p$ , although decreasing from summer to winter (*ca*  $-900$  kPa in February to *ca*  $-1200$  kPa in July, Figure 9), was not significantly different between sites. This could imply that the differences in net radiation between sites were not reflected in the water balance of the plant but may also indicate control of water loss by stomatal closure. Min  $\Psi_p$  also showed a distinct trend towards becoming more negative with decreasing soil moisture, and then increasing to summer levels following the first rains (Figures 7 & 10).

Total daily stress was only occasionally found to differ significantly between sites (Figure 11). These differences arose principally as a result of base  $\Psi_p$  becoming more negative (Figure 6) because min  $\Psi_p$  remained more or less constant during the study. Since min  $\Psi_p$  consistently declined to *ca*  $-1100$  kPa despite increasingly negative base  $\Psi_p$ , which is indicative of low  $\Psi_{soil}$ , it can be postulated that min  $\Psi_p$  was controlled by stomatal closure.



**Figure 10** The seasonal pattern of soil moisture (%) at the valley bottom and south aspect sites at two depths (i.e. 0-249 and 250-500 mm) during 1976 and 1977. Vertical bars represent the 95% confidence limits.



**Figure 11** Accumulated values of total daily stress ( $\Sigma\Psi_p$ ) calculated from the diurnal water stress ( $\Psi_p$ ) measured periodically throughout 1976 and 1977.

### Soil moisture

At the VBS there was no predictable trend in soil moisture (Figure 10). For example in the 0–249 mm zone it increased from 98 to 123% between June and July 1977 despite no rainfall being recorded. Variability between samples of soil made it impossible to develop a reliable moisture characteristic curve and thus to infer the amount of available soil moisture (Everson 1979). The Bainsvlei-Wilgenhof soil at the VBS has a diagnostic G horizon which is by definition saturated with water for a greater part of the year by the presence of a more or less permanent water table (MacVicar *et al.* 1977). The fact that the VBS is situated in low lying land and that base  $\Psi_p$  was always low, would favour the hypothesis that water was freely available for most of the year, even during the dry months. In contrast, soils at the SAS sites had moisture contents of 60% in August 1976 and 53% in July 1977 which are at or below the –1500 kPa permanent wilting point (PWP) for this soil (Everson 1979). Since the plants did not wilt and die at this site their PWP must be less than –1500 kPa and therefore the generally accepted –1500 kPa PWP is not applicable to *P. evansii*.

There was generally more available water in the deeper soil (Everson 1979), but the stress patterns evident in the seasonal study of xylem pressure potential (Figures 5 & 6), together with the observation that *P. evansii* is shallow rooted with most roots radiating outwards at about 100 mm depth (Everson 1979), imply that this was not available to the plants.

### Discussion

#### Xylem pressure potential: relationship with net radiation and VPD

Sutcliffe (1968) and Slavik (1974) have emphasized the significance of solar radiation as a factor governing the water relations of plants. In this study,  $\Psi_p$  was significantly correlated with net radiation and VPD at both sites (Table 1). Similar observations led Haas & Dodd (1972) to suggest that an accumulated value of VPD ( $\Sigma\text{VPD}$ ) could be used to predict daily water stress in honey mesquite. Their results indicated that net daily  $\Psi_p$  (net  $\Psi_p = \Psi_p - \text{base } \Psi_p$ ; Ritchie and Hinckley 1975) was sensitive to more of the environmental variables than  $\Psi_p$  and showed a close linear relationship between net  $\Psi_p$  and  $\Sigma\text{VPD}$  when soil moisture relationships were favourable. In this study the regression of net  $\Psi_p$  on  $\Sigma\text{VPD}$  for the 24-hour diurnal curves was not significant (Table 1), perhaps because water was not always freely available and base  $\Psi_p$  became more negative, reducing net  $\Psi_p$ .

The regression of  $\Psi_p$  on  $\Sigma\text{VPD}$  was, however, significant but because the 95% confidence limits were extremely broad ( $\pm 3790$  kPa) over a total range of only 5800 kPa during the study, it was not possible to use  $\Sigma\text{VPD}$  to predict  $\Psi_p$ . Thus it was not possible to use estimates of relative humidity and air temperature to predict daily water stress in *P. evansii*.

#### Xylem pressure potential: relationship with soil moisture

Ritchie & Hinckley (1975) have suggested that if plants are able to reach equilibrium with the soil overnight then base  $\Psi_p$  can be used as an index of soil moisture potential. In this study base  $\Psi_p$  was significantly negatively correlated with soil moisture at the SAS but not at the VBS (Table 1). This supports the contention that in the soils at the VBS, water was usually freely available whereas it was not at the SAS.

The minimum xylem pressure potential ( $\text{min } \Psi_p$ ) reflects the balance between transpirational flux and water uptake (Ritchie & Hinckley 1975). Thus as the availability of soil water declines,  $\text{min } \Psi_p$  is expected to decrease unless the plant exerts control over transpiration. The significant negative correlation found between  $\text{min } \Psi_p$  and soil moisture at the SAS indicates that  $\text{min } \Psi_p$  became more negative as soil water availability declined (Table 1). This evidence was insufficient to suggest that *P. evansii* had no control over transpirational flux, because control is effected at different leaf water potentials in different species (Bannister 1971; Tobiessen & Kana 1974). In an investigation of  $\text{min } \Psi_p$  at six sites on clear sunny days during June and July of 1976,  $\text{min } \Psi_p$  was not found to vary significantly, reaching a mean minimum of –1078 kPa with a range of –910 to –1200 kPa (Everson 1979). Since soil water availability was known to be below the –1500 kPa PWP at one of the sites during these observations and not at others, these data show that *P. evansii* closed its stomata when the  $\text{min } \Psi_p$  was ca –1100 kPa. Richter (1976) has summarized the range of minimum values for total water potential; they range from –16300 kPa in the desert plant *Artemisia herba-alba* to –3200 kPa in *Prosopis glandulosa* growing in an area experiencing pronounced drought periods. The  $\text{min } \Psi_p$  value for *P. evansii* was high, even for woody plants of mesic sites, and it must be concluded that it is sensitive to water stress. Bannister (1964), in a study of members of the Ericaceae, concluded that the *Erica tetralix* may be restricted to the wetter areas because of its greater sensitivity to water stress, whereas *Calluna vulgaris*, which is more widespread, was more tolerant of a wide range of water deficits. *P. evansii* appears to be most similar to *E. tetralix*.

**Table 1** Correlation coefficients for plant water stress ( $\text{min } \Psi_p$ ; base  $\Psi_p$ ; net  $\Psi_p$ ;  $\Psi_p$ ) with soil moisture, VPD and net radiation at both the low radiation (SAS) and high radiation (VBS) sites

Correlation	Number of samples	Coefficient	Significance
$\Psi_p$ on net radiation (SAS)	57	0,63	$p < 0,001$
$\Psi_p$ on net radiation (VBS)	50	0,55	$p < 0,001$
VPD on net $\Psi_p$ (SAS & VBS)	24	0,20	ns
VPD on $\Psi_p$ (SAS & VBS)	24	0,45	$p < 0,02$
Soil moisture on base $\Psi_p$ (SAS)	12	0,47	$p < 0,05$
Soil moisture on base $\Psi_p$ (VBS)	12	0,43	ns
Soil moisture on $\text{min } \Psi_p$ (SAS)	12	0,61	$p < 0,05$
Soil moisture on $\text{min } \Psi_p$ (VBS)	12	0,0	ns

## Conclusions

The results demonstrate that aspect and site influence the amount of radiation intercepted and this affects significant differences in vapour pressure deficit. The *P. evansii* growing on the southern aspect slope experience considerable water stress during the dry winter months when soil moisture may decline below the  $-1500$  kPa permanent wilting point. The plants are sensitive to water loss and stabilize xylem pressure potential at *ca*  $-1100$  kPa by controlling transpiration. Conditions are expected to be more extreme on north aspect slopes in the southern hemisphere (Armesto & Martinez 1978; Holland & Steyn 1975), perhaps more than can be tolerated by the shallow-rooted *P. evansii*. The data therefore support the hypothesis of Granger & Schulze (1977) that water stress may be a major factor restricting the colonization of north aspect slopes by *P. evansii*. An enigma remains however; why has *P. evansii* been so successful in colonizing the south aspect sites where it experiences considerable water stress and yet it has been singularly unsuccessful in expanding its range in the valley bottom where it suffers much less water stress? Clearly, water stress is only one of a number of factors controlling succession.

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## References

- ARMESTO, J.J. & MARTINEZ, J.A. 1978. Relations between vegetation structure and slope in the mediterranean region of Chile. *J. Ecol.* 66: 881–889.
- BANNISTER, P. 1964. The water relations of certain heath plants with reference to their ecological amplitude, II. Field Studies. *J. Ecol.* 52: 481–497.
- BANNISTER, P. 1971. The water relations of heath plants from open and shaded habitats. *J. Ecol.* 59: 51–64.
- BOYER, J.S. 1967. Leaf water potentials measured with a pressure chamber. *Plant Physiol.* 42: 213–217.
- EVERSON, C.S. 1979. Autecological studies on *Philippia evansii* N.E. Br. with particular reference to water relations. M.Sc. thesis. University of Natal, Pietermaritzburg.
- GARDNER, W.H. 1965. Water content. In: Methods of Soil Analysis 1, eds. Black, Evans, White, Ensminger & Clark. Number 9 in the series Agronomy, Ch. 7, American Society of Agronomy Inc., Madison, Wisconsin, U.S.A. pp.82–127.
- GRANGER, J.E. 1976. The plant succession and some associated factors in Catchment IX, Cathedral Peak Research Station, Ph.D. thesis, University of Natal, Pietermaritzburg.
- GRANGER, J.E. & SCHULZE, R.E. 1977. Incoming solar radiation patterns and vegetation response: examples from the Natal Drakensberg. *Vegetatio* 35(1): 47–54.
- HAAS, R.H. & DODD, J.D. 1972. Water stress patterns in honey mesquite. *Ecology* 53: 674–680.
- HOLLAND, P.G. & STEYN, D.G. 1975. Vegetational response to latitudinal variations in slope angle and aspect. *J. Biogeogr.* 2: 179–183.
- KILLICK, D.J.B. 1963. An account of the plant ecology of the Cathedral Peak Area of the Natal Drakensberg. *Bot. Surv. Mem., S. Afr.* No. 34 Govt Printer, Pretoria.
- MACVICAR, C.N., LOXTON, R.F., LAMBRECHTS, J.J.N., LE ROUX, J., DE VILLIERS, J.M., VERSTER, E., MERRY-WEATHER, F.R., VAN ROOYEN, T.H. & VON M. HARMSE, H.J. 1977. Soil classification. Science Bulletin 390. The Department of Agricultural Technical Services, Republic of South Africa.
- RICHTER, H. 1976. The water status in the plant: experimental evidence. In: Ecological Studies 19, Water and plant life problems and modern approaches, eds. Lange, O.L., Kappen, L. & Schulze, E.D., Springer-Verlag.
- RITCHIE, G.A. & HINCKLEY, T.M. 1975. The pressure chamber as an instrument for ecological research. *Adv. Ecol. Res.* 9: 165–254.
- SCHOLANDER, P.F., HAMMEL, H.T., BRADSTREET, E.D. & HEMMINGSEN, E.A. 1965. Sap pressure in vascular plants. *Sci.* 148: 339–346.
- SCHULZE, R.E. 1974. Catchment evapotranspiration in the Natal Drakensberg. Ph.D. thesis, University of Natal, Pietermaritzburg.
- SLAVIK, B. 1974. Methods of studying plant water relations. Springer-Verlag, Berlin.
- SUTCLIFFE, J.F. 1968. Plants and water. Institute of Biology's Studies in Biology no. 14, Edward Arnold Ltd.
- TOBIESSEN, P. & KANA, T.M. 1974. Drought-stress avoidance in three pioneer tree species. *Ecology* 55: 667–670.
- WALTER, H. 1979. Vegetation of the earth and ecological systems of the geo-biosphere. Springer-Verlag, New York.