

**COMPARATIVE WATER RELATIONS OF PROTEA NITIDA
SEEDLINGS AND SPROUTERS AFTER FIRE**

BY

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PROTEA NITIDA

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ABSTRACT

This study was undertaken to determine the effect of vegetation structure (the ratio of re-seeding to re-sprouting plants) on post-fire catchment water yield. Plant communities are the only components of mountain catchments which can be manipulated to augment water supplies on any practical scale. Burning, which is one of the options available to catchment managers, reduces plant biomass and increases water yield by reducing transpiration and interception losses.

Communities dominated by re-seeding species tend to recover more slowly after fires than when sprouters predominate. The rate of vegetation recovery will determine the rate at which streamflow returns to pre-fire levels. Sprouters may use more water than seeders in the early post-fire period by virtue of their greater leaf area, which both increases interception and transpiration losses. Leaf area development could be used as a simple determinant of post-fire water yield if transpiration losses per unit leaf area are similar in seedlings and sprouters.

In this study, a comparison was made of the transpiration rates of seedlings and sprouters of Protea nitida after a fire in Swartboskloof (Cape Province) in 1987. Plant water potentials were determined (index of the degree of stress) and leaf stomatal conductances were measured.

Results indicate that transpiration rates are similar throughout the year except during the short summer drought period when the seedlings have comparatively low transpiration rates ($< 1 \text{ mmol m}^{-2} \text{ s}^{-1}$ compared to 2-3 $\text{mmol m}^{-2} \text{ s}^{-1}$ of the sprouter), and

immediately after the first winter rains where the seedlings have comparatively high rates (approximately $4 \text{ mmol m}^{-2} \text{ s}^{-1}$ compared to $2 \text{ mmol m}^{-2} \text{ s}^{-1}$). The low summer rates are thought to be the result of drought stress induced by limited water supply and the shallow root systems of the seedlings. The higher winter rates suggest that the shallow surface roots of the seedlings respond quickly to increased surface moisture. Differences in root structure (i.e. shallow seedling roots and well-developed deep sprouter roots) rather than regeneration mode appear to be responsible for the marginal differences observed in transpiration rates. These differences are expected to disappear as seedling roots develop and occupy the profile. Leaf area could therefore, be used as a determinant of catchment water yield

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Plant communities are the only components of mountain catchment ecosystems which may at present be manipulated for water supply control on any practical scale (Kruger and Wicht, 1976; Bosch *et al.*, 1984; Versfeld, 1985). Changes in water yield are therefore directly related to changes in plant biomass (Wicht, 1971) with most water vapour being lost through transpiration in vegetated areas (Kattlemann *et al.*, 1983). On a catchment scale, the water balance equation for a gauged, leakproof catchment is as follows:

$$\text{PRECIPITATION} = \text{EVAPOTRANSPIRATION} + \text{STREAMFLOW} \pm \text{STORAGE}$$

The storage term is frequently ignored in the long term when dealing with annual water balance, and the evapotranspiration term comprises largely of transpiration losses in vegetated areas - the rest being soil and water evaporation and rainfall interception by vegetation (Kruger and Wicht, 1976; Versfeld, 1985).

The sclerophyllous shrubland vegetation characterising the catchments of the southwestern Cape Province, South Africa, is commonly known as fynbos and comprises three basic components: Proteaceae, Restionaceae and Ericaceae. In these catchments, the percentage of water lost by evapotranspiration is less than that from afforested catchments, varying from 40 % to 60 % in comparison with 50 % to 90 % in afforested catchments. In fynbos catchments where transpiration losses are higher than 50 %, a 10 % increase in the transpiration rate will lead to a proportionally larger drop in streamflow.

Catchments in South Africa are managed primarily to maintain an optimum sustainable yield of water of the highest possible quality (Wilson, 1985). Burning, which is one of the management options available in mountain catchments (Kruger and Wicht, 1976), is carried out to reduce fire hazard, maintain streamflow, control invasive plants and rejuvenate the fire-adapted vegetation (Wilson, 1985). Burning reduces plant biomass and therefore has a marked influence on catchment water yield by reducing

transpirational losses (Bosch *et al.*, 1984). Results from experimental burns in South African shrublands are inconsistent but show that fires usually produce short-lived increases in catchment water yield (Bosch *et al.*, 1984; Lindley, 1985; Lindley *et al.*, 1988). Bosch *et al.* (1986) have argued that the length of time over which streamflow remains higher than baseflow will depend on the vegetation type or condition (pristine or degraded) and on the canopy recovery rate.

The rate of canopy recovery depends on the pre-fire composition of the fynbos community, especially the ratio of re-seeding to re-sprouting plants. The relative abundance of these life forms is influenced by fire frequency; short fire cycles (i.e. intervals less than the juvenile period of seeders) favour sprouters (especially graminoids), longer fire cycles favour seeders with the shrub communities becoming senescent (van Wilgen, 1982; Kruger & Bigalke, 1984).

Virtually all fynbos plants attain reproductive maturity within 10 years post-fire. Obligate seed regenerating species are often eliminated from a community should fires occur before they reach maturity. Therefore frequent burning (< 10 years) reduces biomass by eliminating most obligate re-seeding shrubs (Van Wilgen & Kruger, 1981) which usually make up the greatest part of the biomass (Van Wilgen *et al.*, 1985). Sprouters are more resilient to changes in fire frequency as they start producing flowers and fruit at a much earlier stage post-fire (3-4 years) (Keeley, 1986). Therefore it is theoretically possible to manipulate the relative abundance of seeders and sprouters in a fynbos catchment by manipulating the fire regime.

Little is known, however, of the water relations of plants following fire in fynbos ecosystems. Sprouters, with their rapid post-fire canopy development, will obtain their full biomass at an early stage post-fire while seeders will take longer to develop their canopies, but may eventually equal or exceed sprouter biomass (Figure 1). Sprouters may therefore use more water than seeders in the early post-fire period by virtue of their greater leaf area, which increases both interception and transpiration losses. It may be possible to use leaf area development as a simple determinant of post-fire catchment water yield if transpiration losses per unit leaf area of seedlings and sprouters are similar.

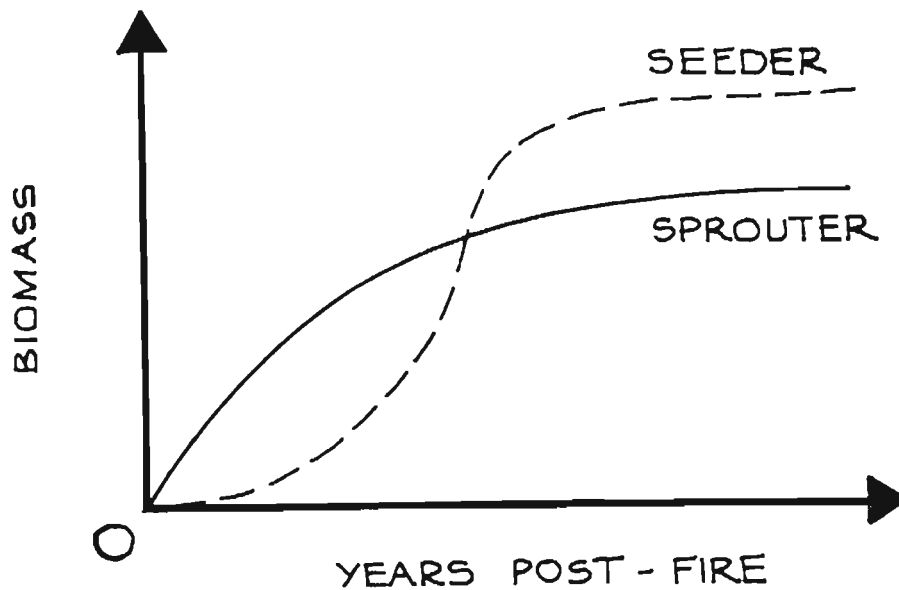


Figure 1: The hypothetical development of seeder and sprouter dominated canopies after a fire in a fynbos catchment.

Mediterranean ecosystems are heterogenous in composition and exist as a mosaic comprising xeric as well as mesic elements, with a wide variety of root systems (Kummerow, 1981). Adequate information on the below ground biological processes is needed to complete the picture of plant community dynamics (Hoffmann and Kummerow, 1978), especially with the development of ecophysiological and other models used to simulate plant growth, catchment water balance, or to predict effects of fire on water yield (Kruger *et al.*, 1985; Bosch *et al.*, 1986). Most studies in the past have concentrated on above-ground plant parts and processes, with data on below-ground processes being relatively scant. This is due to the difficulties in assessing root growth dynamics and due to frustrating difficulties with root excavations because of the extreme rockiness of mediterranean ecosystem terrains (Kummerow, 1981). This is also true for fynbos where the only studies conducted have been by Low (1983, 1984), Hoffmann and Mitchell (1986), Rutherford (1981) and Higgins *et al.* (1987), contributing to information on the fynbos root systems but leaving immense scope and need for further studies.

This study tests the assumption that seedlings and sprouting individuals of Protea nitida have similar transpiration rates and hence that leaf area (cover or above-ground biomass) can be used as a simple determinant of post-fire changes in water yield. It forms part of a broader study (Smith and Richardson, in prep) encompassing a number of obligate and facultative seeders and sprouters of representative fynbos species. Protea nitida was chosen for this study because of its ability to regenerate successfully after fire both vegetatively and by seedling establishment. This enables comparisons to be made between these regeneration forms without the additional complexities of anatomical and morphological differences which could arise should different species have been used. Obligate and facultative seedlings may however have different growth rates or may differ in their ability to endure environmental stress for instance, and therefore care must be taken in generalising or extrapolating these results without verification from other re-seeders and sprouters. Leaf xylem pressure potentials (as a indicator of water stress) and stomatal conductances were determined for both regeneration forms throughout the study period, and transpiration rates were estimated. The relationships between environmental and plant response factors were also examined. Root systems of both regeneration forms were excavated to determine their lateral and vertical distributions.

CHAPTER 2: MATERIALS AND METHODS

2.1 RESEARCH SITE AND SPECIES DESCRIPTION

2.1.1 The research site

The study was conducted in the Swartboskloof catchment in the Jonkershoek Valley (33° 57'S, 18° 55'E) near Stellenbosch in the south-western Cape Province. Swartboskloof is a 373 ha catchment which was under mature (29 yr old) sclerophyllous heathland until a planned fire cleared the area in March 1987. It has a mediterranean climate with warm, dry summers and cool, wet winters. Mean maximum and minimum temperatures for February (hottest month) are 27.3 and 14.5 °C and those for July (coldest month) are 16.8 and 6.2 °C. Mean annual rainfall is 1 475 mm of which 67 % falls between May and September (Richardson and Fraser, in press). The site indicated by an arrow on Figure 2 has a slope of four degrees, an altitude of 350 m and is north-facing. The soil is a mixture of granite and quartzite and its form is classified as Oakleaf (Series 31/34) (Macvicar *et al.*, 1977). It is moderately drained with a varying percentage of stones and boulders in the profile (Fry, 1987) being as shallow as 40 cm in places.

The dominant vegetation type on the study site is Jonkershoek Mesic Proteoid Fynbos which comprises a tall (2-3 m), open to closed, overstorey of proteoid shrubs with a 1 m high understorey (Campbell, 1985; Mc Donald, 1985).

2.1.2 Species distribution, description and regeneration features

Protea nitida Mill. was chosen for this study because of its ability to regenerate after fire both vegetatively (sprouter) and generatively (from seedlings). This enabled valid comparisons to be made between seeders and sprouters without the additional complexities of anatomical and morphological differences which could arise should different species have been used. Differences (should they occur) in transpiration rates or plant water relations in general, can therefore be ascribed almost entirely to differences between mature shrubs and seedlings. Sprouters differ from seedlings, having

well-established deep root systems capable of extracting water from larger areas and from greater depths. Their canopies are fully exposed to sunlight and not shaded by the mid-high re-sprouting shrub layer. Inter- and intra-specific competition is less than for seedlings.

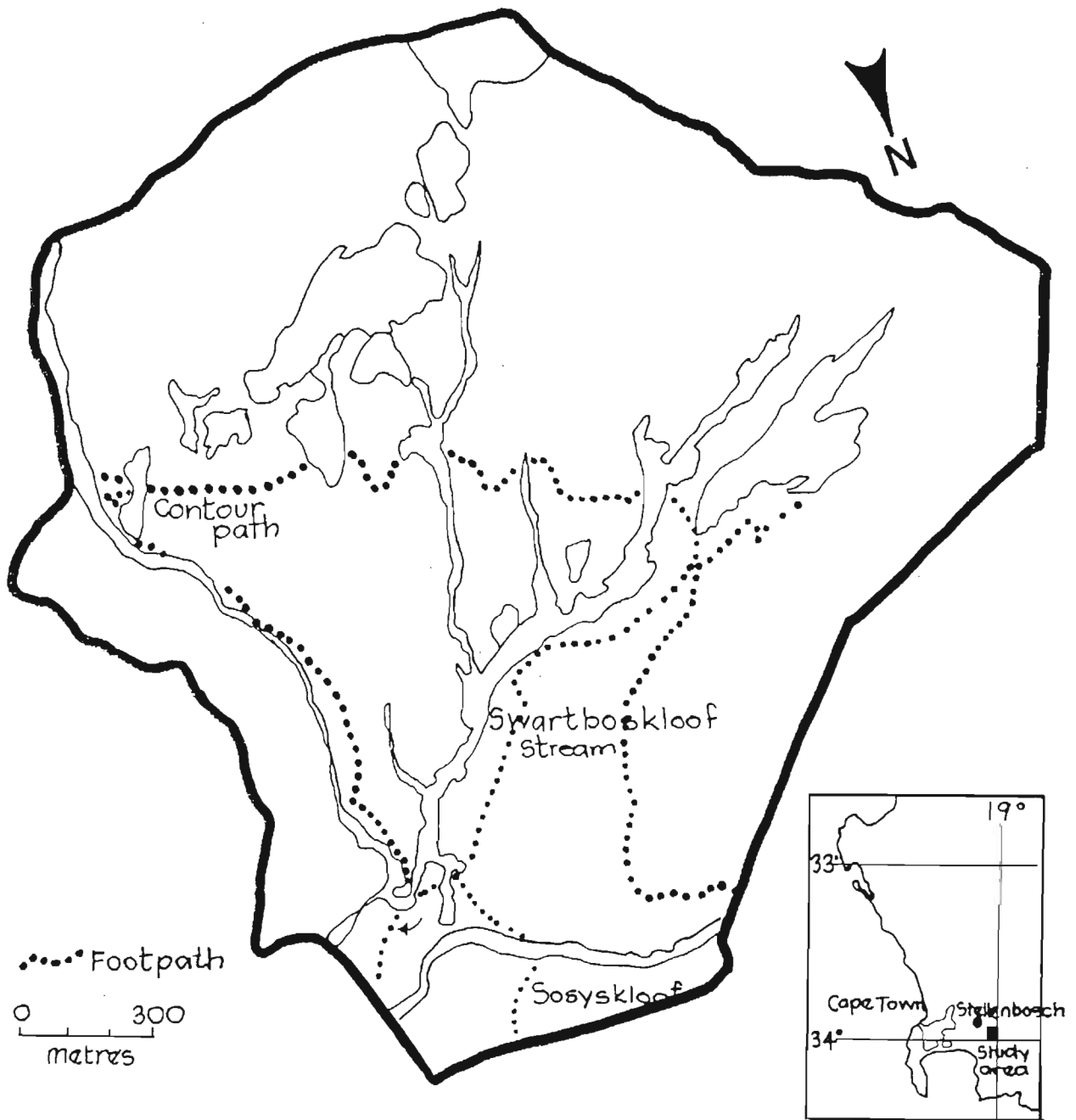


Figure 2: The study site situated in the Swartboskloof catchment of the Jonkershoek Valley near Stellenbosch. The site is indicated by an arrow.

Protea nitida is found throughout the southern and south-western folded mountain region with its distribution stretching from Van Rhynsdorp in the north-west Cape to the Van Stadens mountains near Port Elizabeth in the eastern Cape (Rourke, 1980). It is considered to be an element of a distinct community throughout most of the fynbos zone (Kruger, 1979). Protea nitida is typically a small, gnarled tree up to 5 m tall, with a whitish bark and grayish-white foliage arranged in an irregular crown. The leaves are sessile, oblong and glabrous and glaucous grey (Rourke, 1980). Leaf angle is approximately 12.5 degrees from the vertical (Kruger et al., 1988). It is rarely solitary and usually occurs in a low open woodland formation. Flowering occurs erratically through the year, peaking in winter (Rourke, 1980). Protea nitida normally grows on rocky slopes at altitudes below 1200 m (Vogts, 1982) on relatively mobile talus slopes, or coarse colluvial fans (Kruger, 1979). The soils are generally sandy loams or stony loamy sands, moderately acid with low organic content in the A-horizon (Bond, 1981).

Protea nitida regenerates after a fire predominantly by means of dormant epicormic buds protected beneath a thick layer of bark (up to 40 mm) on the stems and branches, or from subterranean lignotubers, or both (Kruger, 1979; Rourke, 1980). Seed reproduction also occurs freely after fire, with the seedlings forming lignotubers within two to three years (Kruger, 1979). This variety of post-fire regeneration modes illustrate a high degree of fire resistance. Seed regeneration however, is usually the less effective survival strategy in a fire climate as recurrent fires at short intervals (less than 5 to 10 years) threaten the survival of some of the re-seeding species which require five or more years before producing seed (Wicht, 1945; Van Wilgen, 1982). Protea nitida populations remain stable under different fire regimes, although post-fire recruitment is higher with longer fire-free intervals (Higgins and Manders, in prep).

Protea nitida is non-serotinous, releasing its seeds less than a year after flowering with less than 4% of the cones retaining their seeds for as long as a year (Bond, 1985). Seed generally takes approximately 4 weeks to germinate. The seedlings remain more or less static for several years after germination, developing a strong lignotuber first and then placing effort into shoot growth. They may take up to 8 years to reach 1 m in height. Flowering can only be expected approximately 12 years after germination (Rourke, 1980).

2.2 METHODS

This study formed part of a larger study on several fynbos seeders and sprouters in Swartboskloof. The number of replications of measurements of xylem pressure potentials and stomatal conductance was therefore limited by the time needed for each reading, the large number of species (seven species measured at half-hourly to hourly intervals). The lack of a larger number of instruments and skilled operators was an additional limitation on the scope of this study.

2.2.1 Edaphic and climatic variables

Soil water potentials were monitored with porous cup Jet Fill tensiometers (Model 2724, Soil Moisture Equipment corp., California) at three different depths (30, 45 and 60 cm). The presence of a shallow rocky layer prevented insertion of tensiometers to greater depths. These tensiometers are limited to soil water potentials higher than -80 kPa. During summer, soil water potentials often fell below this value. Soil samples were also taken during each field run to determine the gravimetric soil moisture content (SMC). Three samples from two depths were taken each field day (upper 20 cm, and 20 cm down to the rocky layer - usually 20-45 cm).

Diurnal courses of relative humidity, temperature, solar radiation, rainfall and wind speed were available from two nearby weather stations, approximately 500 m from the study site. Mean hourly values for each field day were calculated from readings made at one minute intervals.

2.2.2 Xylem pressure potentials

A Scholander pressure chamber (Scholander *et al.*, 1965) was used to determine leaf xylem pressure potentials on three leaves, each from a different plant. The number of leaves used was limited due to the low number of seedlings on the study site. Additional leaves were measured only when the variation between leaves exceeded 0.15 MPa. The xylem potentials were determined twice a month (in most cases) from March 1988 (approximately one year after the fire) to November 1989. Measurements commenced before dawn (between 4:00 and 6:00 depending on the season) and were repeated at two-hourly intervals throughout the day until dusk. The sample plants were in close proximity of the chamber (within five to 10 m) and therefore measurements were usually taken within 30 seconds of the leaves being cut. Evaporative losses whilst the leaf was in the chamber were minimal. A trial study on a warm, clear day (temperature 17 °C; relative humidity 45%) showed no significant differences ($p < 0.05$) between pressure chamber readings taken with or without moist blotting paper in the chamber. Water loss is greatest prior to putting the leaves in the chamber (Pammenter, pers. obs.), and therefore it is important that the sample leaves are enclosed within plastic bags from the time of cutting until the measurements are made.

An attempt was made at constructing pressure-volume curves using the pressure chamber technique described by Tyree and Hammel (1972). This method provides a means of assessing whether seedlings and sprouters of *P. nitida* show signs of seasonal osmotic adjustment. Details on the methodology and problems experienced are given in Appendix A.

2.2.3 Stomatal conductance and transpiration

Diurnal courses of stomatal conductance were also determined twice a month, on the same days that the xylem pressure potentials were determined. Conductance and the ambient relative humidity and temperature in the vicinity of sample leaves were measured with a null-balance diffusion porometer (MSC 301 Null Balance Porometer, M C Systems, Plumstead). The principles and operation of a null-balance porometer are

described fully by Beardsell *et al.* (1972). Five leaves, one per plant for each of the seedlings (each seedling having between three and five leaves at the start of the study) and five leaves on one adult sprouter were selected from similar positions in the canopy. Due to variation in stomatal conductance between leaves within the canopy of the sprouter, a decision was made to sample more intensively within one canopy (five leaves on one tree) rather than to do one or two leaves on different plants.

Measurements were repeated on these ten leaves (five for each of the seedlings and sprouter) throughout the day at half-hourly intervals from daybreak (6:00 to 8:00 depending on season) until dusk (17:00 to 19:00). The days on which measurements were taken were standardised as far as possible with regards to weather, with clear, still days being preferable. Measurements were discontinued on days where the weather changed markedly (heavy cloud cover, rain, strong wind). The areas of the sample leaves were determined after each diurnal run and projected leaf area was used for conductance and transpiration calculations.

A comparison of the following three methods of determining transpiration is shown in Appendix B: (1) transpiration determined directly from the porometry flow rate measurements, (2) using stomatal resistances in a simplified form of the Penman-Monteith equation, and (3) the cutshoot technique. The first method using the flow rate data was chosen. Estimates of total transpiration per unit leaf area per day were obtained by determining the area under the diurnal hourly transpiration rate curves.

2.2.4 Statistical analyses: climatic, transpiration and xylem pressure potential data

A stepwise regression analysis (PROC STEPWISE in SAS; SAS inc., 1985) was done to provide some insight into the relationships between mean hourly transpiration rate, and the variables mean hourly solar radiation, ambient temperature, relative humidity and xylem pressure potentials, for the seedlings and sprouter during each season in the year. The partial correlation coefficients were calculated to determine the relative contribution of each of the independent variables to the model. Transpiration rates and xylem pressure potentials at each sampling time were taken to be the median of the readings

for each time. The climatic variables are hourly means.

The significance of the seasonal differences in daily water use of seedlings and sprouters was determined by a multiple comparison Tukey test (SAS inc., 1985) on the daily water loss (transpiration) per unit leaf area data. A 5% significance level was used.

2.2.5 Root study

Five young seedlings were excavated to determine the depth and distribution of their root systems. The sites chosen were situated on a slight (3-5 degrees) slope to facilitate water movement during the excavation process. Care was taken not to break the finer roots by using the fine spray adjustment on the nozzle as soon as the roots were exposed. The stem of each seedling was supported during the excavation. Sketches of both the lateral and vertical distribution of the roots were made (using a one by one meter grid which was sub-divided into one hundred 10 cm by 10 cm squares) when the excavations were complete. The above-ground biomass and total leaf area of each seedling was determined. The root systems were divided into 10 depth intervals (0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-40, 40-50, 50-60, 60-70 cm) and into four diameter categories (<0.5 mm; 0.5-2 mm; 2-5 mm; >5 mm) within each depth interval.

Two adult shrubs sprouters were selected 25 m away from the river: one on a steep slope (30°) and a second on a level area. The projected canopy area was determined using a vertical pole to establish co-ordinates on a set of axes. The trunk and canopy were removed and the above-ground biomass and leaf area were determined. The lateral root distribution was mapped in a similar manner as the seedlings, with the soil being divided into 10 cm levels. Root diameters and biomass were determined for each soil depth. The following diameter classes were used: < 0.5 mm, 0.5-2 mm, 2-5 mm, 5-10 mm, 10-20 mm, >20 mm. During excavations, finer roots became brittle and often broke and were lost in the soil/water debris.

CHAPTER 3: RESULTS

3.1 EDAPHIC AND CLIMATIC VARIABLES

Soil moisture content ranged from 2 % in summer to 22 % in winter (dry mass basis) in the upper 40 cm of the soil surface (Figure 3a). The data in Figure 3a are means of three readings. All three sets of tensiometers showed the same pattern of soil moisture potential throughout the year. Potentials ranged between -5 and -40 kPa throughout the season with the exception of December to March (summer to early autumn) where, due to water potentials less than -80 KPa, the tensiometers were unable to register (Figures 3d-3f). Variation in soil moisture potential at 600 mm was less than at 300 and 450 mm.

Vapour pressure deficits (Figure 3b) were highest during the dry summer period (4 kPa) and lowest during the wet winter months (dropping to 0 kPa on occasions). The soil moisture potentials and water contents also mirrored the rainfall pattern (Figure 3c) with the soil being driest between November and March where rainfall was at its lowest. Approximately 68 mm of rain fell from December to February which is less than 5 % of the total annual rainfall.

3.2 XYLEM PRESSURE POTENTIALS

Diurnal xylem pressure potential patterns were similar for seedlings and sprouters for most of the study period excluding the dry months (December to March) with hourly values (calculated as the median of the individual values) seldom more than 0.5 MPa apart (Figures 4a-d). Greater differences (up to 2.5 MPa) were evident during the summer drought.

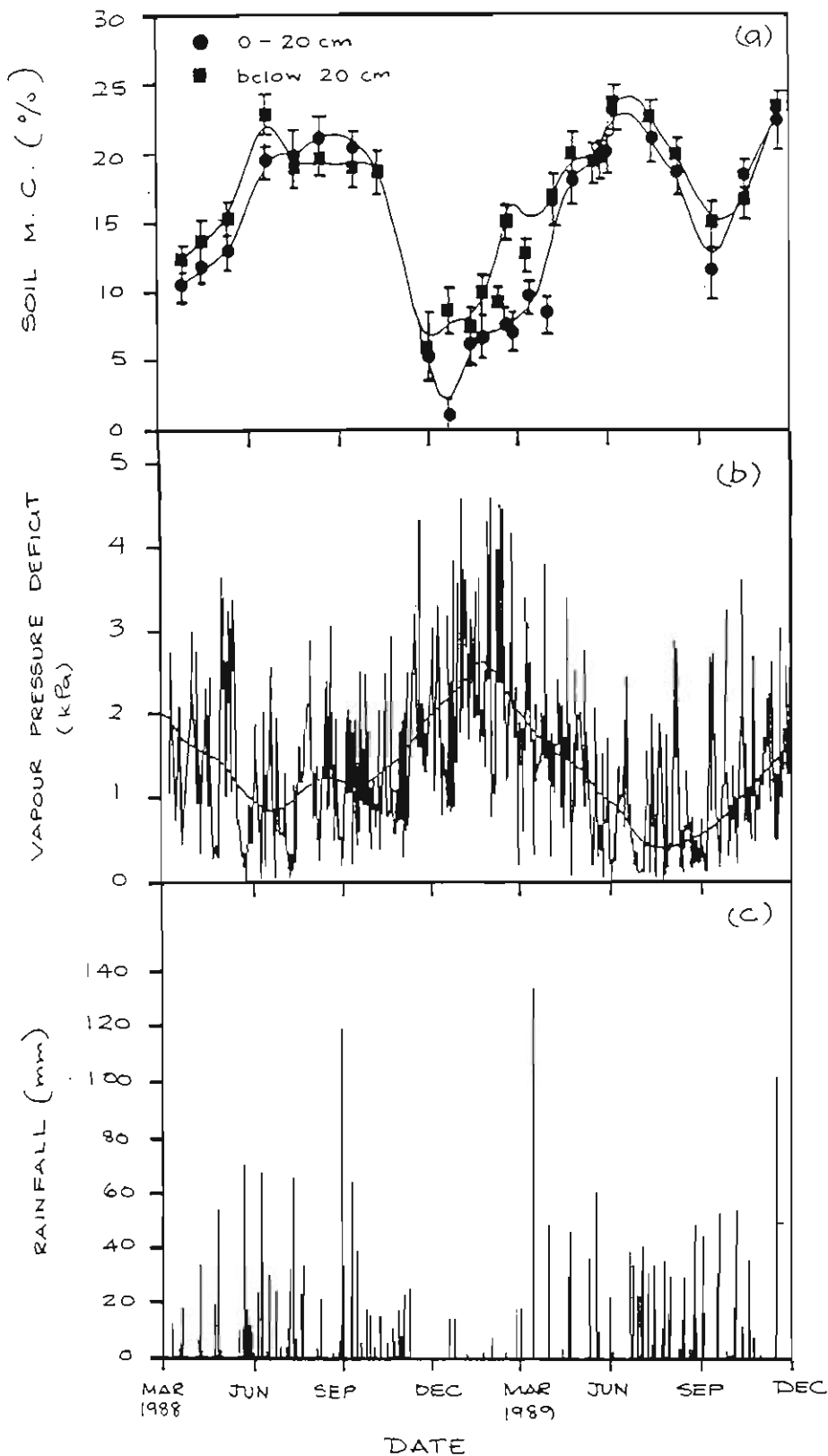


Figure 3: Seasonal fluctuations in (a) soil moisture content where the circles represent the moisture content in the upper 20 cm of the soil and the squares represent the soil from 20 cm down to approximately 45 cm (bars represent the standard deviation); (b) maximum vapour pressure deficit (the solid line is a spline function indicating the seasonal trend); (c) rainfall, for the period March 1988 to November 1989.

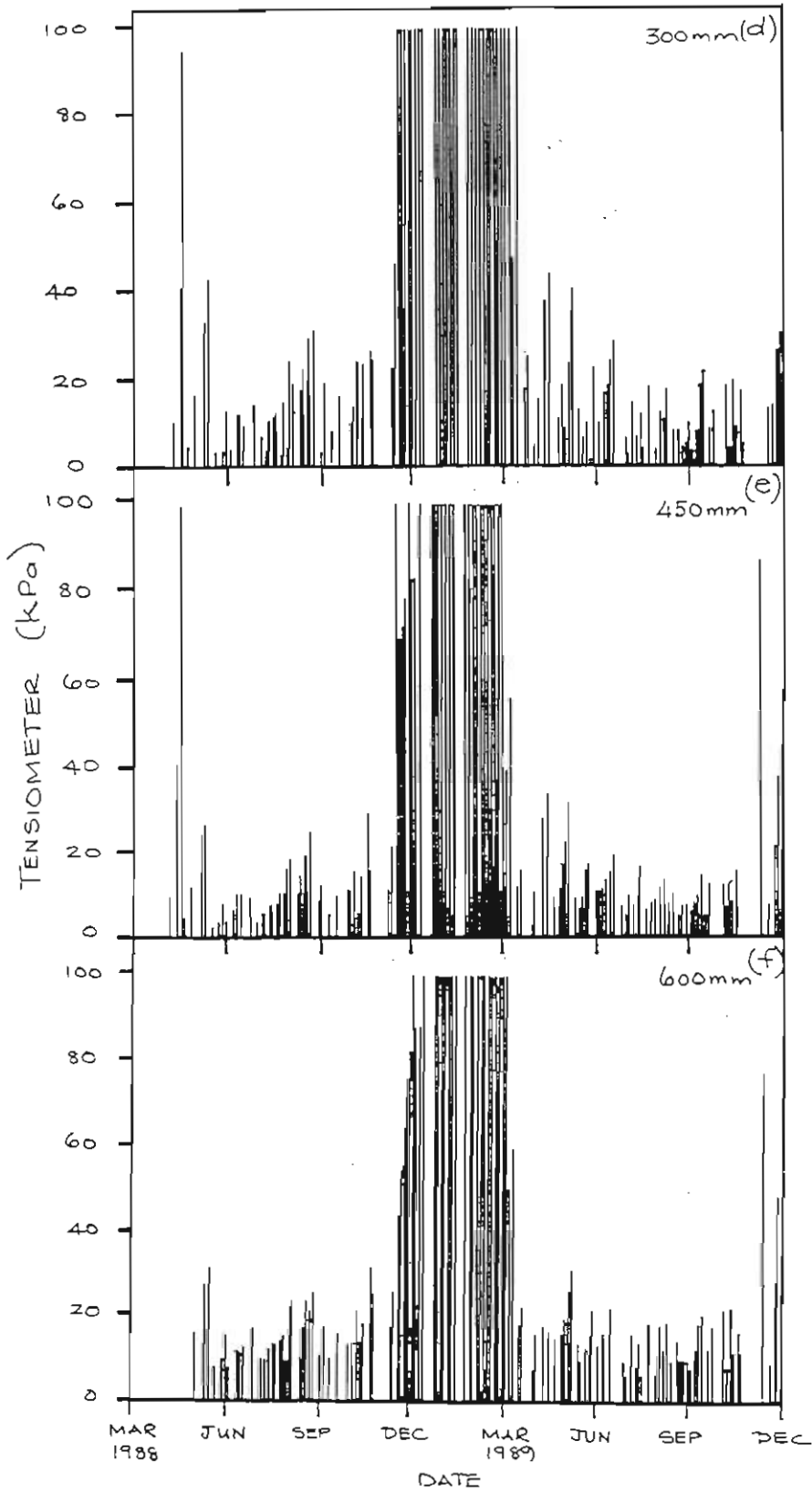


Figure 3: Seasonal fluctuations in soil moisture potentials at a depths of (d) 300, (e) 450 and (f) 600 mm respectively.

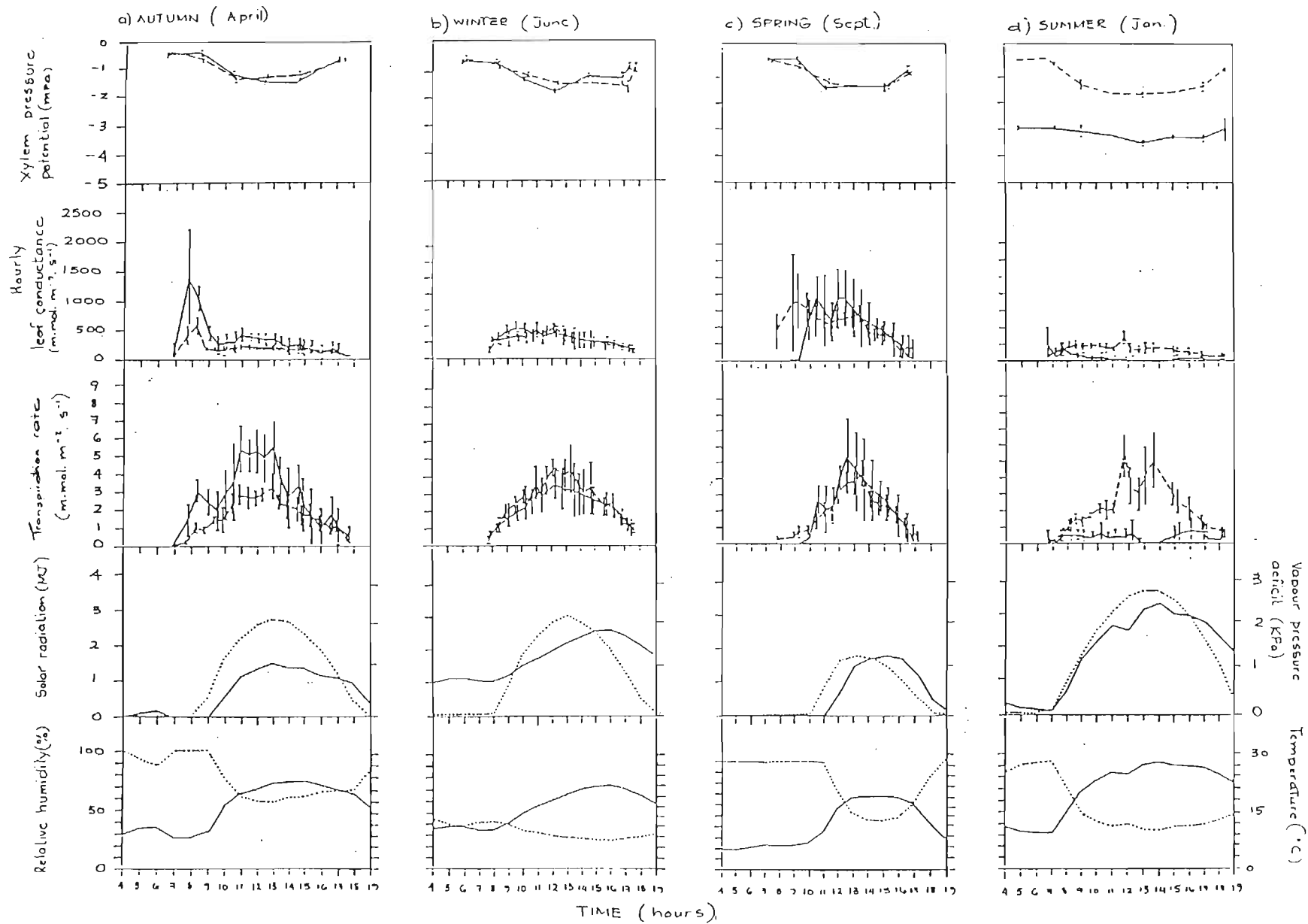


Figure 4: Characteristic diurnal xylem pressure potential (top segment), stomatal conductance (second segment) and transpiration (third segment) patterns for autumn (April 1989), winter (June 1989), spring (September 1988) and summer (January 1989) for the seedlings (solid line) and sprouter (dotted line). The bars represent one standard deviation. The solar radiation (dotted line) and vapour pressure deficit (segment 4), and relative humidity (dotted line) and temperature measurements (segment 5) are also given for each of the days.

Dusk potentials for both regeneration forms usually returned to within 0.5 MPa of predawn potentials. Sprouter potentials dropped only slightly during summer.

Seedling pre-dawn and midday leaf xylem pressure potentials (Figure 5) also varied seasonally. In the dry summer period, their pre-dawn potentials were approximately -3 MPa compared to -0.5 MPa for the sprouters (Figure 5), while midday readings dropped to approximately -4.5 MPa compared to -2 MPa for the sprouters. During the rest of the year, soil moisture levels were higher and pre-dawn and midday potentials for seedlings and sprouters were similar. The seedlings showed decreasing midday potentials with decreasing pre-dawn potentials, but this was not apparent for the sprouters (Figure 6).

3.3 STOMATAL CONDUCTANCE AND TRANSPIRATION

3.3.1 Diurnal and seasonal patterns of stomatal conductance

Diurnal patterns of stomatal conductance for seedlings resembled those of the sprouter with peak conductances usually occurring within the first three hours after stomatal opening. Characteristic diurnal stomatal conductance curves for each season are given in the second segment of Figures 4a-4d (half-hourly conductance values were calculated as the median of the five individual leaf conductances). The sprouter did not show complete midday stomatal closure, although decrease in stomatal conductance was evident during the middle of the day when temperatures and vapour pressure deficits were highest.

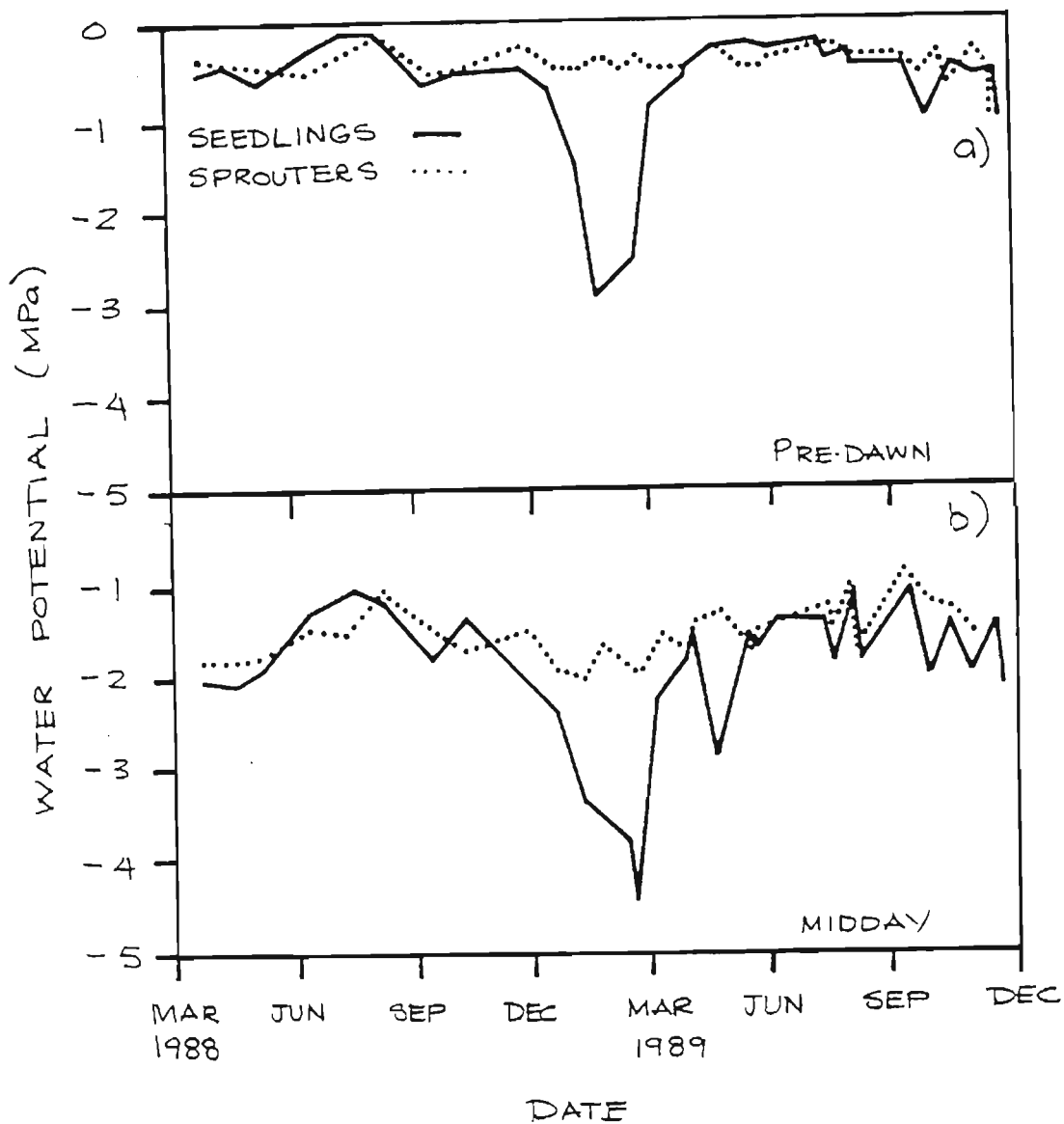


Figure 5: Seasonal pattern of (a) pre-dawn and (b) midday xylem pressure potentials for *P. nitida* seedlings (solid line) and sprouters (dotted line). Values are medians of the 3-4 measurements taken pre-dawn and at midday.

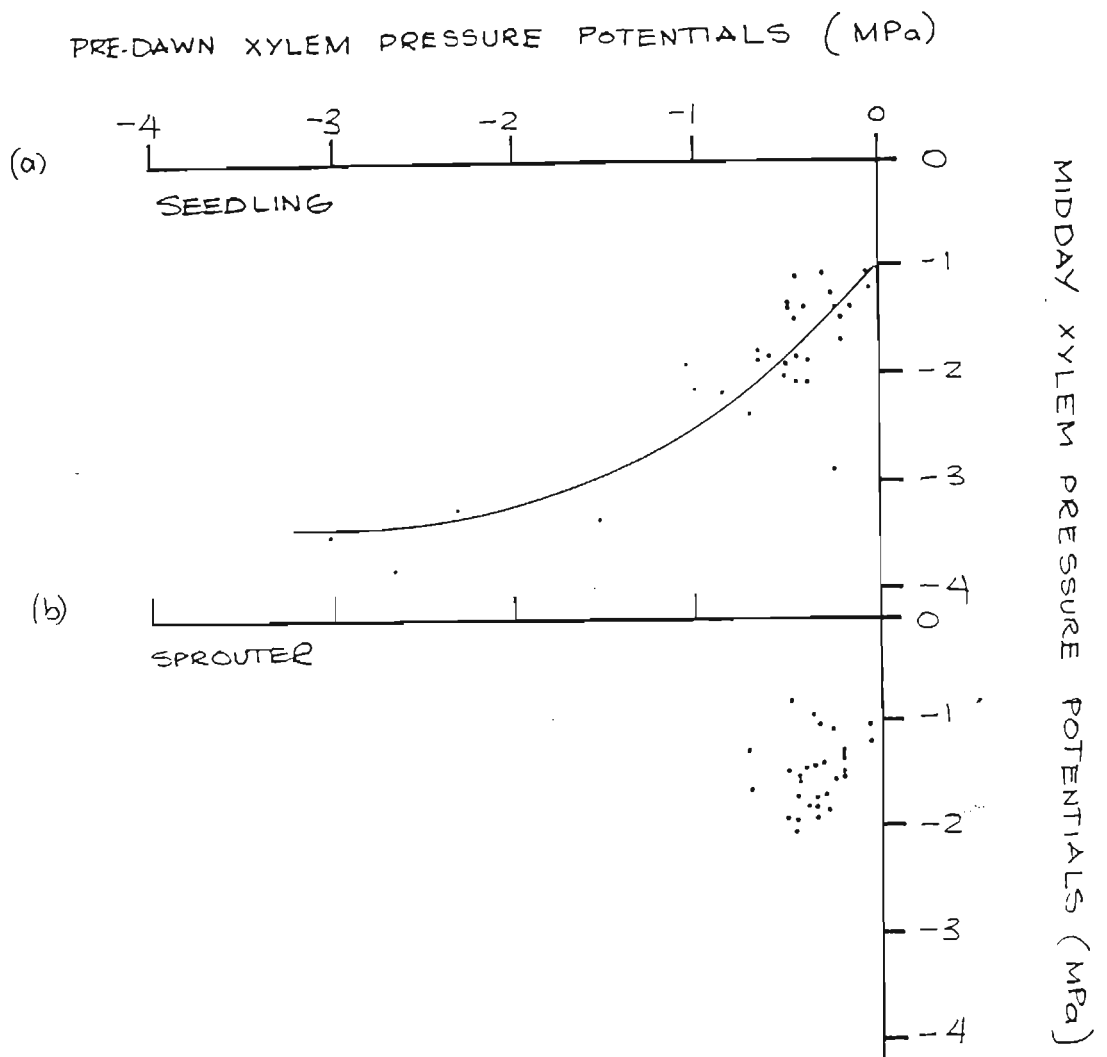


Figure 6: The response of midday xylem pressure potentials to decreasing pre-dawn xylem pressure potentials for (a) seedlings and (b) sprouters of *Protea nitida*, with the solid line in (a) indicating the trend (subjectively drawn). Values are medians of the 3-4 measurements taken pre-dawn and at midday.

During late January to mid February, seedlings closed their stomata to restrict water loss as a result of growing soil moisture deficits (seedling roots were less than 70 cm in depth in comparison with a depth of 2-3 m for the sprouters cf. Section 3.5), or increased vapour pressure deficits.

Mean (mean of all half-hourly conductances in a day) and peak (highest half-hourly conductance recorded in a day) daily stomatal conductances were similar for seedlings and the sprouter from March 1988 to early January 1989, with mean conductances ranging from 80 to 150 $\text{mmol m}^{-2} \text{s}^{-1}$ and peak conductances ranging from 100-200 $\text{mmol m}^{-2} \text{s}^{-1}$ (Figure 7). Seedling conductances dropped at the end of January until February during the worst of the summer drought period, with mean conductances ranging from 0 to 50 $\text{mmol m}^{-2} \text{s}^{-1}$ (peak conductances of 100 $\text{mmol m}^{-2} \text{s}^{-1}$). In March, seedling conductances increased to equal sprouter levels and both seedling and sprouter conductances increased as water became more freely available after the first winter rains of about 400 mm between March and April. Mean conductances for the seedlings and sprouter were similar from April 1989 until November 1989, ranging from 150-220 $\text{mmol m}^{-2} \text{s}^{-1}$, with seedlings showing fractionally higher conductances than the sprouter (Figure 7). Peak conductances however, displayed considerable fluctuations (Figure 7). Some leaf characteristics including specific leaf mass (leaf density) and stomatal densities which may have a bearing on stomatal conductances are given in Table 1.

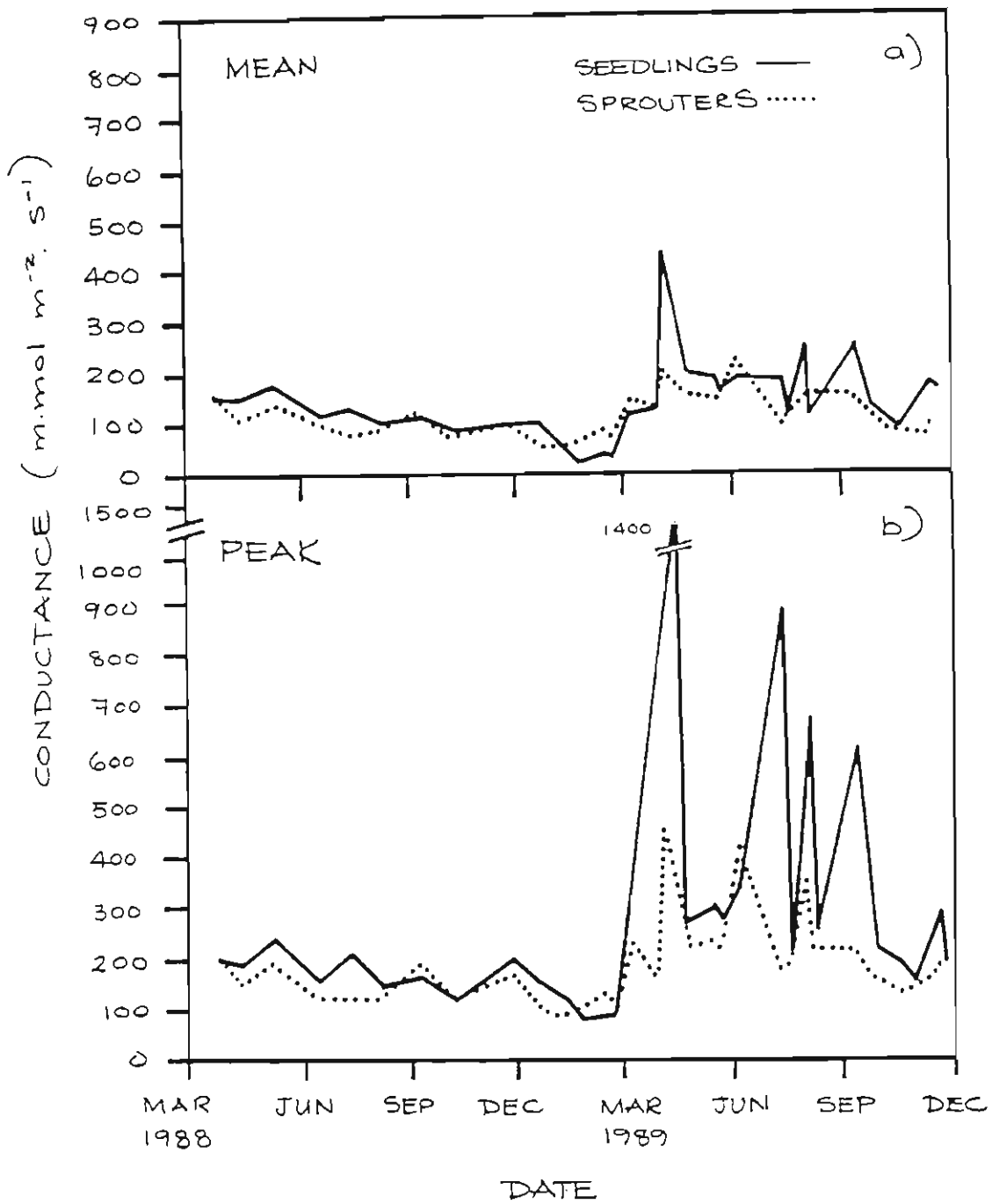


Figure 7: Mean (a) and peak (b) stomatal conductances for *Protea nitida* seedlings (solid line) and sprouter (dotted line). Values are (a) the means of the hourly median conductance and (b) the maximum hourly median conductance for each measurement day.

Table 1: Leaf characteristics of *Protea nitida* seedlings and sprouters in Swartboskloof. Data are means with standard errors in parentheses. Sample sizes: leaf area and width (n=30); specific mass (n=10); stomatal density (n=5 or 6).

	Area (mm ²)	Width (mm)	Specific leaf mass (g m ⁻²)	Stomatal density per mm ² adaxial abaxial		Abaxial/ adaxial
Seedlings	455 (19.1)	14 (0.8)	171 (6.7)	80 (2.1)	91 (3.4)	1.14
Sprouters	3581 (137)	37 (0.8)	502 (17.3)	109 (5.2)	122 (9.7)	1.12

3.3.2 Responses of stomatal conductance to changes in solar radiation, vapour pressure deficit, temperature and xylem pressure potential

Solar radiation appears to have little effect on the stomatal conductance of re-seeding (Figure 8) and re-sprouting (Figure 9) *P. nitida* plants, with high radiation values producing a similar range of conductances as lower values. As expected, increasing vapour pressure deficits cause a decrease in conductance for seedlings and sprouters, with the effect being greater on the seedlings. The sprouter shows no clear response to increasing temperatures (Figure 9), whereas the seedlings show declining conductances with increase in temperature, possibly mediated through a temperature effect on vapour pressure deficit. Only the seedlings displayed declining conductances with decreasing xylem pressure potentials, but this was mostly because the sprouter potentials were never really sufficiently low to make this effect noticeable (Figure 8).

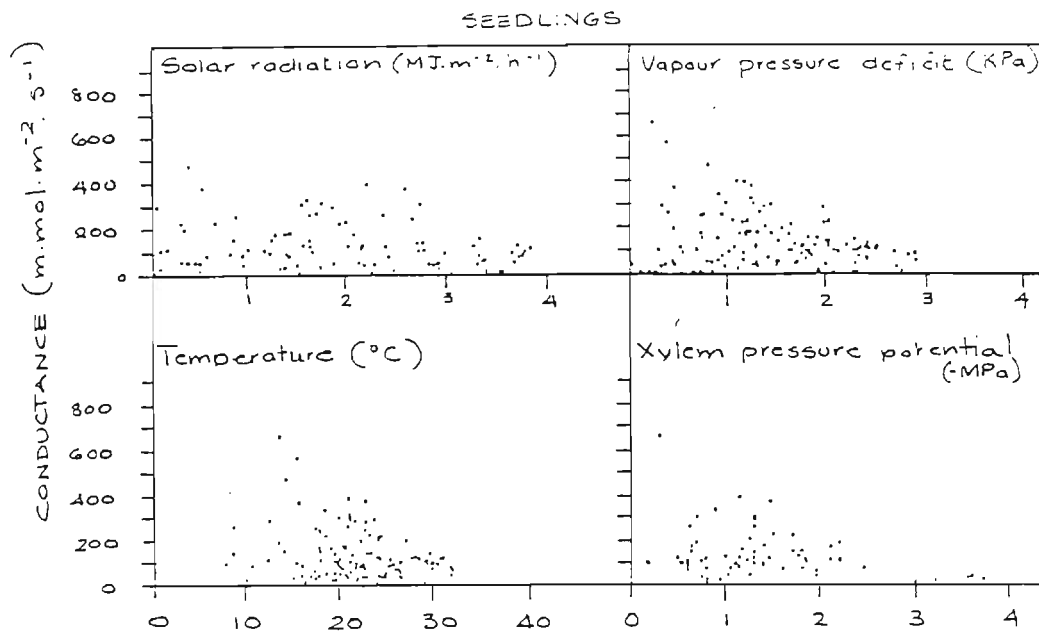


Figure 8: The response of stomatal conductance to changes in (a) solar radiation, (b) vapour pressure deficit, (c) temperature and (d) xylem pressure potential changes for *Protea nitida* seedlings. Values are means of the hourly values for all variables.

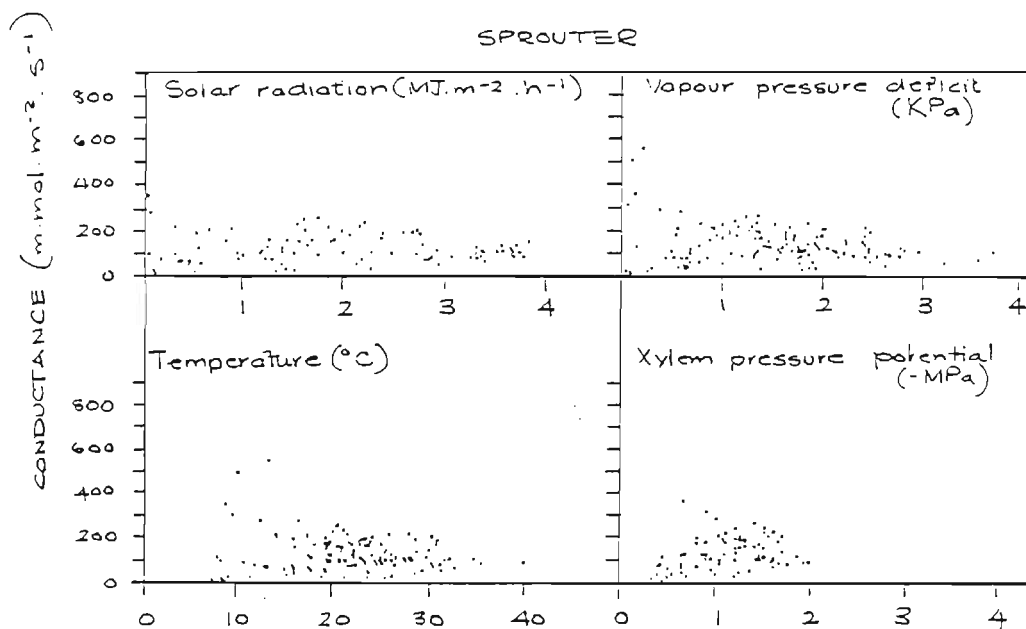


Figure 9: The response of stomatal conductance to changes in (a) solar radiation, (b) vapour pressure deficit, (c) temperature and (d) xylem pressure potential changes for the *Protea nitida* sprouter. Values are means of the hourly values for all variables.

Vapour pressure deficits, solar radiation and ambient temperatures are however, related in that as solar radiation increases through the day, ambient temperatures rise and vapour pressure deficits generally fall, and therefore the effects of these three variables must not be seen in isolation.

3.3.3 Diurnal and seasonal patterns of transpiration rates

Transpiration patterns for seedlings were similar to those of the sprouter, except during the summer drought where relatively moderate transpiration rates were maintained by the sprouters, while seedling rates were low, dropping to zero during the period that stomata were shut. Characteristic diurnal curves of transpiration rates (half-hourly values calculated as the median of the five individual leaf transpiration rates) for both regeneration modes for each season are given in the third segment of Figures 4a-4d.

Daily mean (calculated as the mean of all the half-hourly transpiration rates in a day) and peak (the highest half-hourly transpiration rate recorded in a day) transpiration rates were similar for seedlings and the sprouter (Figure 10) for most days between March 1988 and early January 1989, with mean rates ranging from 1 to 3.5 $\text{mmol m}^{-2} \text{s}^{-1}$ for the sprouter and 1 to 5 $\text{mmol m}^{-2} \text{s}^{-1}$ for seedlings. During the worst part of the summer drought (late January to early March), seedling transpiration rates dropped to half of those of the sprouter, while the sprouter showed little response. Seedling transpiration rates increased considerably to equal or exceed those of the sprouter after the first winter rains, while the sprouters again showed very little response. Generally, seedlings had higher mean and maximum transpiration rates for the rest of the study period. Peak rates ranged from 3.0 to 8.5 $\text{mmol m}^{-2} \text{s}^{-1}$ for the seedlings and 2.5 to 6 $\text{mmol m}^{-2} \text{s}^{-1}$ for the sprouter (Figure 10) from March 1989 to November 1989.

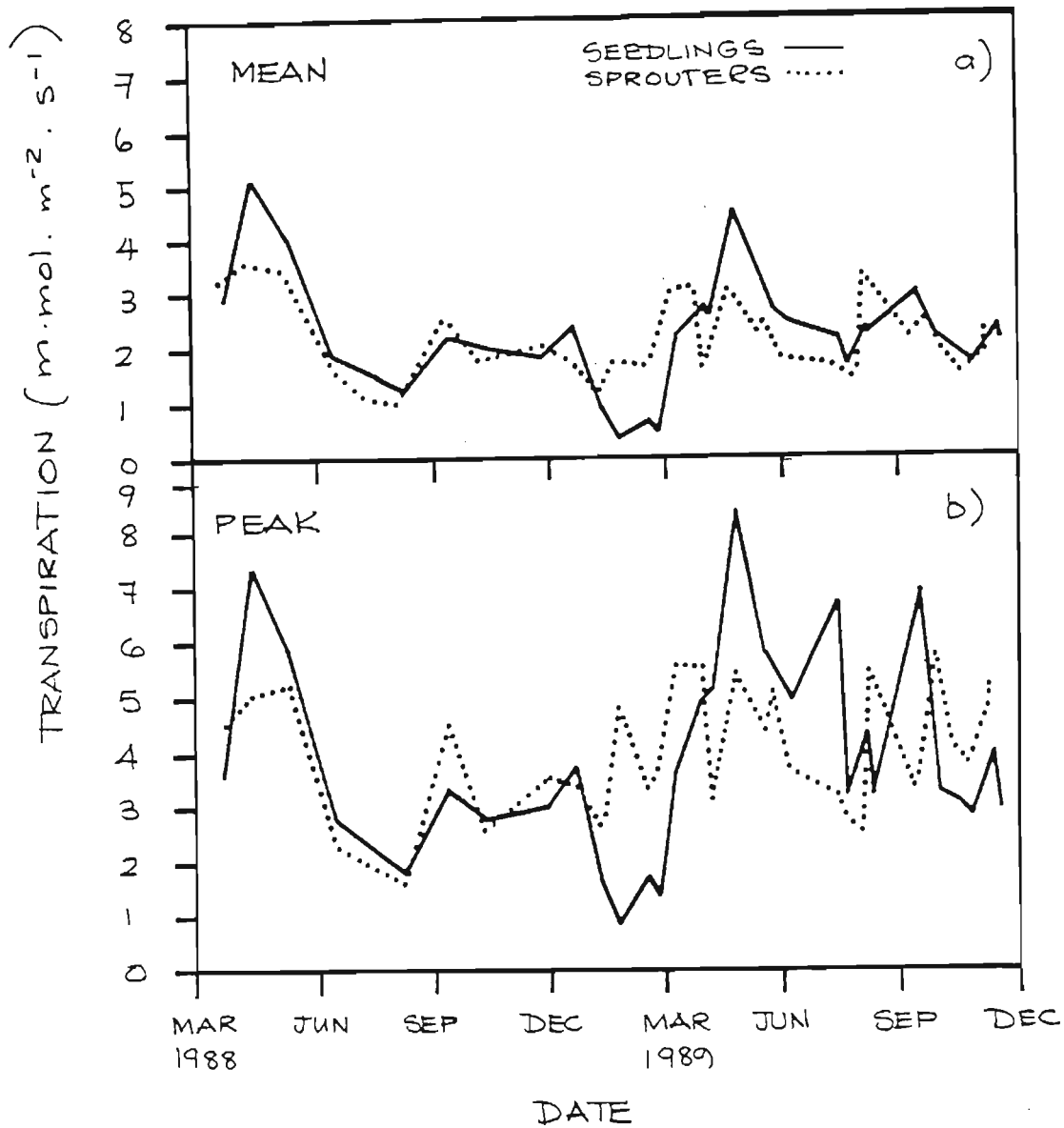


Figure 10: Mean (a) and peak (b) transpiration rates for *Protea nitida* seedlings (solid line) and sprouter (dotted line). Values are (a) the means of the hourly median transpiration rates and (b) the maximum hourly median transpiration rates for each measurement day.

Both seedlings and sprouters displayed evidence of a shift in transpiration rate with change in season, although the effect was more marked in the seedlings. They displayed lower rates in winter (low vapour pressure deficits and solar radiation) and in summer (low soil water, low conductances) and higher rates in the intermediate seasons, especially in autumn (adequate soil water, less extreme atmospheric conditions and high conductances).

3.3.4 Response of transpiration rate to changes in solar radiation, vapour pressure deficit, temperature and xylem pressure potential

The sprouter displayed a steady increase in transpiration rate with increase in solar radiation (Figure 12) from rates of approximately $2 \text{ mmol m}^{-2} \text{ s}^{-1}$ at $0.5 \text{ MJ m}^{-2} \text{ hr}^{-1}$ to $4 \text{ mmol m}^{-2} \text{ s}^{-1}$ at $4 \text{ MJ m}^{-2} \text{ hr}^{-1}$ while the transpiration rates of the seedlings increased until radiation levels of approximately $2.5 \text{ MJ m}^{-2} \text{ hr}^{-1}$ (transpiration rates of $4 \text{ mmol m}^{-2} \text{ s}^{-1}$) were reached and then remained more or less constant (Figure 11), probably indicating a saturation effect. The sprouter (Figure 12) responded positively to increasing vapour pressure deficits, whereas the seedlings did not respond as strongly to increasing vapour pressure deficits. Responses to temperature were similar to the response to vapour pressure deficits (Figures 11 and 12), which is not surprising as the two variables are not independent of each other. Sprouter and seeder xylem pressure potentials declined as transpiration rates increased (Figures 11 and 12), with the effect being more marked on the seedlings than the sprouters. As the seedlings experience water stress (-3 MPa), their stomata shut, causing transpiration rates to drop.

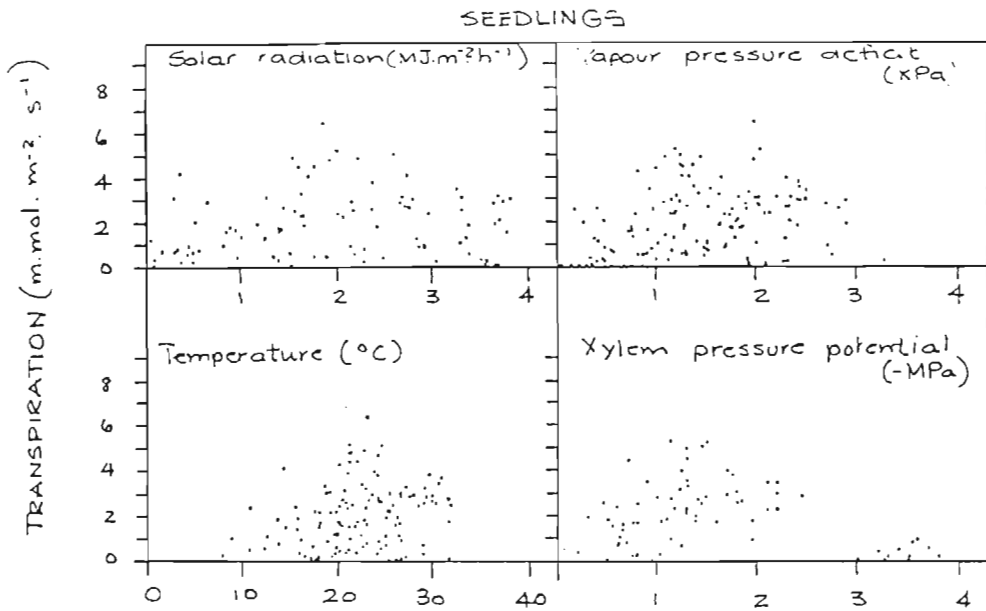


Figure 11: The response of transpiration rates to changes in (a) solar radiation, (b) vapour pressure deficit, (c) temperature and (d) xylem pressure potential changes for *Protea nitida* seedlings. Values are means of the hourly values for all variables.

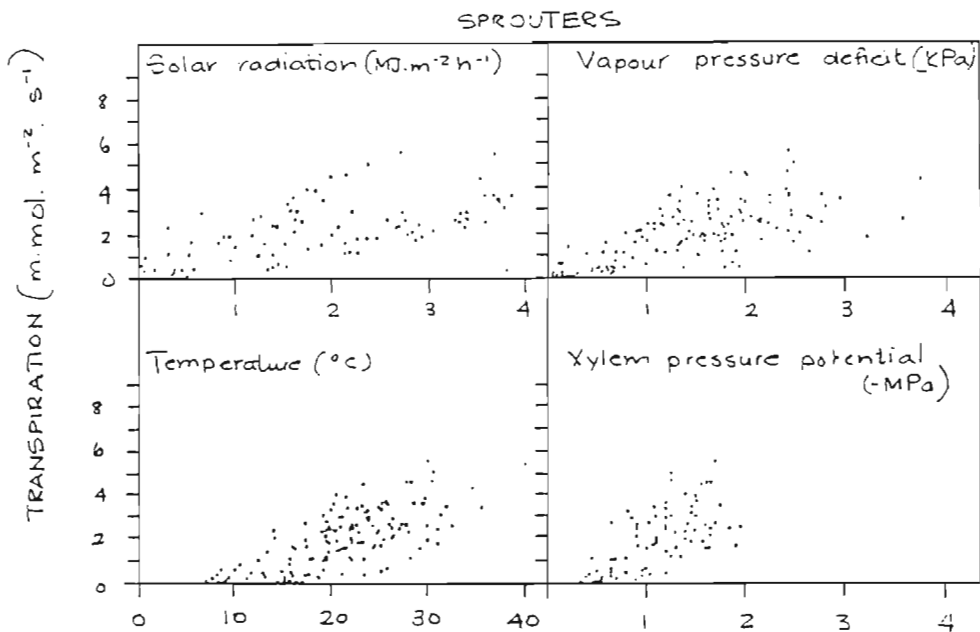


Figure 12: The response of stomatal conductance to changes in (a) solar radiation, (b) vapour pressure deficit, (c) temperature and (d) xylem pressure potential changes for the *Protea nitida* sprouter. Values are means of the hourly values for all variables.

3.4 STATISTICAL ANALYSES: CLIMATE, TRANSPIRATION AND XYLEM PRESSURE POTENTIAL DATA

As expected, transpiration rates of the sprouters were strongly correlated with stomatal conductance. They were also strongly correlated with xylem pressure potentials (or soil moisture levels) during autumn, winter and spring (partial correlation coefficients of 0.64, 0.60 and 0.27 respectively), with the climatic variables playing a more minor role (Table 2). Similarly, seedling transpiration rates were also more highly correlated with water potentials than with the climatic variables during these three seasons (partial coefficients of 0.35, 0.10 and 0.11 respectively), although to a lesser extent than for the sprouters (Table 2). In the dry summer months, both seedling and sprouter transpiration rates were highly significantly correlated with solar radiation (coefficients of 0.20 and 0.71 respectively), with the effect being greater for the sprouters than the seedlings (Table 2). Comparatively more of the variation in transpiration rate of the sprouters is explained by these four variables (solar radiation, relative humidity, temperature, and xylem pressure potential) than for the seedlings (Table 2), while stomatal conductance appears to play a greater role in explaining the variation in seedling rates.

Total daily water use was calculated by determining the area beneath the diurnal transpiration curves on each measurement day. A t-test was then performed on this data. The t-test revealed no significant differences between the total daily water use per unit leaf area of the seedlings and sprouter for most of the year (Table 3). Significant differences were however detected during the dry summer months of January and February 1989 where the sprouter had higher rates than the seedlings and in April (1988 and 1989) after the first winter rains when the seedlings had significantly higher rates.

Table 2: The partial and model correlation coefficients for *Protea nitida* sprouters and seedlings for the dependant variable transpiration rate, calculated as the mean of the five half-hourly transpiration readings. The independant variables all represent hourly means, except for the xylem potentials which are two-hourly means.

<u>Protea nitida</u> (sprouter)				
Season	Independent Variables	Partial R ²	Model R ²	Level of Significance
Summer	Solar radiation	0.71	0.71	***
	Xylem potential	0.01	0.72	
	Temperature	0.01	0.73	
	Relative humidity	0.00	0.73	
Autumn	Xylem potential	0.64	0.64	***
	Solar radiation	0.05	0.69	
	Temperature	0.03	0.72	
	Relative humidity	0.00	0.72	
Winter	Xylem potential	0.60	0.60	***
	Temperature	0.12	0.72	
	Relative humidity	0.02	0.74	
	Solar radiation	0.01	0.75	
Spring	Xylem potential	0.27	0.27	***
	Solar radiation	0.08	0.35	
	Relative humidity	0.01	0.36	
	Temperature	0.01	0.37	
<u>Protea nitida</u> (seedlings)				
Summer	Solar radiation	0.20	0.20	**
	Xylem potential	0.13	0.33	
	Relative humidity	0.01	0.34	
	Temperature	0.02	0.36	
Autumn	Xylem potential	0.35	0.35	***
	Solar radiation	0.04	0.39	
	Temperature	0.12	0.51	
	Relative humidity	0.01	0.52	
Winter	Xylem potential	0.10	0.10	**
	Solar radiation	0.02	0.12	
	Relative humidity	0.04	0.16	
	Temperature	0.03	0.19	
Spring	Xylem potential	0.11	0.11	*
	Relative humidity	0.02	0.13	
	Temperature	0.01	0.14	
	Solar radiation	0.03	0.17	

Table 3: The results of a t-test analysis of the daily transpiration rates per unit leaf area ($\text{mmol m}^{-2} \text{ day}^{-1}$) of *Protea nitida* seedlings and sprouters; daily rates were obtained by determining the area under the diurnal transpiration curves. The mean transpiration rates (mean of the half-hourly median transpiration rates in a day) with their standard errors of the mean and the level of significance are given: one asterisk represents $P < 0.05$; two represent $P < 0.01$; three represent $P < 0.001$.

Date	Seedlings	Sprouters	Significance level
	Mean daily water use ($\text{mmol m}^{-2} \text{ d}^{-1}$) (\pm S.E.; n = 5)		
Mar88	19.4 \pm 7.3	24.2 \pm 5.0	
Apr88	42.9 \pm 3.5	28.1 \pm 2.2	*
May88	35.1 \pm 0.8	28.4 \pm 8.9	
Jun88	12.2 \pm 1.0	10.1 \pm 1.7	
Jul88	10.4 \pm 1.2	8.1 \pm 1.1	
Aug88	47.4 \pm 2.2	35.1 \pm 1.1	**
Sep88	24.2 \pm 2.4	27.7 \pm 2.6	
Oct88	12.8 \pm 3.1	18.2 \pm 0.7	
Nov88	24.0 \pm 4.6	26.2 \pm 7.1	
Dec88	30.1 \pm 7.1	26.3 \pm 1.9	
Jan89	13.3 \pm 1.7	17.1 \pm 1.5	
Jan89	4.6 \pm 1.0	26.1 \pm 2.5	***
Feb89	9.1 \pm 1.8	22.5 \pm 0.9	***
Feb89	7.6 \pm 1.5	26.1 \pm 1.4	***
Mar89	28.7 \pm 6.2	38.6 \pm 2.9	
Mar89	9.9 \pm 1.1	10.0 \pm 1.5	
Apr89	30.5 \pm 2.2	18.5 \pm 1.4	**
Apr89	33.4 \pm 5.8	35.1 \pm 2.4	
May89	29.5 \pm 4.3	23.5 \pm 1.1	
May89	24.6 \pm 2.8	25.3 \pm 1.8	
Jun89	19.6 \pm 3.5	17.5 \pm 1.1	
Jul89	19.3 \pm 2.8	16.3 \pm 1.0	
Jul89	14.6 \pm 1.0	15.8 \pm 1.5	
Aug89	20.1 \pm 2.4	13.9 \pm 0.7	
Aug89	24.6 \pm 5.2	37.4 \pm 4.2	*
Sep89	39.0 \pm 5.7	23.4 \pm 1.8	*
Sep89	22.8 \pm 1.5	28.1 \pm 1.6	
Oct89	21.3 \pm 2.3	22.4 \pm 1.7	
Oct89	12.1 \pm 1.8	15.9 \pm 0.9	
Nov89	57.5 \pm 11.3	25.1 \pm 2.7	*
Nov89	18.7 \pm 1.7	22.6 \pm 1.4	

There were also four isolated instances (between August and November 1989) where significant differences were detected between the seedlings and sprouter, but these were not consistent. Seedlings had significantly higher rates than the sprouter in only three out of the four cases. These may have been exceptions as no significant differences were detected in other field days during this period.

An estimate of the total transpiration loss per unit leaf area over the entire study period for the seedlings and sprouter was also made by determining the area under the daily water use per unit leaf area curve. The sprouter was found to have an annual water use of $13300 \text{ mmol m}^{-2}$ in comparison with $14080 \text{ mmol m}^{-2}$ of the seedling. The seedlings therefore had a higher total water use per unit leaf area than the sprouter for this study period.

3.5 ROOT STUDY

The seedlings (30 months post-burn) all developed primary roots averaging 52 cm (standard error of 8) in length and resembled Cannon's (1949) type 3 root system. Figure 13 gives a brief layout of Cannon's six primary root types. There were few lateral roots and no evidence of proteoid roots. The average radius of lateral root development was 21 cm (standard error of 3). The horizontal and vertical rooting patterns are illustrated in Figure 14. Root:shoot biomass ratios (root biomass to total above-ground biomass), root:leaf biomass ratios (root biomass to leaf biomass), root:shoot area ratios (area of soil covered by roots to the projected canopy area), maximum rooting depths, and an estimate of the total soil volume (area of soil covered by roots multiplied by the rooting depth) exploited per unit leaf area for each seedling, are given in Table 4 and the mean root phytomass (g) at each soil depth for each root diameter class are given in Table 5.

The average root:shoot biomass ratio for the seedlings was 2.3, indicating that the root biomass is at least double that of the shoot biomass, whereas the root:shoot area ratios indicated that the roots occupied an area at least five times greater than the projected

canopy area (Table 4). The root biomass is therefore spread over a much wider area than the canopy biomass. Root and leaf biomass appear to be similar, being on average 1.1. The average volume of soil exploited per unit leaf area is approximately $633 \text{ cm}^3 \text{ cm}^{-2}$ for the seedlings (Table 4). The majority (77%) of the seedling root biomass occurs in the upper 30 cm of the soil surface (Table 5), and the fine water absorbing roots ($< 2 \text{ mm}$) make up 50% of the total seedling root biomass (Table 5).

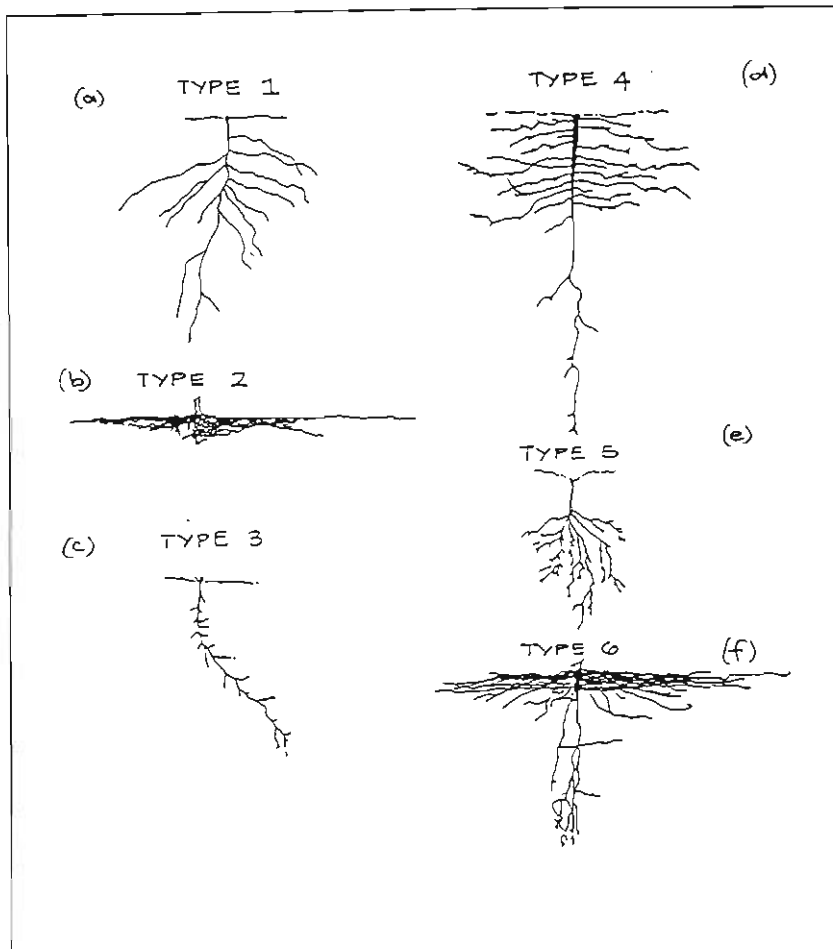


Figure 13: Cannon (1949)'s six different root types: (a) Type 1 - long primary root with acropetalous lateral roots, (b) Type 2 - short fibrous primary root with long first order lateral roots, (c) Type 3 - Long fibrous primary root, with short well-branched first order lateral roots evenly distributed down the primary root, (d) Type 4 - long, slender primary root, with well-branched first order laterals; those closest to surface are longer than those further down, (e) Type 5 - Primary root forked or branched with few first order laterals, (f) Type 6 - primary root also branched. First order laterals are mainly in the upper portion of the primary root and are thus superficial.

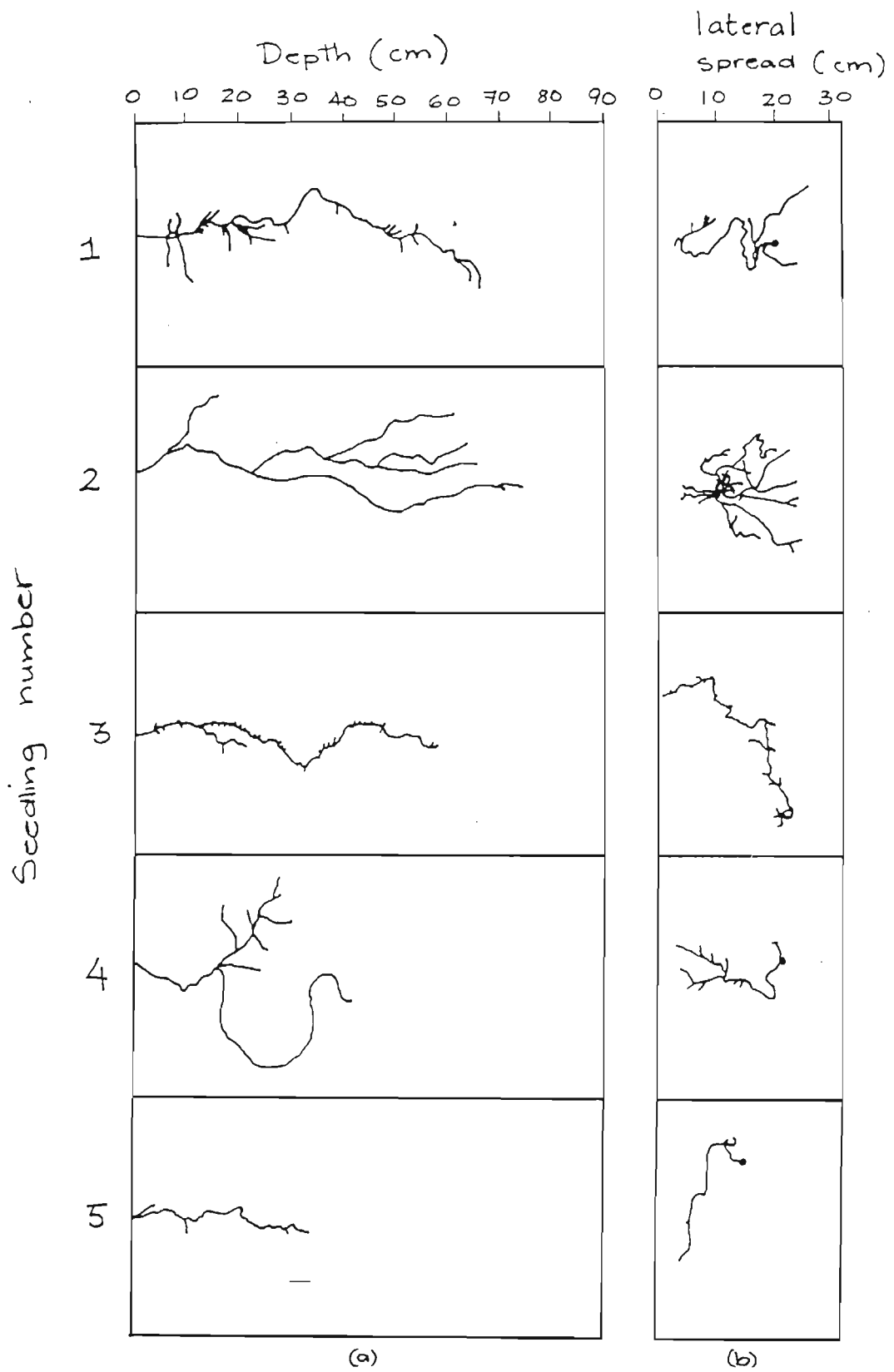


Figure 14: The horizontal and vertical rooting patterns of five *Protea nitida* seedlings indicating their maximum depths (a) and lateral extent (b) of their distributions.

Table 4: Root:shoot biomass ratios (root biomass to total above-ground biomass), root:leaf biomass ratios (root biomass to leaf biomass), root:shoot area ratios (area of soil covered by roots to the projected canopy area), rooting length, and the minimum soil volume exploited per unit leaf area for each of *Protea nitida*'s seedlings and sprouters. The mean and standard errors are given except for root length, and volume of soil utilized per unit leaf area of the sprouters.

Regeneration form	Root:Shoot Biomass Ratio	Root:Leaf Biomass Ratio	Root:Shoot Area Ratio	Root length (cm)	Soil volume per unit leaf area (cm ³ cm ⁻²)
Seedling 1	1,89	1,00	6,00	67,0	1100
Seedling 2	1,80	1,00	5,46	70,0	821
Seedling 3	3,97	1,20	4,12	54,0	517
Seedling 4	2,01	1,20	5,00	41,0	414
Seedling 5	1,98	1,10	5,00	28,5	313
Mean	2,33	1,10	5,12	52,1	633
S.E.	0,41	0,40	0,31	78,0	144
Sprouter 1	0,49	5,20	2,86	150+	284+
Sprouter 2	0,43	3,20	4,99	120+	152+
Mean	0,46	4,20	3,92		
S.E.	0,03	1,00	1,07		

Table 5: The mean root phytomass (mg) for each soil depth class in each diameter class for the seedlings. Standard deviations are given in parentheses).

	Root diameter class (mm)				Total
	0-0,49	0,49-2	2-4,9	>5	
0 - 5	2.0 (1.7)	36.8 (33.6)	165.8 (79.2)	148.0 (107.0)	352.6
5 - 10	11.7 (10.5)	54.7 (36.2)	139.6 (54.9)	.	206.0
10 - 15	3.7 (3.2)	46.7 (13.9)	111.6 (2.1)	.	162.0
15 - 20	5.6 (5.7)	69.6 (42.5)	.	.	75.2
20 - 25	9.0 (7.7)	39.8 (22.6)	.	.	48.8
25 - 30	4.6 (3.3)	37.2 (16.7)	.	.	41.8
30 - 40	1.7 (1.9)	74.5 (61.5)	.	.	76.2
40 - 50	2.8 (2.9)	47.5 (32.7)	.	.	50.3
50 - 60	4.5 (4.4)	43.2 (31.8)	.	.	47.7
60 - 70	3.3 (0)	88.2 (0)	.	.	91.5
Total	48.9	538.2	417.0	148.0	1152.1

The first of the sprouters (on the slope) had a sprawling root system which did not appear to resemble any particular root type in Cannon's (1949) classification system. It resembles type 2 root systems in that the base of the stem (bole) led into a short, thick primary root which gave rise to several long lateral roots close to the surface of the substratum. The plant was approximately 12 m from the stream and it was expected that the plant would anchor itself with two or three lateral roots for stability on the relatively steep slope and then send down a primary root ("sinker") to tap ground water resources. Contrary to expectations, the primary root diminished in size rapidly, while the lateral roots spread out in several directions (Figure 15, in envelope at back of thesis). Roots were excavated to a depth of at least 1.50 m but "sinker" roots (roots acting as tap roots) extended much further (possibly a further 1-2 m) than this. The maximum radius of root extension from the position of the primary root was 12.5 m. There were relatively few fine roots within the drip zone of this sprouter.

The second sprouter (level site) had many more fine roots within the drip zone of the canopy. The maximum depth of excavation was 1.20 m (with "sinkers" again being deeper). The maximum root radius was 7.5 m. The roots of this sprouter were of a similar nature to the first sprouter, spreading out in several directions (Figure 16, in envelope at the back of thesis).

The removal of the two sprouters was extremely time-consuming (5-6 months) with the presence of many large rocks and boulders hampering progress and preventing deeper excavations. Poor weather conditions during the greater part of the root study period also slowed the excavation process down. Roots, due to exposure and the time consuming nature of the study, became brittle, breaking easily and were lost in the debris.

Compound, open proteoid roots were found on both the sprouters. Proteoid roots are compound if the rootlets are produced in groups of three or more clusters and they are open if they do not produce second and third degree proteoid roots (Lamont, 1983).

Root:shoot biomass ratios (root biomass to total above-ground biomass), root:leaf

biomass ratios (root biomass to leaf biomass), root:shoot area ratios (area of soil occupied by roots to the projected canopy area), rooting depths (as deep as it was possible to excavate), an estimate of the minimum soil volume (area of soil covered by roots multiplied by the rooting depth) exploited per unit leaf area for each sprouter are given in Table 4. The mean and standard deviations are given except for root length, and volume of soil utilized per unit leaf area, because maximum root depth was not determined. The mean root phytomass (g) at each soil depth for each root diameter class is given in Table 6.

An average root:shoot ratio of approximately 0.5 was obtained for the sprouters, indicating that the root biomass is approximately half that of the shoot biomass. One must bear in mind however, that a large proportion of the shoot biomass of the sprouters comprises the woody stem and branches, which the seedlings lack at this stage in their development. It may therefore be more correct to compare the root:leaf biomass ratios. The root:leaf ratio for the sprouters was 4, indicating that the root biomass is considerably larger (four times) than the leaf biomass, and also indicating the large influence that the stem and branch biomass have on the root:shoot biomass ratios. The sprouters therefore have a much larger root:leaf biomass ratio than the seedlings, but have a lower root:shoot biomass ratio, due to the high proportion of woody tissue. The soil area occupied by the roots of the sprouters was on average four times as large as the shoot canopy, similar to the trend shown by the seedlings. The average (minimum) volume of soil exploited by the sprouters is $218 \text{ cm}^3 \text{ cm}^{-2}$, which is approximately a third of that exploited by the seedlings. This may have been higher if it had been possible to excavate the entire root systems of the sprouters. Approximately 70 % of the total sprouter root biomass is found in the upper 30 cm of the soil surface (Table 6) and only 0.1 % of the total biomass comprises the fine water absorbing roots (<2 mm).

Table 6: The mean root phytomass (g) for each soil depth class in each root diameter class for Protea nitida sprouters. Standard deviations are given in parentheses).

	Root diameter class (mm)						Total
	0-0,49	0,5-1,9	2-4,9	5-9,9	10-19,9	>20	
0 - 10	0.3 (0)	1.4 (1.2)	8.6 (10.5)	53.6 (7.7)	222.4 (166.1)	1265.4 (201.4)	1551.7
10 - 20	1.4 (1.1)	4.7 (2.0)	56.0 (4.2)	217.8 (165.4)	1160.8 (26.3)	3511.6 (1297.6)	4951.7
20 - 30	0.7 (0.7)	2.2 (1.7)	14.1 (11.4)	114.8 (45.9)	561.7 (209.1)	3146.6 (2811.8)	3840.1
30 - 40	0.4 (0)	2.9 (0.8)	20.3 (15.1)	102.4 (43.1)	200.9 (220.2)	1552.0 (552.4)	1878.9
40 - 50	0.1 (0.3)	0.5 (0)	22.4 (25.3)	122.0 (112.3)	265.8 (361.5)	1128.0 (650.4)	1538.8
50 - 60	.	0.1 (0)	3.6 (2.4)	50.5 (34.3)	234.5 (265.1)	15.8 (0)	304.5
60 - 70	.	.	5.0 (0)	22.7 (12.5)	68.0 (41.2)	15.0 (0)	110.7
70 - 80	.	.	1.0 (0)	5.2 (4.8)	127.5 (142.9)	8.8 (0)	142.5
80 - 90	.	.	1.0 (0)	.	11.3 (14.5)	.	12.3
90 - 100	.	.	0.2 (0)	9.7 (0)	10.9 (0)	.	20.8
100 - 120	.	.	.	9.5 (0)	6.6 (0)	.	16.1
120 - 150	.	.	.	8.7 (1.2)	.	.	8.7
Total	2.9	11.2	132.2	716.9	2870.4	10643.2	14376.8

CHAPTER 4: DISCUSSION

4.1 PLANT WATER PROCESSES

Water availability is one of the major ecological factors determining plant community productivity in many areas of the world (Specht, 1972; Poole *et al.*, 1981; Jones, 1983). Soil moisture replenishment through rainfall is usually unpredictable, and therefore plants are sometimes unable to survive due to drought, exacerbated by their own activity (growth). Plants most essential substrate, carbon, is gained only at the expense of losing water, and therefore, they need to adapt so as to allow them to grow quickly, without diminishing their probability of survival (Cowan, 1982).

Stomata are the most rapid means available to the plant for adjusting to changes in the environment of photosynthetic organs, with stomatal movements being reversible and inexpensive in terms of energy. Leaves have certain rates of assimilation of CO₂ (A) and transpiration (E) per unit leaf area at any point in time. These fluxes are determined in part by the degree of stomatal opening. Variations in A and E with surface area and time are optimal if A cannot be increased without increasing E. If one considered A to be 'benefit' and E 'cost', the slope of the E versus A curve would define the unit marginal cost (in economic terms). Plants need to maintain the marginal cost uniform for all the leaves and constant over time. Optimisation will therefore require that under certain circumstances, the stomata will have to respond directly to external environmental conditions affecting transpiration and carbon assimilation (feedforward control - explained in more detail later in this section). This will cause transpiration rates to decrease when environmental changes tend to increase transpiration (Cowan, 1982).

Plants lose water predominantly through transpiration, which is driven by the leaf-to-air vapour pressure gradient. As water is lost from plants through transpiration, the leaf water potential decreases, setting up a gradient in water potential between the soil and leaf, causing water to flow at a rate limited by the plant resistances (R) (Jones, 1983). This is illustrated in the following equations:

$$J \text{ (flow through plant)} = \frac{\psi(\text{soil}) - \psi(\text{leaf})}{R(\text{plant})} \quad \text{.....1}$$

The flow through a plant is a function of transpiration (E), which can be represented by:

$$E = g*(e_i - e_o) \quad \text{.....2}$$

where (g) is the total water vapour conductance of the pathway and (e_i) and (e_o) are the vapour concentrations at the internal leaf surface and of the air respectively. Leaf water potential can then be described as:

$$\psi(\text{leaf}) = \psi(\text{soil}) - g*(e_i - e_o)*R(\text{plant}) \quad \text{.....3}$$

(Jones, 1983)

$\psi(\text{leaf})$ is therefore controlled by $\psi(\text{soil})$, R and E (or g). Most environmental factors (temperature, solar radiation, vapour pressure deficit) are linked to each other and changes to any one factor will affect E. These environmental factors can affect g by either feedforward or feedback control mechanisms. In feedforward control, an increase in vapour pressure deficit (VPD) causes peristomatal evaporation to increase, lowering guard cell water potential, which in turn causes the stomata to close, limiting E. In feedback control, the increase in VPD causes E to increase, lowering $\psi(\text{leaf})$, which causes stomatal closure (Jones, 1983). It is however, virtually impossible to distinguish between these two control mechanisms in the field.

If $\psi(\text{soil})$ drops, either $\psi(\text{leaf})$ will also drop or stomatal conductance will have to decline to prevent $\psi(\text{leaf})$ from becoming more negative. Root distribution with depth is important in this regard. Deep-rooted plants probably have almost constant access to soil moisture and leaf water potentials will therefore remain relatively high with little need for control of water vapour conductance. Shallow-rooted plants will experience periodic drought stress as the upper soil layers usually dry out rapidly. To prevent the

leaf from desiccating, control over water vapour conductance will be necessary, which is possible through stomatal closure.

Transpiration rates are also influenced by environmental factors which affect the water potential difference between the internal leaf surfaces and the air ($e_i - e_o$). Transpiration increases with decreasing ambient humidity and increasing temperature, and is greater when the air is moving. Irradiation warms surfaces, leading to a larger vapour pressure difference and more rapid evaporation.

Plants cannot influence environmental factors to prevent desiccation in times of low soil moisture. Desiccation of the plant can be prevented by mechanisms that allow it to maintain a favourable tissue water content. This is achieved either by improving water uptake or reducing water loss. Water uptake is usually improved by the development of an extensive root system with a large active surface area, whereas restricted loss is achieved by early stomatal closure and effective cuticular control against transpiration, or by reduction of the transpiring surface of the plant (Larcher, 1983). *Protea nitida*'s seedling and sprouter root systems are discussed in section 4.6.

Specht (1972) hypothesized that some plants adjust stomatal resistance to moderate transpiration so that soil moisture is not limiting in any season, thus ensuring photosynthesis, and with it productivity, throughout the year (Cowan's (1982) optimality model). Following this hypothesis, one would expect *P. nitida* seedlings (shallow roots) to moderate stomatal behaviour so as to maximise water use efficiency. Sprouters (deeper roots) would most probably have access to water in lower soil layers and therefore water supply should keep up with demand. The need for moderating stomatal behaviour to restrict water use would be less and therefore water loss may be high even during drought. One must bear in mind however, that fynbos comprises a large number of different plant species with different rooting depths, growth rates and water use efficiencies and therefore mutual competition between species for water may limit the applicability of such a model.

4.2 XYLEM PRESSURE POTENTIALS

In this study, xylem pressure potentials (estimate of leaf water potential) of both the seedlings and sprouters remained similar throughout the study period, except during the dry summer months of January and February, where seedling potentials were markedly lower (by 2 MPa) than sprouter potentials. This difference in potential between the seedlings and sprouters is therefore either the result of lower $\psi(\text{soil})$, and/or the result of increased E , if equation 3 is followed. As mentioned above, rooting depth influences the $\psi(\text{soil})$ that the plant is experiencing. From the root study (Sections 3.5 and 4.6), it is evident that the seedlings have shallow roots in comparison with those of the sprouter, and will naturally experience a lower $\psi(\text{soil})$. During summer, conductances and transpiration rates of the seedlings actually dropped, probably as a consequence of a feedback mechanism of leaf water potential on stomatal conductance, and therefore the lower $\psi(\text{leaf})$ of the seedlings can be ascribed almost entirely to the drop in $\psi(\text{soil})$ due to their shallow root system. Transpiration rates were low and therefore low leaf water potentials are not due to excessive transpiration. The deeper roots of the sprouter probably penetrate moist soil layers near to the water table, and therefore $\psi(\text{soil})$ remains high and E is not limited in summer.

The seedling xylem pressure potentials also respond similarly to those of shallow-rooted plants from other studies in the fynbos, both within Swartboskloof (Miller *et al.*, 1983; Miller *et al.*, 1984; Kruger *et al.*, 1988; Smith and Richardson, unpublished data), and in other fynbos areas (Miller *et al.*, 1983; Miller *et al.*, 1984; Miller, 1985). Likewise, the sprouter responded similarly to deep-rooted shrubs in these same studies.

Neither the seedlings nor sprouters in this study experienced severe drought in a mediterranean-climate context (cf. Roberts *et al.* 1981; Roberts, 1982; Blake-Jacobsen, 1987 where water potentials for selected chaparral shrub species in summer dropped to -7 MPa). Xylem potential patterns of *P. nitida* seedlings and sprouters also resembled those of shallow- and deep-rooted plants respectively, in other mediterranean climate regions other than fynbos (Poole and Miller, 1975; Roberts *et al.*, 1981; Dodd *et al.*, 1984; Davis and Mooney, 1986; Hart and Radosevich, 1987).

4.3 STOMATAL CONDUCTANCE

Daily stomatal conductance patterns for *P. nitida* seedlings and sprouter were similar for most of the study period. During the dry summer drought period (December to March) where temperatures and vapour pressure deficits were high, both the seedlings and sprouter had low conductances. The limiting effect of these conditions was more evident in the seedlings with the stomata remaining closed over large parts of the day. The low seedling conductances are due to a feedback mechanism responding to low leaf water potential, which was a consequence of low soil water potential. The shallow roots of the seedlings cause them to experience a lower $\psi(\text{soil})$ than the sprouter, causing $\psi(\text{leaf})$ to drop. Transpiration without stomatal control would accelerate during summer due to the increased leaf to air gradient created by the high vapour pressure deficit, temperature and solar radiation experienced by the plants. These environmental variables also cause the stomata of the sprouter to close slightly, decreasing conductances during summer, thus preventing excessive water loss through transpiration. The primary response of the sprouters appears to be to the large leaf-air water vapour concentration difference.

Conductances of the seedlings and sprouter were similar to those of shallow- and deep-rooted plants respectively, measured in fynbos (Miller *et al.*, 1983; Miller *et al.*, 1984; Miller, 1985; Kruger *et al.*, 1988; Smith and Richardson, unpublished data) and other mediterranean regions (cf. Poole and Miller, 1975; Miller and Poole, 1979; Roberts *et al.*, 1981; Hart and Radosevich, 1987).

4.4 SCLEROPHYLLY

Protea nitida sprouters have a higher degree of sclerophylly (Table 1) than seedlings, possibly enabling them to withstand water-stressed conditions or moderate water loss to a greater degree. Their stomata are not highly sensitive to environmental stress, closing only partially under extreme conditions. The seedlings on the other hand, proved to be less sclerophyllous, having a leaf density almost a third of that of the sprouters (Table

1). Their stomata close completely under conditions of low soil moisture (low $\psi(\text{soil})$), high temperatures, irradiance and deficits, either as a result of their stomata being sensitive to these conditions, or as a feedback response to water stress. Oechel *et al.* (1981) commented that the specific leaf mass (leaf density) is usually higher for sclerophyllous plants than for mesophylls. Poole and Miller (1975) found that shallow-rooted shrubs had the most xerophytic leaves and stomata least sensitive to water stress, while Davis and Mooney (1986) found in contrast that shallow-rooted *Rhamnus*, like *P. nitida* seedlings, was the least xerophytic and the most sensitive to stress.

Protea nitida seedlings and sprouters both possess amphistomatous leaves. Amphistomaty may assist translocation in thick (sclerophyllous) leaves like *P. nitida* sprouters, where there are long diffusion pathways. Plants capable of higher stomatal conductances have a competitive advantage when conditions are favourable for water uptake. They can use water quickly and grow while water is available before it is lost either to other competitive plants or by percolation and evaporation (Mott *et al.*, 1982).

Protea nitida seedlings and sprouters have more stomata on their lower (abaxial) leaf surfaces than on their upper (adaxial) surfaces (Table 1). The seedlings had a lower stomatal density than the sprouters. The number of stomata per unit leaf area usually increases with increasing exposure to the sun and with increasing plant height (Slavik, 1974), and so differences in stomatal densities are expected to disappear in time as seedling canopies develop.

Protea nitida seedling leaves remain considerably smaller than the sprouter or adult leaves for at least 3-4 years after fire (Table 1). This is possibly because most of the biomass allocation appears to go into root development at this stage in the plants development (Sections 3.5 and 4.6). Limited leaf area growth as a mechanism to prevent excessive water loss is common to plants experiencing water stress (Jones, 1983).

4.5 TRANSPIRATION RATES

Diurnal transpiration trends of *P. nitida* seedlings and sprouter were generally similar for most of the study period. Large differences in these trends were only found during the height of the summer drought (January to February 1989) and immediately after the first winter rains had fallen (March to May 1988/1989). The effects of water stress on transpiration rates were more evident in the seedlings than in the sprouter, as shown by the extremely low transpiration rates of the seedlings in summer (Figure 10). The sprouter experienced little if any water stress (as was shown by the consistently high xylem potentials through the year), maintaining only slightly lower mean and peak transpiration rates during this period in comparison with the rest of the study period (Figure 10).

The shallow-rooted nature of the seedlings (Section 3.5; Figure 13a) enables them to utilize surface water from the first winter rains rapidly after the summer drought. This is illustrated by the comparatively larger response of the seedling transpiration rates after the April rains (Figure 10). These first rains may not wet the soil to any great depth, as the upper soil layers were so dry at this stage that most water was probably absorbed by this layer. The sprouter probably has access to soil moisture throughout the season due to its deep root system (Section 3.5; Figures 14 and 15) and therefore does not show as marked a response.

The seedlings and sprouters have similar transpiration rates to those of other shallow- and deep-rooted fynbos plants respectively (irrespective of regeneration mode), measured in Swartboskloof before and after the 1987 fire (Miller *et al.*, 1984; Smith and Richardson, unpublished data). There is however little information on the transpiration rates of fynbos species.

The slightly higher peak conductances and transpiration rates and lower water potentials of seedlings in contrast with the sprouter (immediately following rain), suggest that *P. nitida* seedlings at times, tend to extract water quite rapidly (perhaps extravagantly) whenever it is available, resulting in lower xylem tensions in the face of high atmospheric

demands. The sprouter tends to be a more moderate water user, seldom showing very high conductances or transpiration rates and maintaining high xylem pressure potentials throughout the year. This behaviour of the seedlings and sprouter supports Cohen's (1970) prediction (in contrast to Specht's (1972) hypothesis (cf. Section 3.1)), that shallow-rooted, drought-adapted plants with overlapping root systems, would extract water rapidly when available, while deep-rooted plants with non-overlapping roots would be more conservative in their soil moisture utilization. The sprouters therefore appear to follow Cowan's (1982) optimality theory (Section 4.1) more closely than the seedlings at this stage, responding to environmental conditions (feedforward control) and reducing conductances during the summer drought before water stress occurs. The seedlings possibly respond by feedback control (although this is difficult to ascertain in the field) and close their stomata in response to low $\psi(\text{leaf})$.

Seasonal daily water use per unit leaf area for *P. nitida* seedlings and sprouter was similar through most of the study period (Table 2), with differences occurring predominantly during the dry summer months (January to February 1989) when seedlings had low rates in response to serious water deficits, and after the first winter rains (April 1988/1989) when seedlings had higher rates, responding to the abundant surface water. The four other incidences where water use of *P. nitida* seedlings and the sprouter were found to be significantly different, were unexpected. In three of the four instances (August 1988, September 1989 and November 1989) the seedlings had higher rates. A possible explanation for this is that in each of these cases, fairly heavy rain fell (after a dry period) in the days prior to measurement, which may have elicited the same response as the April rains.

Generally daily water use was lowest for both regeneration modes during winter (low irradiance, temperatures and vapour pressure deficits) and for the seedlings during the dry summer period. Neither of the regeneration forms had consistently higher daily water use throughout the study period. Total water use per unit leaf area integrated over the entire study period was however, slightly higher for the seedlings than the sprouter.

4.6 ROOT STUDY

4.6.1 Root structure and distribution

Re-sprouting *Protea nitida*'s root structure was interesting in that it did not conform strictly to any of Cannon's Root Type classes, whereas the seedlings were easily classified as Root Type 3. Dodd *et al.* (1984) in their study in the kwongan (fynbos-like vegetation type in Australia) found that most mature obligate seeders and facultative seeder-sprouters had Cannon's (1949) Type 1 root system, which are considered to be the least specialized, while obligate sprouters had the more advanced Type 3 or Type 4 root systems. Higgins *et al.* (1987) found that all the mid-high to tall Proteaceae shrubs (*Leucadendron salignum*, *P. neriifolia* and *P. repens*) excavated in Swartboskloof (irrespective of regeneration mode) were examples of Cannon's Type 4 root system and it was expected therefore, that *P. nitida* would follow suit, growing in the same environment on similar if not identical soils.

The root structures of *P. nitida* seedlings were consistent with those of other Proteaceae excavated by Higgins *et al.* (1987), having a single primary root extending downward with finer lateral roots arranged radially around it. These Proteaceae all appeared to utilize the drip zone of the canopy for water absorption and therefore had the majority of their fine roots (and most of their thicker support roots) concentrated within this zone. The first (larger) sprouter in contrast, had large sprawling lateral roots spreading out in all directions, with fine root masses concentrated at its tips, while the second (smaller) sprouter had a higher concentration of fine roots within the drip zone, conforming to the pattern shown by the other Proteaceae. These differences in the root structure of the *P. nitida* sprouters may be age related in that seedlings would need a Type 3 root pattern to fully utilize all surface soil moisture and would therefore concentrate roots within the more moist drip/shade zone of the canopy, although one could argue that the seedling canopies would probably not offer much in the way of canopy-drip. Fully-developed mature plants with deep root systems would have adequate access to water in the deeper soil layers and the positioning of roots within the drip zone would decrease in importance. Judging by the small leaf canopies of the seedlings in comparison with their

relatively long primary roots and their comparatively larger root:shoot biomass ratios (Table 3), it appears as if most energy in the first two years goes into developing a primary root. These primary roots are needed for anchorage and for enabling plants to survive prevailing drought conditions by penetrating more moist soil layers at greater depths.

Most of the root biomass for the *P. nitida* seedlings (75%) and sprouters (70%) was concentrated in the upper 30 cm of the soil surface. Higgins *et al.* (1987) also found that the roots of all the fynbos species that they excavated were concentrated in the upper soil layers (sixty-seven percent of the total root phytomass was found in the upper 10 cm of the soil surface). Miller and Ng (1977) and Kummerow *et al.* (1977) confirmed this for Californian and Chilean chaparral plants as well.

Unfortunately, it was impossible to excavate *P. nitida* sprouter roots below 1.5 m due to the rocky (boulder) nature of the terrain, but judging from the root diameters of some of the sinker roots at this depth, these roots may well have extended down to at least 3 m. This surmise is supported to an extent by results from Higgins *et al.* (1987), where the average depth for other Proteaceae was over 3 m and the lateral spread from the primary root was 1-2 m. The lateral spread of *P. nitida*'s roots (Figures 14 and 15) was far greater than for these other Proteaceae, which generally extended their roots only to the periphery of their leaf canopies. These long lateral extensions were not expected and reasons for this atypical rooting structure in *P. nitida* are not clear. Long lateral roots were evident in some of the other mediterranean climate regions, where certain woody shrubs in the southern Californian chaparral had horizontal extensions of 1.5 to 10 m and reached depths of 1.5 m to greater depths than 4 m (Hellmers *et al.*, 1955). Shadori *et al.* (1967 *ex* Hoffmann and Kummerow, 1978) found that some of the Israeli *Machis* species had roots extending down to 9 m deep.

4.6.2 Proteoid roots

Proteoid roots are analogous to mycorrhizal roots in function (Lamont, 1982) and appear to be natural components of virtually all southern African Proteaceae (Low, 1980;

Lamont, 1983). It was therefore expected that *P. nitida* would follow suit. The sprouters were found to have proteoid roots similar in structure to those found by Lamont (1983) in his study, but the seedlings at two years of age showed no evidence of proteoid roots. These roots were concentrated in the upper 20 cm of the soil surface for the sprouters, similar to those found by Lamont (1983). The function of these roots appears to be to improve the plant's ability to survive environments of low nutrient status and water availability (Low, 1980) similar to conditions found in the fynbos (especially during summer). Proteoid roots were found to be more effective than ordinary roots in absorbing phosphorus and potassium from soils, although being less effective in translocating the elements (Smith and Jooste, 1986; Vorster and Jooste, 1986a; Voster and Jooste, 1986b). The presence of proteoid roots in the sprouters (and corresponding absence in the seedlings) may be an additional factor contributing to their comparatively low level of water stress during the summer drought.

4.6.3 Root:shoot biomass and area ratios

Protea nitida seedlings were found to have root:shoot biomass ratios of 2.2 two and a half years after the fire, indicating that more biomass is allocated to the roots than to the shoots during this period. In contrast, the sprouters had ratios of 0.5. The sprouters have a well-developed root stock immediately post-fire, and therefore virtually all their resources are able to be used for above-ground biomass development. Higgins *et al.* (1987) found that re-sprouting fynbos plants (26 year old vegetation) had consistently higher ratios (mean of 2.3) than mature re-seeding plants (mean of 0.2). *Protea nitida* sprouters therefore have relatively low ratios in comparison to these other sprouters, whereas the seedlings have high ratios in comparison with other re-seeders. The seedlings however, are in a growing phase at this stage and therefore these ratios will change in time. For the calculation of the sprouter ratios, the burl (thickened portion of the stem just above the root) was included as part of the shoot biomass. The presence of this burl may partially explain the high canopy biomass, although it comprises only 15-20 % of the total shoot biomass. If one includes the burl as part of the root biomass, the biomass ratio increases to 0.7.

Kummerow (1981) considered root:shoot biomass ratios to be of questionable value in frequently burnt environments with large re-sprouting components.

Sprouters that form large burls (as is the case with *P. nitida*) are difficult to divide into root and shoot tissue and any decisions made in this respect are purely arbitrary, leading to questionable root:shoot ratios. Assessments of root:shoot ratios are both time-consuming and labour intensive. The only reliable estimates appear to be those obtained during hydraulic excavations in chaparral, but even during the most careful excavations, an unknown fraction of the finer root biomass will be lost (Kummerow *et al.*, 1977; Kummerow and Mangan, 1981). Fortunately, the finer roots are of little consequence for root:shoot biomass ratios in chaparral because of their small contribution to the total root biomass (Kummerow *et al.*, 1977). Fine roots (< 2.5 mm in diameter) are however, vitally important to the plant in that they perform the chief physiological functions of the root systems (Kummerow, 1981).

Protea nitida seedlings and sprouters appear to fall into a broadly similar root:shoot biomass ratio category as plants from other mediterranean climatic regions. Hellmers *et al.* (1955) found that most of the Californian chaparral shrubs that they excavated had ratios between 1.6 and 4, irrespective of their regeneration form or rooting type. Kummerow (1981) found ratios of less than one to be typical for chaparral in Chile and California, although higher ratios were also evident. Dodd *et al.* (1984) found most ratios to be less than one for the kwongan, but ratios of up to 10 were also found. Hoffmann and Kummerow (1978) also found most ratios of the plants that they excavated to be less than one, although the deeper-rooted species had higher ratios (1.4 to 4.9). It does not appear as if root:shoot biomass ratios can be used to distinguish between seeders and sprouters or between deep- and shallow-rooted plants in general, as no consistent patterns of this nature were evident from the literature.

Protea nitida seedlings had slightly higher root:shoot area ratios (Table 3) than the sprouters (Table 6), but generally both seedlings and sprouters had large root systems in comparison with their canopies. The projected crown area of chaparral and fynbos plants is usually much smaller than the root area, despite most of the roots being concentrated in the canopy dripzone (Hellmers *et al.*, 1955; Kummerow, 1981; Higgins

et al., 1987).

This section confirms that the seedlings and sprouters of *P. nitida* have very different root systems, both in terms of size and structure. This can, from the results of similar plants in other mediterranean regions, be expected to have an effect on their water use patterns. Under conditions of sufficient soil moisture and moderate atmospheric conditions, the seedlings and sprouters do not appear to have different water usage per unit leaf area. Differences occur predominantly during or just after periods of serious soil water deficit, and these differences can therefore be ascribed almost solely to differences in their root structures. These differences are expected to disappear as the seedling roots develop with age.

4.7 BIOMASS/LEAF AREA DEVELOPMENT

In a post-fire biomass and leaf area recovery study in Swartboskloof, *P. nitida* sprouters had generally recovered their above-ground biomass and a stable leaf area per plant one to two years after the fire. The seedlings were still developing their biomass and leaf areas per plant slowly, with the average total leaf area per plant increasing at each determination. In September 1989, the seedlings still had total leaf areas two to three orders of magnitude less than the sprouters (Smith and Forsyth, pers. comm.).

In another study (Forsyth and Van Wilgen, pers. comm.) assessing the pre- and post-fire dominance of seeders and sprouters in Swartboskloof, it was found that at sites where re-seeders were dominant (in terms of biomass) before the fire, sprouters are dominant for possibly up to 6-10 years after the fire. It is expected however, that the re-seeders will regain their dominance after this period.

Therefore despite small seedling canopies initially after a fire, leaf area development within a catchment is rapid due to the rapid post-fire development of sprouters. Once sprouters have acquired their pre-fire canopies, catchment leaf area will continue to develop at a slower rate until the seeder canopies are mature. Transpiration and interception losses are therefore large irrespective of whether there are a number of re-

seeding plants or not, because the sprouters assume leaf area and biomass dominance until seeder canopies develop.

4.8 CONCLUSIONS

It appears from the evidence of *Protea nitida* (supported by evidence from seeders and sprouters in other mediterranean ecosystems) that seedling and sprouters generally do not differ markedly in their daily water use per unit leaf area. The marginal differences which are observed at times, appear to stem from differences in their respective root systems, and hence due to differences in $\psi(\text{soil})$, rather than from differences in their regeneration modes per se.

In almost all studies conducted on the effects of burning in catchments, the water yield increases observed after fire are either short-lived or very small (Bosch *et al.*, 1984). In order to maximise these increases, the only real benefit that could be derived (in terms of augmenting catchment water supplies) from manipulating community structure in favour of seeders, would be that their water use during the critical period (summer drought) would be less due to their shallower root systems during the first few years (two to five) post-fire.

Encouraging a higher proportion of seeding species may lead to a lower biomass and leaf area during the first five to ten years by virtue of slower development; therefore transpiration and interception losses would be concomitantly less, with consequent increases in water yield. Such increases will however, only be of any importance in catchments where very high seeder:sprouter ratios are achieved, and fast-developing sprouter canopies do not overshadow the smaller re-seeder canopies. Leaf area or biomass development therefore, appears to be the best indicator of post-fire catchment water yield changes.

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APPENDIX A: PRESSURE VOLUME CURVE DETERMINATIONS

An attempt was made at constructing pressure-volume curves (PV-curves) for Protea nitida seedling and sprouter leaves. This was done to detect possible differences in osmotic potentials at full and zero turgor and to establish whether the plants adjust osmotically to summer drought conditions. Pressure-volume measurements were conducted at two to three monthly intervals on two leaves of both P. nitida seedlings and sprouters.

PV-curves were constructed in a similar manner to that described by Tyree and Hammel (1972) and Sinclair and Venables (1983). Leaves were cut under water the evening before the day that measurements were taken. The cut leaves were temporarily stored in a container partially filled with water until arrival at the laboratory. Most of the water was then emptied and the leaves were left in a humid environment to hydrate overnight (12 hrs at 22 °C) with their petioles having access to water lying at the base of the container. The leaves were first weighed and then enclosed in the Scholander pressure chamber and the nitrogen pressure was increased (over pressurised) within the chamber until sap flowed out of the cut surface. The sap was collected for a short period of time (2-3 minutes) whereafter the pressure was reduced slightly until sap stopped flowing from the cut surface. This pressure was noted and called the balancing pressure and the weight of expressed sap determined. The above process was repeated with 0.2 to 0.3 MPa pressure increments, with each new balancing pressure and increment of expressed sap recorded. After completion of the pressure measurements, the mass of the leaf was re-determined. The sum of the final mass and the mass of sap expressed was

subsequently subtracted from the initial leaf mass. The remaining mass resulting from evaporative losses was divided equally among the series of mass readings, presuming evaporative losses to be constant during determinations.

The graphical representation of the series of pressure-volume readings is known as a pressure-volume curve and comprises the inverse of the balancing pressure on the y-axis and the weight of water expressed on the x-axis. PV-curves are characteristically two-phase curves (Figure A1) with a linear and a non-linear phase. By extrapolating the linear portion of the curve, the initial osmotic potential (potential at full turgor - A) can be obtained from the intercept on the y-axis while the intercept on the x-axis gives the turgid (osmotic) cell volume (B). The initial osmotic potential is important as it places the upper limit on the turgor pressure which a tissue can develop. The osmotic cell volume is the effective volume of tissue water available for exchange as water content fluctuates within the physiological range of water deficit (Roberts and Knoerr, 1977). The osmotic potential (C) at zero turgor can also be determined from the position where the linear phase of the curve departs from linearity (subjective assessment). These values can be used to determine the range of osmotic and turgor potentials between zero and full turgor (Hofler diagram) at various cell water contents (Sinclair and Venables, 1983). The bulk modulus of elasticity (BE), which provides a measure of cell wall rigidity, can also be determined. BE is calculated as follows:

$$BE = V \cdot dP/dV$$

where dP is the change in cell turgor pressure and dV/V is the corresponding relative change in cell volume (Steudle and Zimmerman, 1977). The elasticity determines the change in cell turgor pressure in response to cell water loss (Lo Gullo *et al.*, 1986). The

ability to increase cell BE is considered to be a drought strategy. Increases in cell wall rigidity lead to large changes in turgor potential with small changes in cell volume. This can result in earlier stomatal closure to prevent water loss.

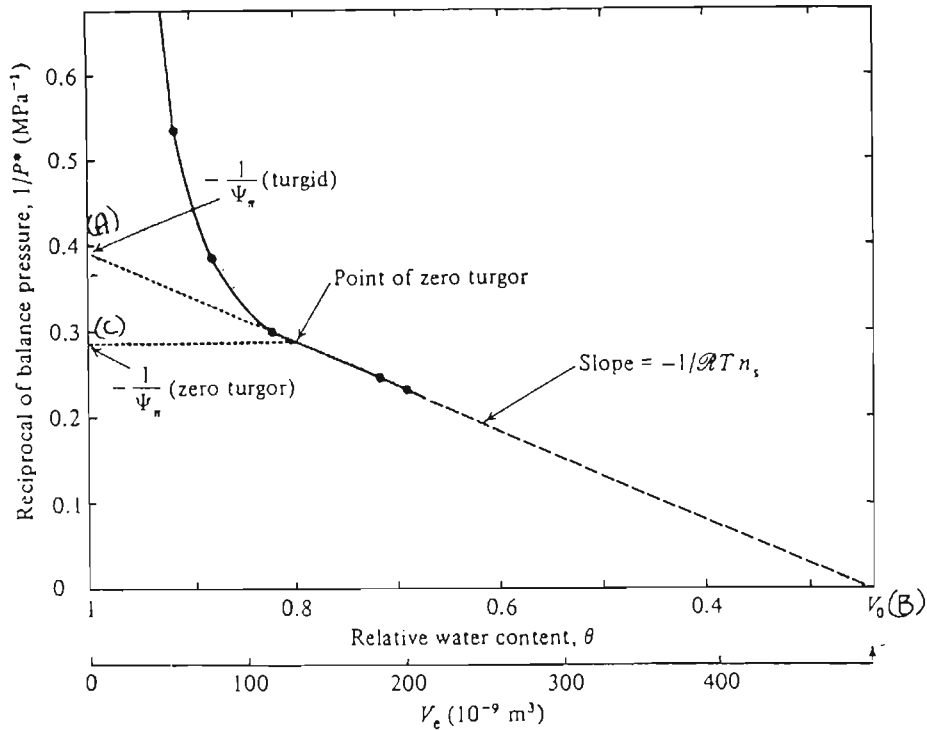


Figure A1: Graphical representation of pressure-volume curve data showing the initial osmotic potential (A), turgid (osmotic) cell volume (B) and the osmotic potential at zero turgor (C) (Jones, 1983).

Typical pressure volume curves obtained during the study in each season for both seedling and sprouter are given in Figure A2 (a-h). The curves appeared similar to those found elsewhere (Tyree and Hammel, 1972; Roberts and Knoerr, 1977; Sinclair and Venables, 1983).

From the data, Hofler diagrams were constructed using the methods outlined by Sinclair and Venables (1983) to determine the reaction of water, osmotic and turgor potential to changes in cell water content. The observed Hofler diagrams for the seedlings and sprouters for each season are given in Figure A3 (a-h). The osmotic potentials at full turgor and zero turgor and the relative water content at zero turgor for the sprouters and seedlings are given in Table A1. No clear seasonal pattern is apparent for either the seedlings or sprouters, with osmotic potentials at full and zero turgor fluctuating throughout the year. In spring, seedlings and sprouters reacted in a similar fashion, both losing turgor at a relative water content of approximately 0.85. During the other three seasons, the seedlings appeared to maintain turgor at lower relative water contents than the sprouters. This data may not be entirely reliable however, as difficulties were experienced with the methodology.

Table A1: The osmotic potentials at full (100) and zero (0) turgor, and the relative water content at zero turgor (with their standard errors in brackets) for the seedlings and sprouters for the study period.

Date	Sprouters		Seedlings			
	$\psi(100)$	$\psi(0)$	RWC(0)	$\psi(100)$	$\psi(0)$	RWC(0)
Apr88	1.58 (0.04)	1.85 (0.1)	0.82 (0.02)	1.55 (0.11)	1.99 (0.17)	0.75 (0.02)
Jul88	1.75 (0.02)	2.16 (0.06)	0.79 (0.02)	1.19 (0.16)	1.49 (0.04)	0.76 (0.02)
Sep88	1.9 (0.09)	2.15 (0)	0.86 (0.03)	1.33 (0.14)	1.75 (0.1)	0.75 (0.1)
Nov88	1.61 (0.05)	1.98 (0.02)	0.8 (0.01)	1.66 (0.06)	2.13 (0.03)	0.78 (0.02)
Jan89	1.89 (0.02)	2.3 (0.05)	0.79 (0)	1.19 (0.06)	2.08 (0.08)	0.56 (0.03)
Apr89	1.81 (0.06)	2.48 (0.38)	0.74 (0.08)	1.28 (0.11)	2.06 (0.10)	0.62 (0.02)
Jun89	1.55 (0.02)	1.84 (0.04)	0.83 (0.00)	2.48 (0.04)	3.66 (0.3)	0.70 (0.02)
Aug89	2.03 (0.10)	2.48 (0.13)	0.80 (0.01)	2.08 (0.08)	3.1 (0.60)	0.69 (0.11)

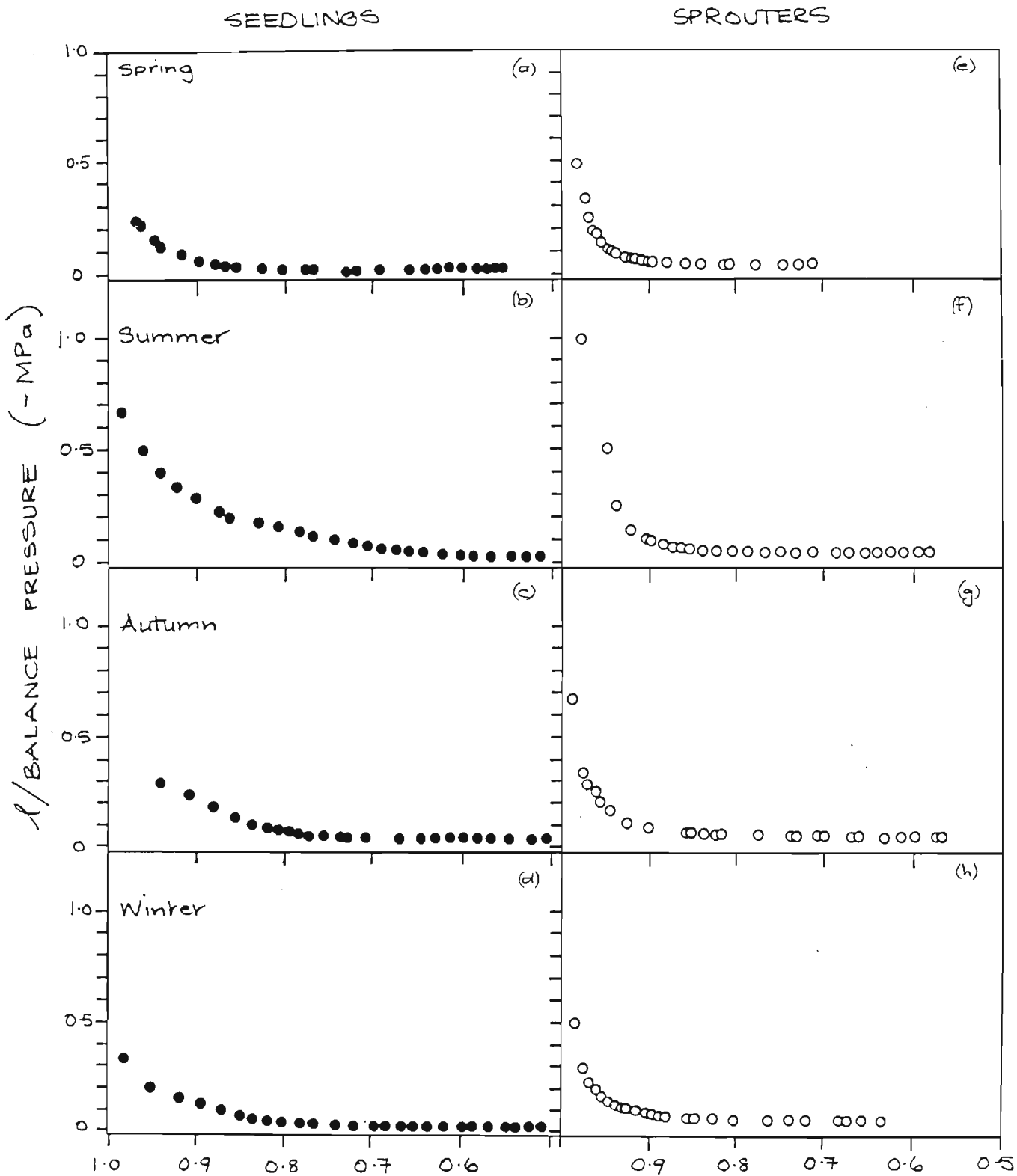


Figure A2: Pressure volume curves for *Protea nitida* seedlings (dots) and sprouters (circles) in (a, e) spring, (b, f) winter, (c, g) autumn and (d, h) summer.

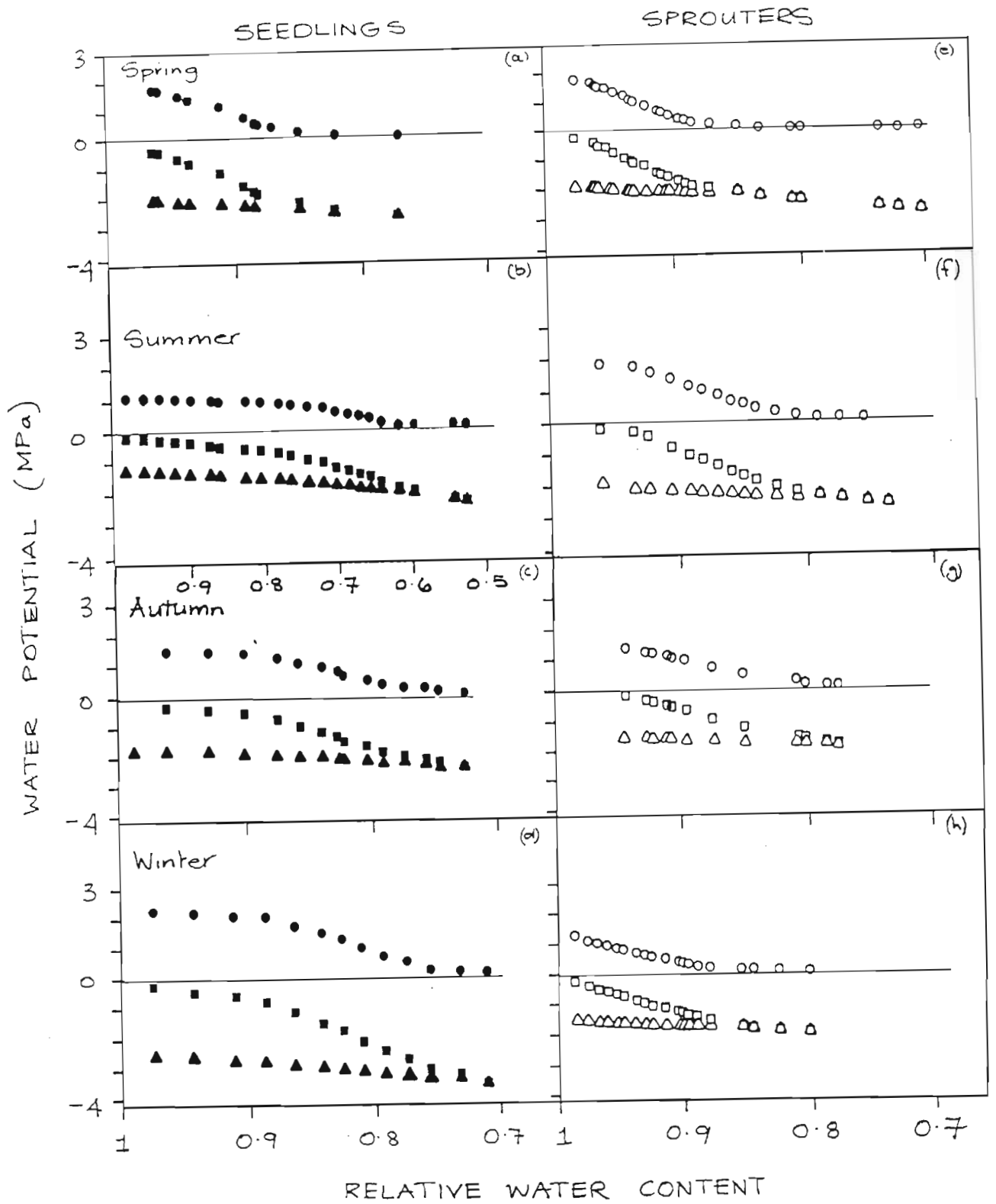


Figure A3: Hofler diagrams for *Protea nitida* seedlings (solid symbols) and sprouters (empty symbols) in (a, e) spring, (b, f) winter, (c, g) autumn and (d, h) summer, illustrating the response of osmotic potentials (triangles), turgor potentials (circles) and water potentials (squares) to a change in relative water content. Circles, squares and triangles indicate turgor, water and osmotic potentials respectively.

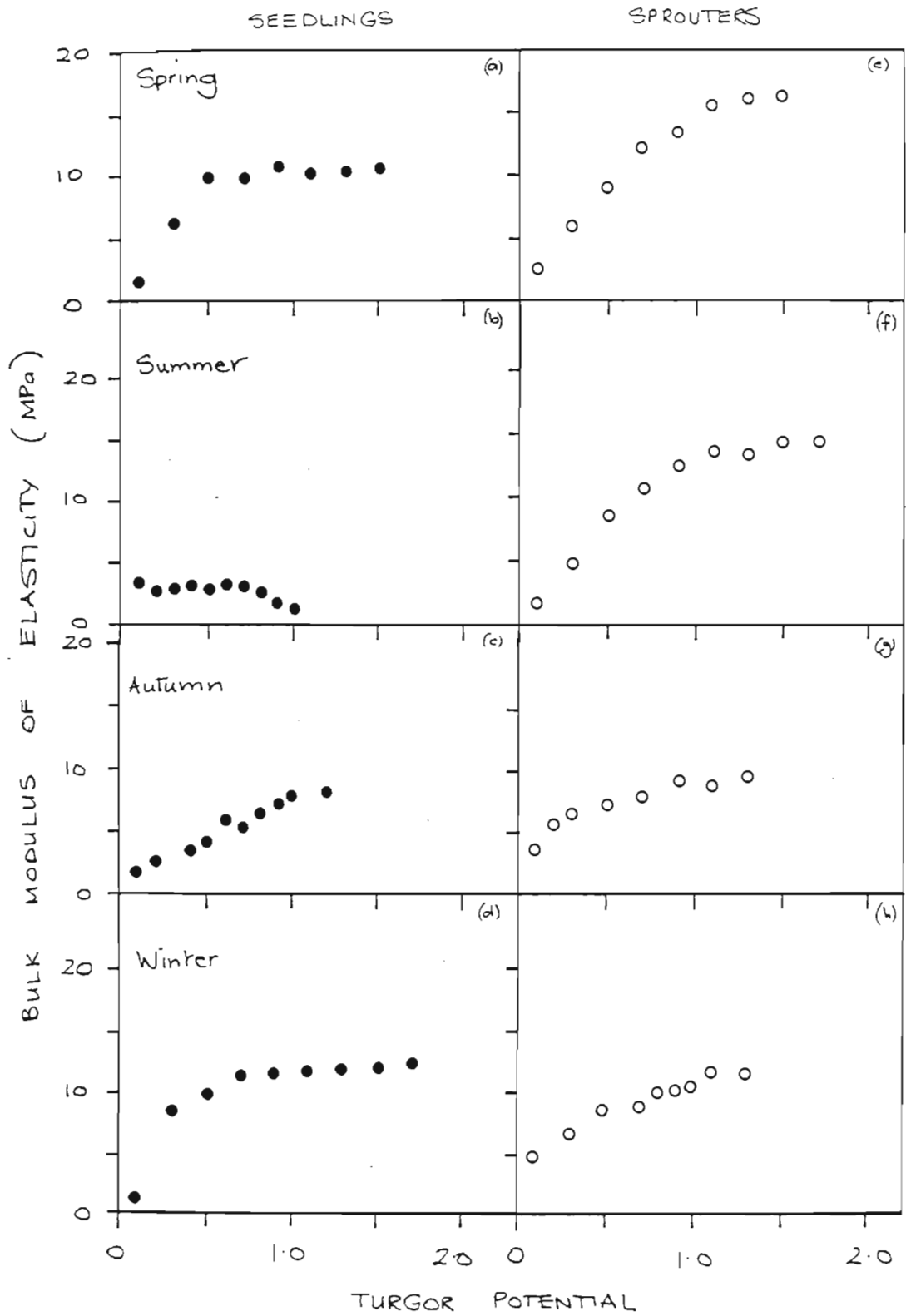


Figure A4: The change in bulk modulus of elasticity with change in turgor potential for *Protea nitida* seedlings (dots) and sprouters (circles) in (a, e) spring, (b, f) winter, (c, g) autumn and (d, h) summer.

The relationship between turgor pressure and relative water content is usually close to exponential (Jones, 1983; Sinclair and Venables, 1983), but *P. nitida* seedlings and sprouters at times displayed an almost sigmoidal relationship between these variables (examples: Figure A3 b, d, e), which is difficult to explain. This atypical turgor potential relationship is also evident in some of the Hofler diagrams presented by Roberts and Knoerr (1977) and Roberts (1982). It affects the calculation of the BE which is determined using the gradient of the turgor potential versus relative water content line.

Graphical presentations of the relationship between bulk modulus of elasticity and turgor potential for the seedlings and sprouters for each season are illustrated in Figure A4 a-h. The greatest differences between seedlings and sprouters are evident in summer where the BE is very low (c. 2.5 MPa) for the seedlings over the entire range of turgor potentials whereas the sprouters has increasingly higher BE values with increasing turgor potentials until a plateau is reached at a BE of approximately 13 MPa. In spring, seedlings also have slightly lower BE values (approximately 10 MPa) in comparison with those of the sprouter (approximately 16 MPa). For the other measurement days, maximum BE is similar for seedlings and sprouters, with a plateau being reached at 10-12 MPa.

The occurrence of the sigmoidal pattern was not consistent throughout the data. The shape of the non-linear section of the pressure-volume curve is the determining factor affecting the shape of the turgor potential versus relative water content curve. The sigmoidal shape may be a consequence of one of the following:

- (1) the time between over pressurizations was far too small to allow for redistribution of water in the tissue between the cells. The time needed for this process can be between 10 and 60 minutes for some species (Roberts and Knoerr, 1977);
- (2) the period in which the leaves were partially submerged in water prior to measurement (on the way to the lab) may have been too long, possibly leading to erroneous data (possibility of water uptake at leaf surface);
- (3) a different technique may have provided better results (air drying where evaporative losses in the chamber are less important for instance).

Each of these possibilities were tested with the original method as control. In the first experiment, leaves were collected in the same manner as the original method, but equilibrium times of 15 minutes instead of 2-3 minutes were used before the balancing pressure was determined. In the second experiment, leaves were cut under water and immediately placed in a plastic bag with only the petiole having access to water, and left to rehydrate overnight. Pressure-volume determinations were carried out in the same fashion (original method) for both experimental and control leaves. In the final experiment, leaves were once again collected in the same manner as the original method, but were left to air dry for 20 minute intervals between each balancing pressure and mass determination (the effect of evaporation within the chamber is unimportant if this method is used). A further source of error could be that the assumption of a constant rate of evaporative water loss within the chamber may also not be true, with water loss being greater initially (leaf turgid), diminishing as the leaf dries out. This was not tested, however.

RESULTS

In the first experiment, longer equilibrium times appeared to reduce the sigmoidal effect considerably, providing a roughly exponential relationship between turgor potential and relative water content. Resulting Hofler diagrams and plots of bulk modulus of elasticity versus turgor potential are given in Figure A5 along with those for the control (experiment 1).

The second experiment (Figure A5 - experiment 2) still revealed a sigmoidal pattern for turgor potential versus relative cell water content. It therefore appears as if the length of time that the leaf is partially submerged in water plays no meaningful role in the shape of the curve.

The air-drying technique also resulted in a sigmoidal pattern, despite the long intervals between each balancing pressure determination. This was also unexpected as this experiment was expected to provide similar results to the first experiment (both with longer equilibrium times). There were no differences due to the method of collection. Results for this experiment are given in Figure A5 (experiment 3).

It can therefore be concluded that longer equilibrium times between measurements may be a means of solving the problem of the sigmoidal shape of the turgor potential versus relative water content curve, but that more extensive verification is necessary.

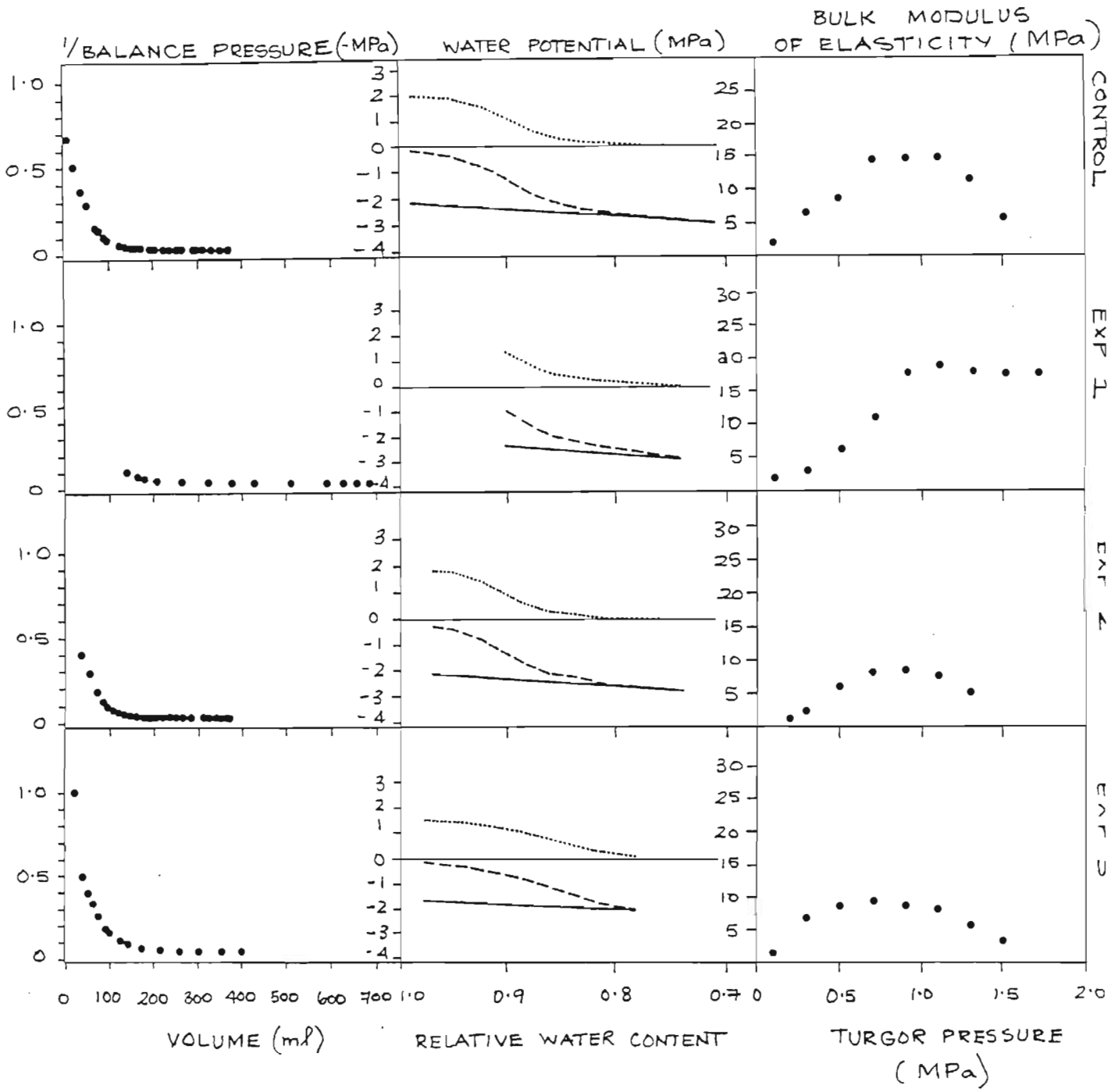


Figure A5: The pressure volume curves, hofler diagrams, and bulk modulus of elasticity curves for each of the experiments and the control.

APPENDIX B: ASSESSMENT OF METHODS OF ESTIMATING TRANSPIRATION

A comparison was made of the following three methods of estimating transpiration rate:

- (1) transpiration estimates determined from porometry flow rate data (Li-cor Product Manual, 1981);
- (2) transpiration estimates using a simplified form of the Penman-Monteith energy budget equation (Tan *et al.*, 1978);
- (3) transpiration estimates using the cut and weigh (cutshoot) technique (Slavik, 1974).

B1: Comparison of Porometry flow rate versus Penman-Monteith energy budget methods:

In a comparison of the first two methods, transpiration was calculated using the following equations:

$$(1) \quad Tr = F/LA * (pc-pa) \quad (g \text{ cm}^{-2} \text{ s}^{-1})$$

(Li-cor Product Manual, 1981)

where F ($\text{cm}^3 \text{ s}^{-1}$) is the flow rate of dry air into the porometer, LA is the leaf area (cm^2), pc (g cm^{-3}) is the water vapour density in the cuvette and pa (g cm^{-3}) is the water vapour density of the dry airstream entering the cuvette (2% relative humidity).

$$(2) \quad E = \frac{p * Cp * VPD}{L * g * r_s} \quad (g \text{ cm}^{-2} \text{ s}^{-1})$$

(Tan *et al.*, 1978)

where E is the rate of diffusion of water vapour ($\text{g cm}^{-2} \text{ s}^{-1}$), p is the density of moist air (1.2 mg cm^{-3}), Cp is the specific heat of moist air ($1.01 \text{ J g}^{-1} \text{ }^\circ\text{C}^{-1}$), L is the latent heat of vaporization of water (2450 J g^{-1}) g is the psychometric constant ($0.066 \text{ KPa }^\circ\text{C}^{-1}$), r_s is the stomatal resistance to water vapour diffusion (s cm^{-1}) and VPD is the vapour pressure deficit between leaf and air.

A t-test (Table B) on hourly transpiration rates estimated by the two equations revealed

significant differences in the rates calculated by the two methods. Transpiration rates using the Li-Cor method were consistently higher than those calculated by the Penman-Monteith formula (by approximately $0.3 \text{ mmol m}^{-2} \text{ s}^{-1}$).

Table B: T-test on difference in transpiration rates for *Protea nitida* calculated by formulae given by the Li-cor Manual and Tan *et al.* (1978) for measurements taken in summer (February 1989) and in winter (July 1989). Ho: no difference between transpiration rates calculated by the two methods.

Season	Mean difference ($\text{mmol m}^{-2} \text{ s}^{-1}$)	S.E	p > T
summer	0.3793	0.0212	***
winter	0.2864	0.0178	***

*** indicates $p < 0.001$

Two assumptions are made for the Penman-Monteith method: one being that boundary layer conductances are considerably higher than stomatal conductances and the second assumes that leaf temperature does not differ significantly from ambient temperature. Although the first of these two assumptions proved to be valid (boundary layer conductances an order of magnitude higher than stomatal conductance - Section B2), the second did not as air temperatures differed significantly from leaf temperature, being on average (80% of measurements) $1.48 \text{ }^\circ\text{C}$ (standard error of mean = 0.117) lower than leaf temperatures.

Transpiration rates are also estimated using stomatal resistances calculated from the porometer flow rates whereas the Li-cor formula uses the actual flow rates for its calculations. The Li-cor method proved to be the more favourable of the two methods, minimising the number of assumptions to be made.

B2: Comparison of the porometry flow rate and the cutshoot methods:

A comparison was then made of transpiration rates calculated with flow rate data (method 1) and those calculated with the cutshoot method (method 3). Transpiration estimates calculated from flow rate data obtained with a porometer, provide an indirect measure of transpiration rate. The conditions within the cuvette of the porometer differ from true ambient conditions due to restricted air flow in the cuvette, compulsory air circulation by the fan, and the shading of the cuvette to prevent an excessive heat build up within the cuvette.

The cutshoot method described by Slavik (1974), however, is also not ideal as the cutting of the leaf eliminates the root and stem resistance components, which are probably the major plant resistances restricting transpiration. This method is based on the assumption that the transpiration rate of a leaf is maintained without significant change during the first few minutes after it has been cut from the plant. The time taken between cutting and the first weighing (10 seconds in this case) should be as short as possible (Slavik, 1974). Protea nitida leaves have a mass of approximately 1 to 4 grams and therefore it is necessary to weigh with a sensitivity of 1 mg for accuracy (Slavik, 1974). A laboratory scale with a 1 mg sensitivity was used. It was completely enclosed in a box with two perspex sliding doors to reduce wind movement over the scale during the weighing procedure.

The time taken for the transpiration rate to decline after the leaf has been cut before measurements could be taken was assessed so as to determine the time period over which a constant transpiration rate is maintained. Five leaves were cut, weighed and suspended on thin wire cradles within the P. nitida canopy, on a warm, cloudless day with a light (< 0.5 m/s) south-easterly wind blowing. At one minute intervals, the leaves were re-weighed and replaced on the cradles for a period of 30 minutes, with the weight loss per minute interval being recorded.

P. nitida leaves appeared to maintain relatively constant transpiration rates for at least 30 minutes after having been cut (Figure B1), making the two to five minute intervals

used in this study acceptable intervals over which transpiration remains constant for cutshoot/porometry comparisons.

To compare the two techniques effectively, measurements had to be made with both porometer and cutshoot techniques on the same plant simultaneously. Transpiration rates were estimated from conductance measurements taken on two *P. nitida* sprouters on two field days (one sprouter for each field day) with differing weather conditions - one warm, cloudless day with slight wind and another slightly hazy day with partial cloud cover. Stomatal conductance readings were taken on 20 leaves within a 30 to 40 minute period and 12 leaves were cut and weighed for the cutshoot technique during the same period. Leaves of a similar age were selected from the same position and aspect in the canopy for both techniques. Those for the cutshoot method were left on the cradle for five minute intervals before being re-weighed. Readings were repeated through the day and transpiration rates were calculated and expressed in $\text{mmol m}^{-2} \text{s}^{-1}$ for comparison.

The results of the two sets of measurements using the porometer and the cutshoot method simultaneously revealed that porometry provides a more conservative estimate of transpiration than the more direct cutshoot method. Cutshoot rates for the first field day (cool) ranged from 0.19 to 3.2 $\text{mmol m}^{-2} \text{s}^{-1}$ (five minute intervals) whilst those of the porometer ranged from 0 to 1.16 $\text{mmol m}^{-2} \text{s}^{-1}$ (Figure B2). On the second (clear, warm) day, the values ranged from approximately 0.19 to 7.4 $\text{mmol m}^{-2} \text{s}^{-1}$ for the cutshoot technique and from 0.46 to 6.9 $\text{mmol m}^{-2} \text{s}^{-1}$ for porometry (Figure B2).

Due to the differences found between the cutshoot and porometry readings in this experiment, a second experiment was planned to determine whether the lack of the plant resistance component in the cutshoot technique, was solely responsible for the discrepancies in the data (porometry measurements were taken on intact leaves (resistance present) and the cutshoot measurements on detached leaves (resistance absent)). The porometer was used to determine transpiration of an attached leaf which was then cut, weighed and suspended on a cradle within the canopy for two minutes. It was then re-weighed and transpiration was determined a second time on the cut leaf. This was repeated on several leaves throughout the day on two field days; one where the

weather was clear and cloudless and another where the weather was partially overcast and cool.

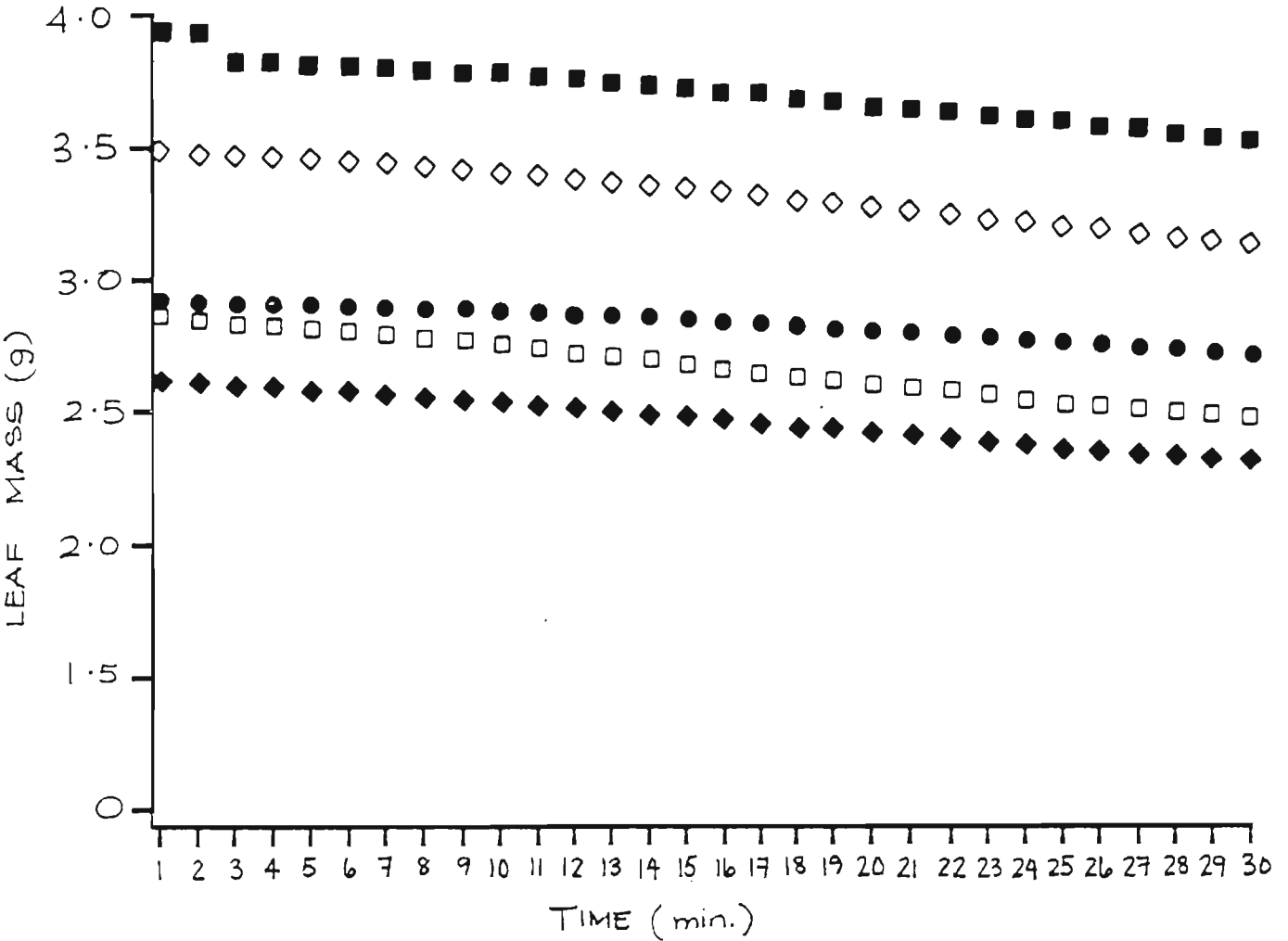


Figure B1: The mass loss of five leaves at one-minute intervals for a period of 30 minutes after being cut, to determine the time period over which water loss from the leaf remains constant. Each symbol denotes a different leaf.

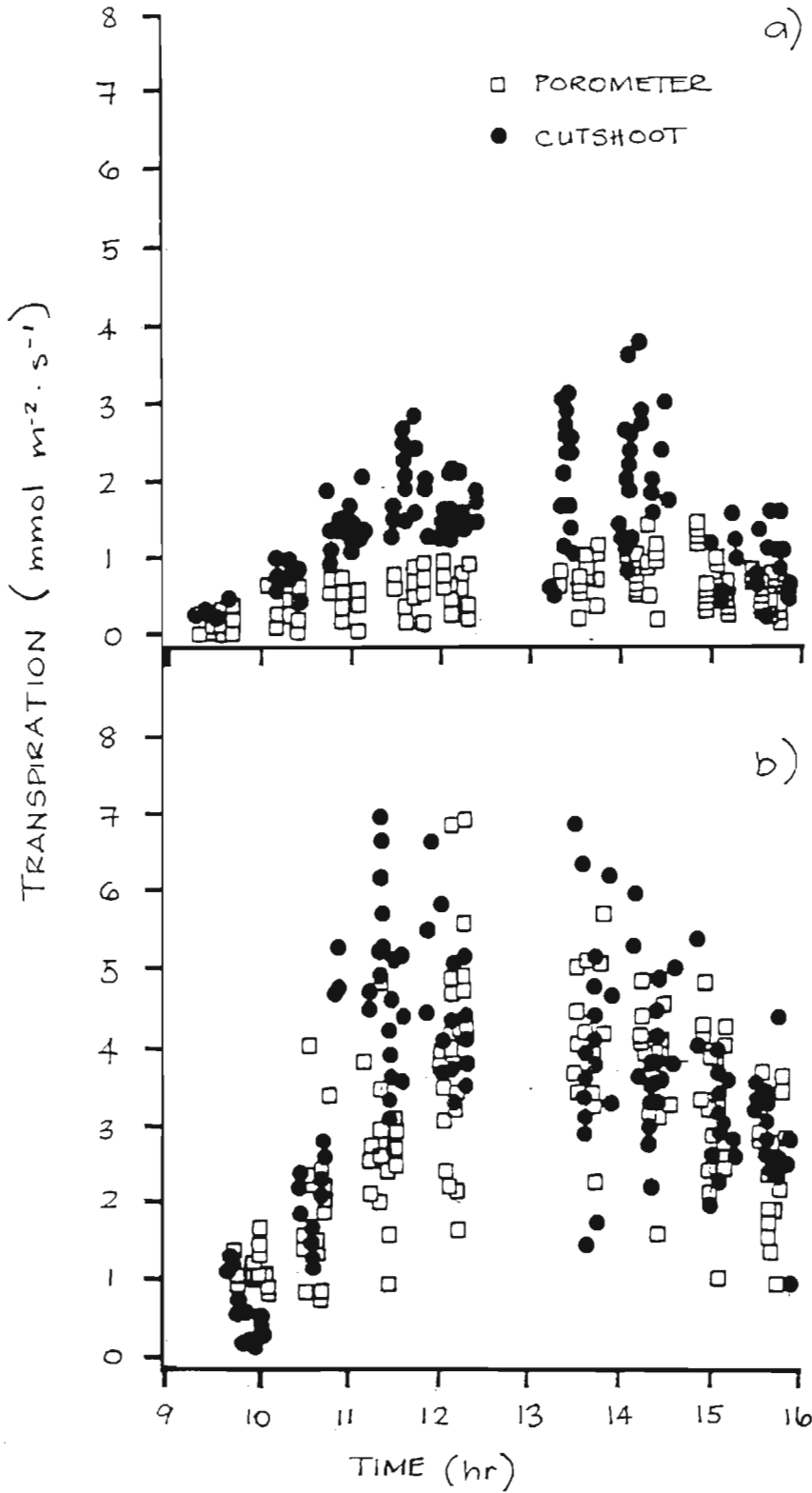


Figure B2: The cutshoot (circles) and porometry (squares) estimates of transpiration rate, measured on (a) a cool, partly cloudy day and (b) a warm, clear day in May 1989.

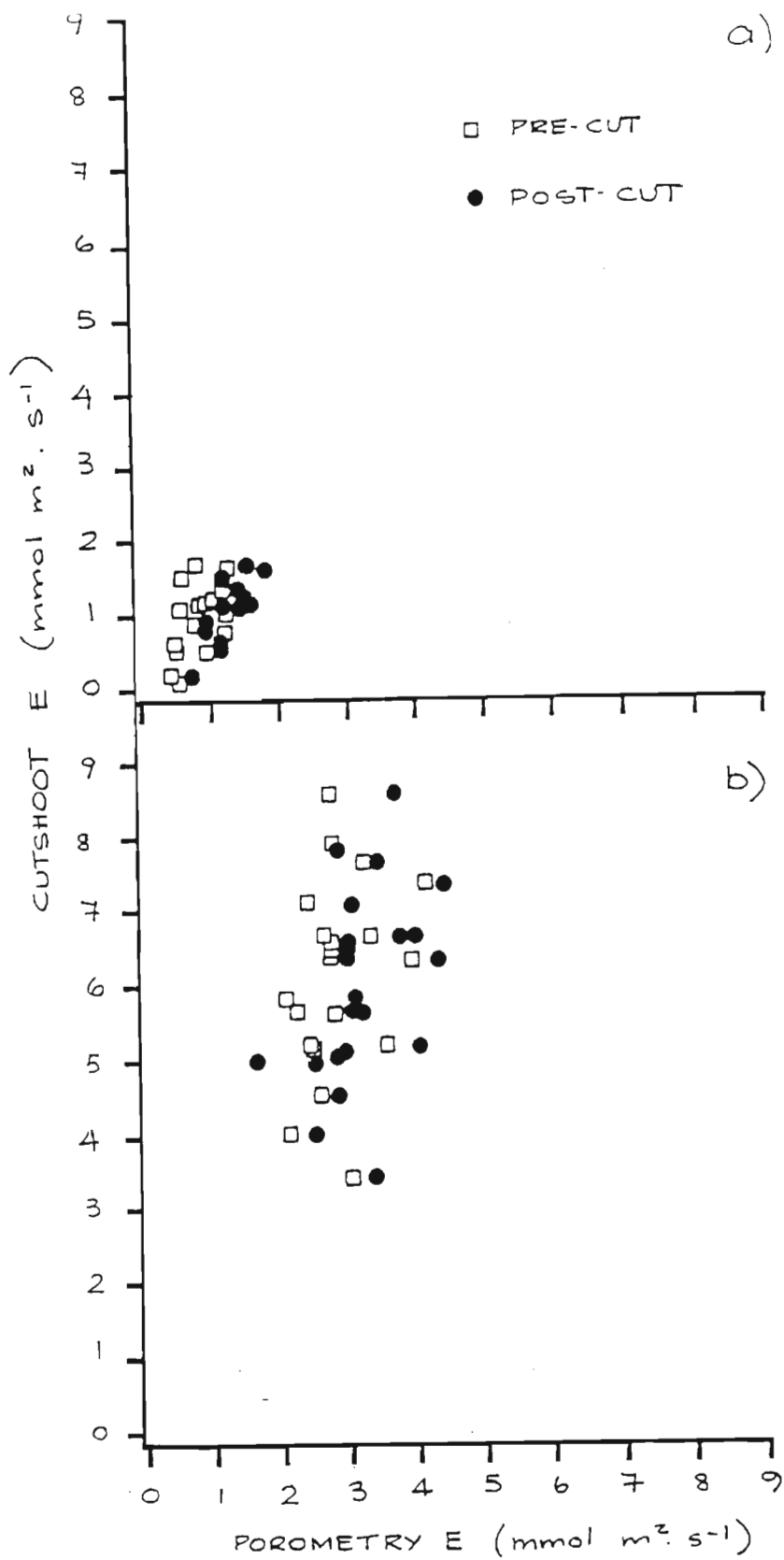


Figure B3: The comparative relationship between transpiration rates measure by the porometry technique before (squares) and after (circles) cutting the leaf and cutshoot rates, on (a) a cool, partly cloudy day and (b) on a warm, clear day in August 1989.

In this experiment, results indicated that removal of root resistance increased stomatal conductance rates slightly. The porometry rates were however, still lower than the cutshoot values (Figures B3).

Further reasons (besides root resistance) were sought to explain the differences in porometry and cutshoot readings, as discrepancies still existed after the second experiment. The modified environment within the cuvette of the porometer may have two possible effects: firstly, the closed cuvette may lead to an increased leaf temperatures within the cuvette. Stomata may be sensitive to these increases per se and therefore may respond by closing their stomata slightly, reducing transpiration rates. Secondly, shading the cuvette from direct radiation may lower PAR, causing stomata to close slightly, thereby restricting transpiration.

Measurements of leaf temperatures were therefore taken both within and outside the cuvette with a thermocouple, to indicate whether leaf temperatures could be a possible source of the discrepancies. The effect of shading the cuvette was also tested by repeating the dual measurements taken with the porometer and cutshoot method on a hot, clear day with and without shading the leaves during the porometry measurements.

Measurements indicated that leaf temperatures were generally 1-3 °C higher within the shaded cuvette than under ambient conditions, although there were also occasions (a quarter of the observations) where the temperatures were slightly (1-3 °C) lower. The effect of shading the cuvette was found to have no marked effect on porometry conductances.

DETERMINATION OF BOUNDARY LAYER CONDUCTANCE

The boundary layer conductance within the P. nitida canopy was determined using a modification of the cutshoot method: a paper leaf with similar dimensions to P. nitida leaves was cut out of blotting paper and saturated with water. It was then suspended by a wire cradle in such a way that its "petiole" had access to a container with water. It

was then placed with cradle and water supply within the *P. nitida* canopy, simulating a *P. nitida* leaf with free access to water (no root resistance) and no stomatal resistance. The system was weighed and then re-weighed at three minute intervals for approximately 90 minutes. The process was repeated on two other "leaves" and conductances were determined.

Boundary layer conductances were found to be one to two orders of magnitude greater than the leaf stomatal conductances ranging between 925 and 1760 $\text{mmol m}^{-2} \text{s}^{-1}$ in comparison with conductances of 90 to 240 $\text{mmol m}^{-2} \text{s}^{-1}$ on the cooler of the two days during early winter, and between 925 and 2400 $\text{mmol m}^{-2} \text{s}^{-1}$ in comparison with rates of between 90 and 325 $\text{mmol m}^{-2} \text{s}^{-1}$ for the warmer, spring day.

It was therefore difficult to ascertain exactly which factors cause discrepancies between cutshoot and porometry estimates of transpiration. This confirms the findings of Rose and Sharma (1984) that despite attempts, it is almost impossible to simulate natural micro-climatic conditions within chamber systems because of the dynamic nature of relative humidity, wind and temperature factors.

Differences between the cutshoot and porometry transpiration rates were not consistent enough to result in the construction of a calibration curve. Method 1 (porometry flow rate estimates) was finally selected for use in this study on the grounds that it was less destructive than the cutshoot method, a relevant factor to consider with the limited supply of seedling material in the study area. It is also based on fewer assumptions than the Penman-Monteith method and provides a good relative (although not absolute) measure of transpiration rate for the seedlings and sprouters, which is all that was necessary in a comparative study such as this one.