

Seasonal variation in photosynthetic capacity with respect to plant water status of five species of the mediterranean climate region of South Africa

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The seasonal variation in net photosynthetic rates of five plant species of the mediterranean climate region of South Africa (fynbos) was investigated. The following species, representing the major fynbos elements, were chosen for intensive investigation: *Erica plukenetii* (ericoid element), *Thamnochortus lucens* (restioid element), *Protea laurifolia*, *Leucadendron salignum* (proteoid element) and *Metrosideros angustifolia*, a shrub of riparian habitat. The shallow-rooted restioid and ericoid species showed the lowest net photosynthetic rates of all the species studied and they also exhibited the greatest summer declines in net photosynthesis. Photosynthetic rate generally decreased with increasing water stress. Those plant species which maintained relatively high photosynthetic rates throughout the year (the proteoid species) and those which were able to control excessive water loss (*E. plukenetii*) were more efficient at utilizing water as a resource than *T. lucens* which exhibited the lowest water-use efficiency.

Die jaargetyverskil in netto fotosintese tempo van vyf plant-spesies van die mediterreense klimaatstreek van Suid-Afrika (fynbos) was ondersoek. Die volgende spesies, wat die hoof-fynboselemente voorstel, was gekies vir intensiewe navorsing: *Erica plukenetii* (ericoïed-element), *Thamnochortus lucens* (restioïed-element), *Protea laurifolia*, *Leucadendron salignum* (proteoïed-element) en *Metrosideros angustifolia*, n struik van oewergroeiplek. Die vlakgewortelde restioïed- en ericoïed-spesies het die laagste fotosintese tempo en die grootste somer-afnames in netto fotosintese tempo van al die spesies vertoon. Fotosintese tempo het algemeen gedaal met toenemende watertekortspanning. Daardie plante wat relatief hoë fotosintese tempo's deur die jaar gehandhaaf het (proteoïed-spesies) en dié wat oormatige waterverlies kon beheer (*E. plukenetii*) was meer doeltreffend in hul watergebruik as *T. lucens* wat die laagste waterverbruiks-doeltreffendheid vertoon het.

Keywords: Adaptation, efficiency of water use, fynbos, photosynthetic capacity, seasonal variation

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Introduction

The mediterranean climate region of South Africa (fynbos biome) is characterized by dry summers and wet to mild winters (Aschmann 1973) and it is also noted for its nutrient-poor soils (Kruger *et al.* 1983). The adaptive significance of plant form in the fynbos biome has generally been interpreted in relation to nutrient-poor soils and gradients of available moisture (Cowling & Campbell 1980; Campbell 1985; Miller 1985; Stock *et al.* 1987).

Studies in the fynbos regions have demonstrated the diurnal and seasonal differences in plant-water relations between plant species growing in various geographical areas (Miller *et al.* 1983; Miller *et al.* 1984; Miller 1985; Jeffery *et al.* 1987; Sommerville 1983). However, little is presently known of the photosynthetic carbon-gaining strategies of fynbos growth forms.

It has been shown that the rates of photosynthetic gas exchange of the evergreen sclerophyll shrubs of the mediterranean-climate regions of California, Chile and the Mediterranean Basin decline in most cases during the summer drought period (Mooney & Dunn 1970; Odening *et al.* 1974; Gigon 1979; Beyschlag *et al.* 1986). Mooney *et al.* (1983) measured the photosynthetic capacities and the photosynthetic temperature and irradiance responses of six fynbos broad-leaf sclerophyll shrubs during spring. The authors observed basic

similarities with the Californian mediterranean climate sclerophylls in stomatal control of gas exchange, constraints on photosynthetic capacity and instantaneous water-use efficiencies.

The objective of this project was to extend the above study by investigating the variation in net photosynthesis of representatives of the three principal fynbos growth forms with season, and to relate the water-use efficiency (in terms of carbon gain) to morphological characteristics of each species.

Methods

The study site was located in the Bain's Kloof Forestry Reserve (33°34'S; 19°06'E) outside Wellington, in the Slanghoek mountain range of the Cape Province. On the basis of the Moll *et al.* (1984) vegetation classification system the study site was considered as consisting of Wet Mountain Fynbos communities. The vegetation at the study area was approximately 4 years old, having regenerated after a fire in 1981. The species studied were *Protea laurifolia* Thunb., *Leucadendron salignum* Bergius, *Metrosideros angustifolia* (L.) Smith, *Erica plukenetii* L. and *Thamnochortus lucens* Pill. Nomenclature is that of Bond & Goldblatt (1984). *P. laurifolia*, *L. salignum* and *M. angustifolia* are deep-rooted, evergreen sclerophyllous shrubs. *L. salignum* and *M.*

angustifolia are both resprouter species and they are very similar in their broad-leaf morphology. *M. angustifolia*, however, is a shrub of riparian habitats while the rest of the study species occur on well-drained soils. *P. laurifolia* is a seed-reproducing species with leaves of approximately three times the area of those of *L. salignum* or *M. angustifolia*. *E. plukenetii* is a low-growing, shallow-rooted shrub with narrow sclerophyllous leaves of which the lower surfaces are deeply grooved. *T. lucens* is a low-growing, shallow-rooted hemicyptophyte with long, erect photosynthetic culms.

The pressure-bomb technique (Scholander *et al.* 1965) for measuring xylem pressure potential was used to estimate plant-water status. Pre-dawn and midday xylem pressure potentials were recorded for vegetative shoots of *E. plukenetii*, *L. salignum* and *M. angustifolia*, flowering culms of *T. lucens* and individual leaves of *P. laurifolia* using a 0–70 bar pressure bomb (PMS Instrument Co., Corvallis, USA). A field-transportable infra-red gas analyser (LCA-2, Analytical Development Company Ltd., Hoddesdon, England) was used for the simultaneous measurement of CO₂ assimilation rate (*A*) and transpiration rate (*E*). Transpiration rate was calculated from the determination of mass flow of dry air through the cuvette and the increase in water vapour pressure in the cuvette due to evaporation from the leaf surface to the dry air passing over the leaf. The values used in this report are therefore overestimates of the true transpir-

ation rates occurring in the field. Transpiration rate was calculated from the determination of mass flow of dry air through the cuvette and the change in water vapour pressure of air in the cuvette during the time of measurement. Net CO₂ assimilation rate was calculated using the differences in mole fractions of CO₂ in the incoming and outgoing airstreams of the cuvette, including a correction for dilution of CO₂ by water vapour from transpiration. The calculations of rates of gas exchange and of stomatal conductance follow the analysis outlined by von Caemmerer & Farquhar (1981).

Field measurements were carried out at monthly intervals on cloudless days. Measurements were always performed on unshaded photosynthetic tissue with maximum exposure to the sun. The naturally occurring orientations were maintained during measurements. Each month, measurements were taken on a diurnal basis which involved the recording of rates of photosynthetic gas exchange at three different times of the day i.e. morning, midday and late afternoon. This report utilizes the midday recordings only. The diurnal variations in the rates of photosynthetic gas exchange will be examined in another research report. Preliminary studies were carried out to identify the photosynthetic regions of the plant that would best represent the maximum photosynthetic capacity for each species. On the basis of these studies only the most recently matured leaves (6–18 months old) were used for gas exchange

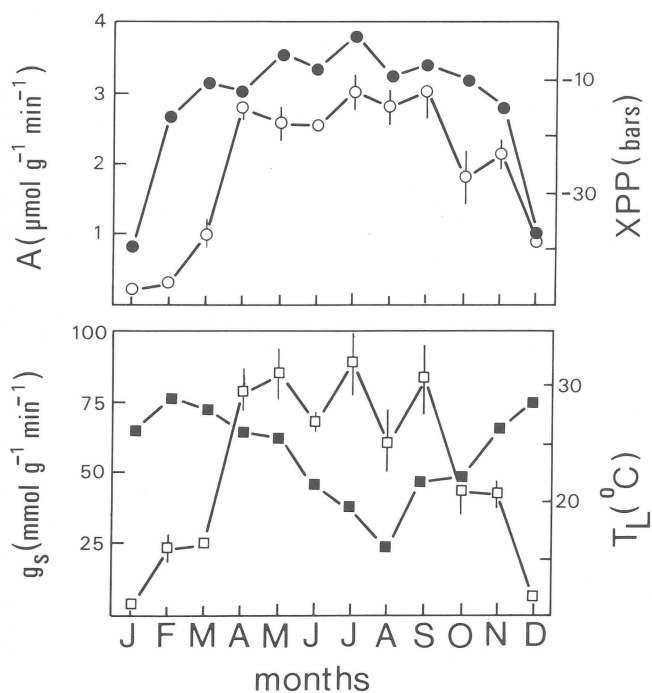


Figure 1 Seasonal variation in midday xylem pressure potential (closed circles), midday net photosynthetic rate (open circles), midday stomatal conductance (open squares) and midday leaf temperature (T_L) (closed squares) of *Erica plukenetii*. Each value is the mean of six replicate measurements and the corresponding vertical bar represents the standard error of the mean. Where there are no bars, the standard errors are too small to show on the scale of the graph.

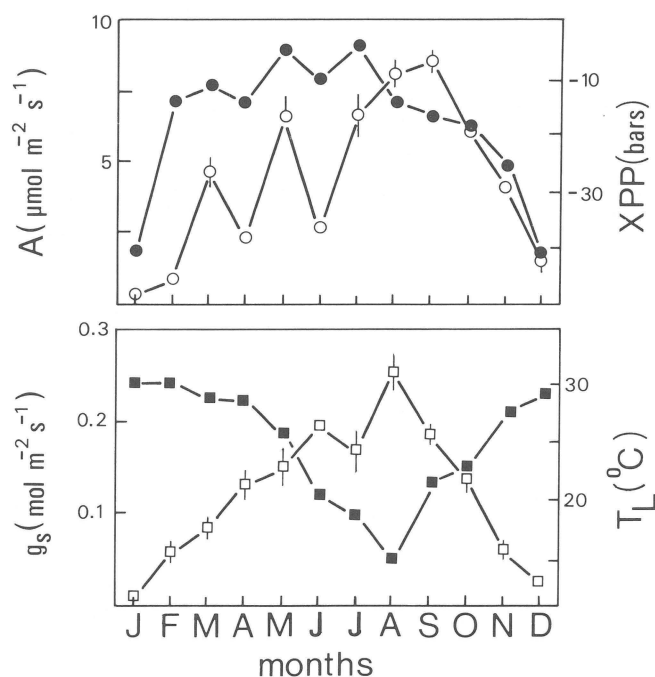


Figure 2 Seasonal variation in midday xylem pressure potential (closed circles), midday net photosynthetic rate (open circles), midday stomatal conductance (open squares) and midday leaf temperature (T_L) (closed squares) of *Thamnochortus lucens*. Each value is the mean of six replicate measurements and the corresponding vertical bar represents the standard error of the mean. Where there are no bars, the standard errors are too small to show on the scale of the graph.

measurements of the broad-leaf species. The leaves of the female individuals of *L. salignum* were used for the measurements since they were almost always larger and showed higher photosynthetic capacities than the leaves of the male individuals. Terminal shoots (0–5 cm from apex) of *E. plukenetii* were used for the gas exchange measurements. First to third internodes below the inflorescence of the photosynthetic culms of *T. lucens* were used, as below this the culms were occasionally shaded and were consequently unsuitable for photosynthetic rate measurements. Rates of photosynthetic gas exchange are expressed on a unit leaf area basis for all species, except for *E. plukenetii*, where methods of leaf area determinations were difficult because of the rolled-leaf architecture of the leaves of this species. The rates of photosynthetic gas exchange of *E. plukenetii* are therefore expressed on a unit dry weight basis. Six individuals of similar size, age and height of each species were selected each month for photosynthetic gas exchange measurements.

Results

Gas exchange in relation to xylem pressure potential

The seasonal patterns of net assimilation rate (A) of *E. plukenetii* and *T. lucens* exhibited some common features (Figures 1 & 2). The lowest photosynthetic rates and xylem pressure potentials (xpp) for both species were recorded from late spring to the summer months.

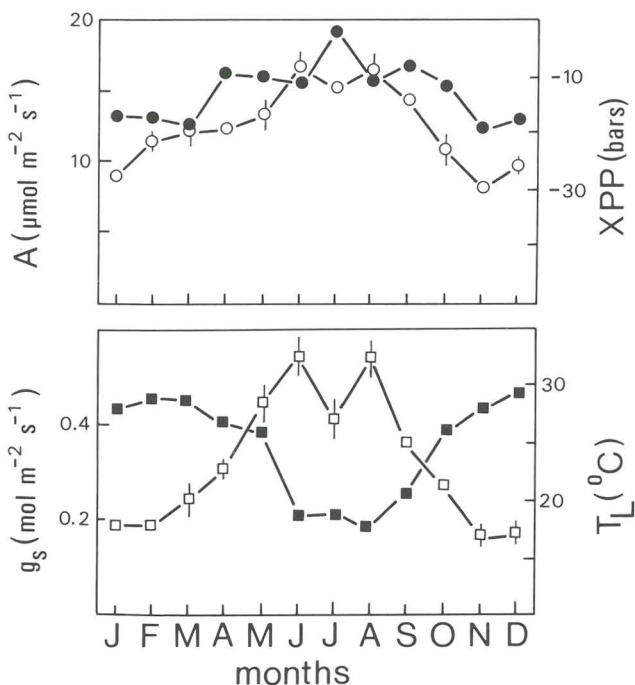


Figure 3 Seasonal variation in midday xylem pressure potential (closed circles), midday net photosynthetic rate (open circles), midday stomatal conductance (open squares) and midday leaf temperature (T_L) (closed squares) of *Protea laurifolia*. Each value is the mean of six replicate measurements and the corresponding vertical bar represents the standard error of the mean. Where there are no bars, the standard errors are too small to show on the scale of the graph.

The rates of decline in gas exchange from the maximum during September to the minimum during January were similar for both species: the midday A of *T. lucens* increased by 97% from January to September while that of *E. plukenetii* increased by 94% over the same period. While *E. plukenetii* exhibited a well-defined seasonal pattern of A , *T. lucens* manifested a high degree of fluctuation, particularly during April and June. The decreases in A during these months were accompanied by similar decreases in xylem pressure potentials.

The seasonal patterns of net assimilation rate of the deep-rooted *P. laurifolia* (Figure 3), *L. salignum* (Figure 4) and *M. angustifolia* (Figure 5) showed the same main features of the patterns observed for *E. plukenetii* and *T. lucens*: the lowest net photosynthetic rates were recorded during summer and the highest during the winter–spring period. The degree of summer decline in net assimilation rate of the deep-rooted species, however, was not nearly as large as the summer net assimilation rate depression recorded for the shallow-rooted species. For example, the midday assimilation rates of *P. laurifolia*, *L. salignum* and *M. angustifolia* during January were 62%, 95% and 43% respectively of their September midday assimilation rates. In contrast, the midday net assimilation rates of *T. lucens* and *E. plukenetii* during January were 3% and 6% respectively of their September midday net assimilation rates. The maximum rates of photosynthesis recorded for the deep-

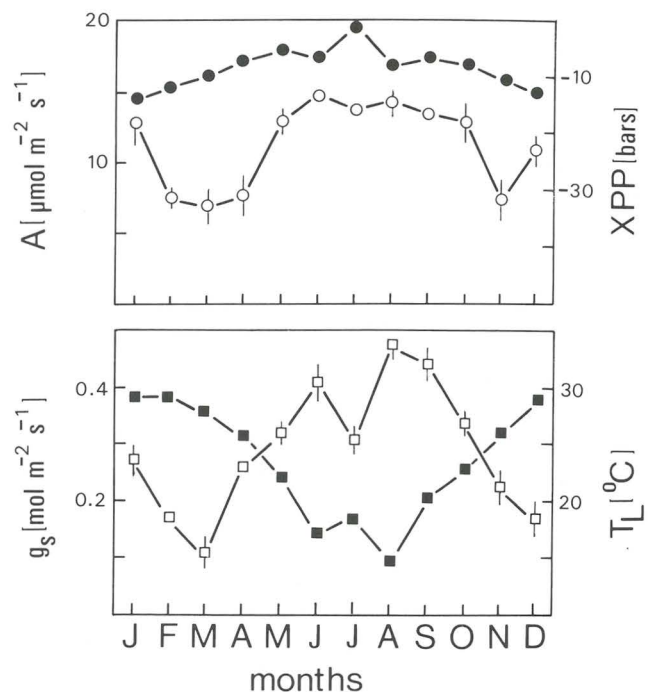


Figure 4 Seasonal variation in midday xylem pressure potential (closed circles), midday net photosynthetic rate (open circles), midday stomatal conductance (open squares) and midday leaf temperature (T_L) (closed squares) of *Leucadendron salignum*. Each value is the mean of six replicate measurements and the corresponding vertical bar represents the standard error of the mean. Where there are no bars, the standard errors are too small to show on the scale of the graph.

rooted species appear to be more than double the rates recorded for the shallow-rooted *T. lucens* and *E. plukenetii*. The magnitude of the differences in A of the three fynbos elements becomes apparent when the net assimilation rate of the three representative species are expressed on a dry weight basis (Figure 6).

Net photosynthesis was more strongly associated with xpp in *T. lucens* (Figure 2) than in the case of the ericoid species (Figure 1) and the deep-rooted proteoid species (Figures 3–5). This is exemplified in the data obtained during April and June when *T. lucens* exhibited decreases in midday xylem pressure potentials (Figure 2). These decreases in xpp were accompanied by similar decreases in net assimilation rate. *E. plukenetii* exhibited similar decreases in xpp during April and June but these were not accompanied by reductions in A . The decreases in A and xpp exhibited during April and June by *T. lucens* (Figure 2) were not associated with decreases in stomatal conductance (g_s). In contrast, more or less parallel patterns were found for the seasonal progressions of net photosynthesis and stomatal conductance of *E. plukenetii* (Figure 1) and the deep-rooted species (Figures 3–5).

Efficiency of water use

Water-use efficiency (WUE) was calculated to assess the efficiency of water usage during photosynthesis and is expressed as net photosynthetic rate/transpiration rate

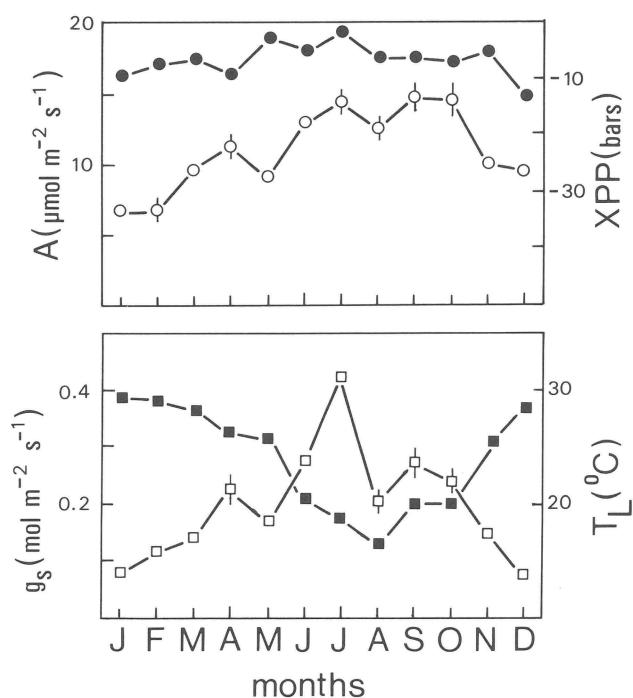


Figure 5 Seasonal variation in midday xylem pressure potential (closed circles), midday net photosynthetic rate (open circles), midday stomatal conductance (open squares) and midday leaf temperature (T_L) (closed squares) of *Metrosideros angustifolia*. Each value is the mean of six replicate measurements and the corresponding vertical bar represents the standard error of the mean. Where there are no bars, the standard errors are too small to show on the scale of the graph.

(i.e. $\mu\text{moles of CO}_2$ gained/ $\text{mmoles of H}_2\text{O}$ transpired). Apart from decreases in WUE experienced by *E. plukenetii* from January to March, relatively constant water-use efficiencies were maintained by this species throughout the year (Table 1). The observed decreases in WUE during these months were possibly responses to higher temperatures and the concomitantly greater evapotranspirative demands. In comparison with the water-use efficiencies calculated for *T. lucens* (Table 1), *E. plukenetii* was relatively economical in its water usage. The ability of *E. plukenetii* to maintain higher water-use efficiencies was probably related to a greater control of transpirational water loss, facilitated by limited stomatal distribution in non-photosynthetic grooves on the lower leaf surfaces. *T. lucens* was most inefficient in its water utilization with respect to C-fixation during February when low rates of net photosynthesis were accompanied by high rates of transpiration. In comparison to *T. lucens*, the deep-rooted species (Table 1) were relatively economical in their water usage with respect to carbon assimilation. These species were able to maintain higher WUE 's by virtue of their generally high net photosynthetic rates.

Discussion

For all species studied the lowest xylem pressure potentials were recorded during spring and summer months. This seasonal pattern corresponds well with the monthly variation in precipitation with the lowest potentials measured at the time of lowest rainfall. The magnitudes of seasonal variations in xylem pressure potentials are comparable to values obtained for mesic fynbos species by Miller *et al.* (1983) and Miller (1985). The values also correspond with xylem pressure potential measurements of several mediterranean-climate sclerophyllous species (Poole & Miller 1975). The highest xylem pressure potentials throughout the study period were found in *P. laurifolia*, *M. angustifolia* and by *L. salignum*. The deeper and more extensive rooting systems of these species probably account for their generally higher xylem pressure potentials and their lower magnitudes of seasonal variation in xylem pressure potentials.

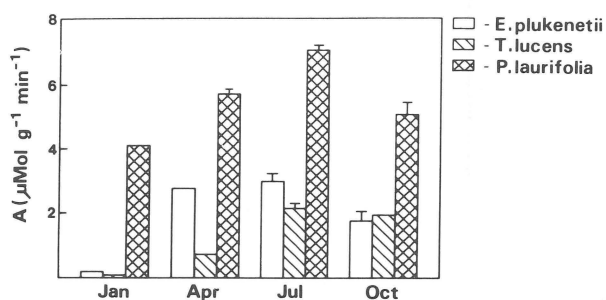


Figure 6 Midday net photosynthetic assimilation rates ($\mu\text{Mol g}^{-1} \text{min}^{-1}$) of three representative mountain fynbos growth forms during January, April, July and October. Each value is the mean of six replicate measurements and the corresponding vertical bar represents the standard error of the mean. Where there are no bars, the standard errors are too small to show on the scale of the graph.

Table 1 Seasonal course of midday water-use efficiency ($\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$). Each value is expressed as the mean of six replicate measurements and the corresponding standard error of the mean

	<i>Erica</i>	<i>Thamnochortus</i>	<i>Protea</i>	<i>Leucadendron</i>	<i>Metrosideros</i>
Jan	1.87±0.26	0.87±0.07	2.48±0.11	1.43±0.09	1.95±0.18
Feb	0.51±0.02	0.36±0.03	2.07±0.12	1.25±0.14	1.25±0.04
Mar	1.51±0.05	1.40±0.09	3.07±0.25	2.48±0.24	1.62±0.08
Apr	2.05±0.10	0.48±0.04	2.03±0.09	0.94±0.05	1.84±0.11
May	2.45±0.31	2.05±0.12	3.29±0.21	2.35±0.08	2.37±0.11
Jun	3.12±0.12	1.05±0.06	4.44±0.09	2.76±0.11	2.82±0.08
Jul	3.55±0.06	2.89±0.14	4.44±0.14	3.03±0.20	2.60±0.03
Aug	4.44±0.09	3.71±0.17	6.28±0.10	3.82±0.14	3.97±0.23
Sep	3.07±0.18	2.71±0.07	3.89±0.26	2.32±0.09	3.14±0.10
Oct	2.29±0.08	2.11±0.05	3.12±0.31	1.67±0.05	2.31±0.20
Nov	2.52±0.17	2.20±0.09	2.24±0.17	1.25±0.11	2.57±0.16
Dec	4.00±0.62	1.56±0.24	2.82±0.18	1.95±0.12	4.17±0.17

On the basis of the photosynthetic data, two distinct groups can be identified: (a) the shallow-rooted *E. plukenetii* (root depth: 0–20 cm) and *T. lucens* (root depth: 0–10 cm), on the one hand, which exhibited relatively low net assimilation rates and which experienced the greatest decline in *A* during the summer months and (b) the deep-rooted species (root depth: +40 cm) which maintained the highest assimilation rates and which showed smaller summer depressions in *A*. The shallow-rooted species showed a greater decline in xylem pressure potential (more negative values) during summer than did the deep-rooted species, and it would appear that their lower CO_2 assimilation rates and their greater summer decline in *A* can be explained in terms of the effects of water stress only. It appears that the effects of decreased plant-water status on the photosynthetic processes of *E. plukenetii* were mediated by stomatal control. In contrast, no experimental support was found to show that the stomata of *T. lucens* imposed limitations on its net assimilation rate under conditions of water stress.

The data suggests that stomatal conductance occasionally limited assimilation rates of the fynbos species studied, although this hypothesis was not explicitly tested. For example, the increases in assimilation rate experienced by most species (except *T. lucens*) with the onset of higher soil-water availability (increased *xpp*) coincided with increases in stomatal conductance. However, changes in assimilation rate and stomatal conductance were not always coincidental, and changes in assimilation rate during these months could have been direct effects of high or low leaf temperatures. Van der Heyden (1988) showed that at saturating light intensities the net photosynthetic rates of three fynbos species declined at temperatures greater than 20–30°C. More detailed experimentation under controlled laboratory conditions is required to determine how stomatal responses contribute to the optimization of water use and photosynthetic processes.

In terms of net assimilation rates, the data compare closely with the results obtained in other mediterranean-climate regions (Mooney & Dunn 1970; Odening *et al.* 1974; Gigon 1979; Beyschlag *et al.* 1986). Most of these studies demonstrated summer and winter depressions in photosynthetic rates. In contrast, net photosynthetic rates of the fynbos species showed only summer depressions. This might be attributed to the fact that measurements in other mediterranean climate ecosystems were performed at lower winter temperatures.

Measurement of water use in relation to carbon fixation (water-use efficiency) provided an insight into the possible strategies employed by the various species in utilizing water as a resource. Essentially three strategies can be distinguished. Firstly, that identified for *E. plukenetii*, which lost minimum amounts of water in relation to carbon gain (i.e. high *WUE*). In this case the ability to maintain the higher *WUE*'s was probably related to an effective control of transpirational water loss facilitated by the unique anatomy of the ericoid leaf where stomata are largely confined to a non-photosynthetic groove on the abaxial side of the leaf. The deep-rooted species, which represent a second strategy, were able to maintain high *WUE*'s relative to the other groups throughout the study period by virtue of their generally high net assimilation rates. *T. lucens* represents the third strategy of water utilization. This species was the least water use efficient, particularly during summer. This species appears to photosynthesize and transpire relatively rapidly when water is available in the upper soil horizons, but under dry conditions low xylem pressure potentials develop and the plant transpires and photosynthesizes at low rates. An analysis of the distribution of vegetation structural characteristics in the mountains of the Cape (Campbell 1985) showed that restioid-dominated fynbos is associated with relatively xeric habitats like the summer-dry northern aspect of mountain ranges, and with very shallow and rocky soils. These soils are frequently subjected to low soil-water

levels because they do not have a large soil volume for moisture retention (Campbell 1985). The unique water-use patterns of *T. lucens* appear to be excellent adaptations for growth and survival in these soils. The data presented suggest that *T. lucens* assimilated carbon at the cost of rapid water loss at times when water was readily available. Consequently, water in the upper soil layers was used quickly as soon as it became available.

It is commonly assumed that plant species with high carbon fixation rates have the advantage of more available carbon which can be used in various ways (e.g. reproductive and vegetative growth) to compete favourably during the successional stages after a disturbance (Mooney *et al.* 1975; Solbrig & Oriens 1977). In one of the first studies to investigate the relationship between plant success and photosynthetic capacity, Oechel & Mustapha (1979) provided support for the assumption that greater photosynthetic capacity is an adaptive advantage. These authors found a strong correlation between plant cover and photosynthetic capacity across a geographical gradient of mediterranean scrub vegetation in southern California. Testing of post-fire regeneration models on a range of fynbos communities (Moll & Hoffman 1984) has shown that approximately 10 years after fire, the proportional representation of the ericoid and the restioid component declines, at which time the proteoid element is contributing an increasingly greater percentage to the total plant population. The photosynthetic data reported in this study support these findings. The greater carbon gain of the proteoid species and an ability to maintain high photosynthetic rates throughout the year could have some adaptive advantage in the later successional stages following fire. Similarly, the low carbon-gaining capacities of the restioid and ericoid species would put them at a disadvantage when plant density and consequently competition for resources increases.

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