Growth and gas exchange responses of *Leucadendron xanthoconus* (Proteaceae) seedlings to different nutrient and water regimes

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Potted seedlings of *Leucadendron xanthoconus* (Proteaceae) were grown in native mountain fynbos soil under different nutrient and water regimes. Nutrient treatments comprised addition of nitrogen, phosphorus and a Long Ashton macronutrient solution (LA). Water was applied at three levels, ranging from near drought to maintained saturation. Rates of gas exchange were measured on a subset of the experimental plants under a range of irradiance levels prior to harvesting of all plants at an age of six months. Measurement of biomass and its distribution showed that increasing water had a significantly positive effect on productivity, and that drought reduced root:shoot ratio and leaf specific weight. Total productivity was highest with LA-addition and lowest in the control, whereas phosphorus and nitrogen additions had an intermediate effect. None of the treatments included in the gas exchange work was shown to affect significantly photosynthetic capacity or water use efficiency. Droughted individuals showed an increased ability to reduce carbon dioxide concentration in the substomatal cavity, and a lower stomatal conductance overall. Stomatal conductance was found to be independent of irradiance in all treatments. The relationships investigated are placed in the context of fynbos utilization and the management of natural fynbos landscapes with regard to the reclamation and maintenance of component natural ecosystems.

Saailinge van *Leucadendron xanthoconus* is in inheemse bergfynbosgrond in potte onder verskillende water-en voedingstofbehandelings gekweek. Die voedingstofbehandelings het uit oplossings van stikstof, fosfor en Long Ashton makrovoedingstof (LA) bestaan. Drie verskillende watervlakke is gehandhaaf, wat gewissel het vanaf droogte tot volgehoue gronddeurweektheid. Voordat die plante op 'n ouderdom van ses maande geoes is, is die tempo van gaswisseling van 'n subreeks experimentele plante onder verskillende ligintensiteite ondersoek. Die bepaling van die biomassa en die verspreiding daarvan het getoon dat 'n verhoogde water-toevoer 'n positiewe invloed op produktiwiteit gehad het, en dat droogtetoestande die wortel:loot-verhouding en die blare se spesifieke gewig verminder het. Algehele produktiwiteit was die hoogste met die LA-toevoe-ging, die laagste in die kontrole, terwyl forfor- en stikstoftoevoegings 'n intermediêre effek getoon het. Geeneen van die behandelings wat tydens die gasuitruilingstudie ondersoek is, het 'n effek op fotosintetiese kapasiteit of waterverbruiksdoeltreffendheid getoon nie. Saailinge wat aan droogte blootgestel is, het 'n verhoogde vermoë om koolstofdioksiedkonsentrasie in die stomakamer te verlaag, getoon. Ligintensiteit het geen effek op blaarkonduktansie uitgeoefen nie. Die verwantskappe wat ondersoek is, is in die lig van fynbosbenutting en die bestuur van natuurlike fynboslandskappe vir die herwinning en die onderhoud van natuurlike ekosisteme bespreek.

Keywords: Fynbos, IRGA, photosynthesis, stress, water use efficiency.

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Introduction

Management of natural ecosystems can be facilitated by an understanding of the stresses which are induced by the disturbance of utilization. For manipulation of vegetation components, especially seed germination and subsequent seedling establishment on disturbed sites in need of revegetation, an insight into ecophysiological relationships is particularly important. In the Fynbos Biome of the Cape, where a large number of threatened taxa require conservation (Hilton-Taylor & le Roux 1989), the environmental factors generally perceived to be sources of plant stress are: (i) limited nutrient availability, especially with respect to phosphorus and nitrogen (Mitchell *et al.* 1984; Witkowski & Mitchell 1987; Witkowski 1989a) and (ii) seasonal drought during the summer period (Kruger 1979; van der Heyden & Lewis 1989; von Willert *et al.* 1989), although Miller *et al.* (1983) and Moll and Sommerville (1985) showed that water

is not a significant stress factor for the deeper rooted species. Arising from his studies of lowland sandplain fynbos in the south-western Cape, Witkowski (1989b; 1989c) suggested that the water regime at a site is an important factor in the relative availability of phosphorus and nitrogen from the soil.

The work described in this paper is based on observations of *Leucadendron xanthoconus* (Proteaceae) growing under field experimental conditions which simulated land management as often practised by commercial wildflower producers (Davis 1990). In this latter study it was shown that, following veld-clearing by burning, self-sown *L. xanthoconus* seedlings growing on soil disturbed by tillage produced more aboveground biomass during the first three years than did those growing on untilled soil. The same study indicated, however, that tillage was associated with a significantly lower overall plant cover, and a higher soil water

content during the relatively dry summer months. From those observations it may be surmised that plants growing on tilled soil were at an advantage with regard to both water and nutrient resources. In this paper it is attempted to determine the relative importance of those two resource factors for seedling growth in *L. xanthoconus*, and the mediation of those influences by physiological processes.

Methods and materials

During the winter of 1988 seeds of *Leucadendron xanthoconus* were sown into sandy (clay content < 10%) mountain fynbos topsoil which had been collected from a site close to Botrivier, Cape, and sieved to 4 mm. Characteristics of this soil are described in Table 1.

Established seedlings were later planted out into individual black plastic bags (500 ml) when most of the plants were developing their first true leaves. Approximately 100 such plants were then randomly distributed between one of three watering regimes, and one of six nutrient supplement regimes.

Experimental regime

Water was administered by dripper devices at three levels of supply. Approximate amounts supplied at each level were: 75 ml once per week (W_1); 300 ml once per week (W_2); and 75 ml daily (W_3). Treatment W_3 maintained plants at or close to field capacity, while occasionally additional water was administered to W_1 to minimize mortality through droughting.

Nutrient additions were based on the Long Ashton nutrient medium with 1 mM NH_4NO_3 as a nitrogen source (Hewitt & Smith 1975), and were applied in 100-ml doses once every six weeks. These were as follows: (i) control (CL) with no additions to the native soil; (ii) 5% Long Ashton (LA_5) solution; (iii) 15% LA solution (LA_{15}); (iv) 50% LA solution (LA_{50}); (v) only the phosphorus component of the LA_{50} solution (P); and (vi) only the nitrogen component of the LA_{50} solution (N). Deviations from this regime included omission of the W_2/N treatment due to insufficient plant material, and a ten-fold concentration overdose in the phosphorus treatment (P) during the second feeding, which resulted in necrosis and abscission of older leaves in most plants of the set. The pattern of height increase and mor-

Table 1 The nutrient status of topsoil at the site from which soil was collected for the experimental work described in this paper[a]

Parameter	Mean	Std. dev.
N (%) (Kjeldahl)	0.0967	0.0176
P (p.p.m.) (Bray extraction)	< 5	—
C.E.C. (me/100 g)	5.803	0.921
Na^+ (me/100 g)	0.117	0.036
K^+ (me/100 g)	0.167	0.063
Ca^{2+} (me/100 g)	3.467	0.917
Mg^{2+} (me/100 g)	1.010	0.132
Al (me/100 g)	0.210	0.089
pH[b] (in 1M KCl)	5.3	0.35

[a] Table values are the mean of three randomly collected samples, as analysed by the laboratory of the Department of Agriculture and Water Supply, Elsenburg, Cape.

[b] Sample taken from sieved experimental soil.

phology was not apparently affected by this latter mishap, and all dead leaves were included in the final total biomass analyses.

Harvesting and measurement of plants

All plants were harvested after six months. The roots, leaves and stems were separated, oven-dried at 75°C, and weighed. Leaf areas were measured on a conveyor belt leaf area meter (Li-Cor 3000).

Gas exchange determinations

An infra-red gas analyser (Li-Cor 6200 with 4-l cuvette), configured as a closed system, was used to investigate CO_2 and H_2O fluxes in response to light intensity. Measurements were made on a subset of plants from the high-water treatment using five replicates from each of the following nutrient supplement classes: CL, LA_{50}, P and N. A set of four plants from the low-water/control-nutrient group was also included. Representative sample sets were removed on consecutive days, starting three days after the last watering for low-water plants, and analyses performed in rotating order with respect to treatment. Plants were allowed to acclimate to the maximum light intensity [maximum photosynthetic photon flux density (PPFD) always greater than 650 $\mu mol.m^{-2}.s^{-1}$] for a minimum of 10 min, and then consecutive sets of three readings were taken at each of approximately seven steps between the PPFD and darkness during which CO_2 efflux was invariably observed.

Natural light through the fibre-glass walls and roof of the greenhouse was supplemented by two fluorescent lamps (15 W each), and three quartz-halogen lamps (500 W each). The lamps contributed a maximum PPFD of approximately 500 $\mu mol.m^{-2}.s^{-1}$ in the position occupied by the plant under analysis. Output from the latter was adjusted by means of a dimmer-switch, and directed through water-filled glass oven dishes as a filter for heat. Irradiance levels lower than ambient were attained by shading with shade-cloth and black plastic sheeting.

Foliar nutrient analyses

Foliar samples were taken from plants used in the gas exchange analysis, oven-dried at 80°C, and milled. Nutrient levels (except nitrogen) were determined by direct current plasma analysis (Barnes 1981), and Kjeldahl analysis was used for determination of nitrogen content (N_{leaf}). All analyses were performed at, and by personnel of, the soil testing laboratory of the Department of Agriculture and Water Supply, Elsenburg, Cape.

Data analyses

Analysis of the gas exchange data was performed in the following ways: (i) maximum photosynthetic rate (A_{max}) was derived from the y-intercept of the plot of $\log_{10}(1/A)$ against $(1/PPFD)$, where A is the net assimilation rate at the associated PPFD; (ii) maximum water use efficiency (WUE_{max},) was similarly derived from the relationship between $WUE = A/E$ and PPFD, where E is the transpiration rate; (iii) a 'light harvesting response' is taken as the area under the irradiance response curve for $0 \leqslant PPFD \leqslant 650$ $\mu mol.m^{-2}.s^{-1}$; and (iv) for each plant's set of light response

data, the largest difference between the measured CO_2 concentration of the atmosphere (C_a), and the associated value derived for the sub-stomatal cavities (C_i) (Li-Cor 1987), hereafter referred to as $(C_a - C_i)_{max}$.

The 'light harvesting response', as defined, is used here as an alternative to measuring the slope of the irradiance response curve at low light (Thompson *et al.* 1988), where data in this study were found to be fairly noisy. Its validity as a comparative measure between treatments does, however, rest on the similarity of associated A_{max} values, a situation which was recorded between all treatments in this study.

Analysis of variance tests (ANOVA) were performed primarily using the General Linear Models (SAS 1985) set of routines, and the Principal Components Analysis (PCA) using the commercial package, STATGRAPHICS (STSC, Rockville, Maryland).

Results

Results of a two-way ANOVA have been separated below with respect to the experimental factors of water and nutrients (Tables 2 and 3). Interactions between water and nutrient effects on all responses except mean leaf area and plant height were insignificant at the 10% level. The interaction for plant height ($p = 0.04$) was in degree rather than in trend, while for mean leaf area ($p = 0.0008$) reversals in trend were apparent. A typical relationship between water and nutrients as factors influencing biomass production is

shown in Figure 1 (where the interaction is non-significant with $p = 0.16$).

Water

As is indicated in Table 2, water stress is related to a response in several parameters of seedling growth. The absence of relative stress produces plants which are generally more productive, with a higher root:shoot ratio, and more, bigger leaves with a higher leaf specific weight (mass/area).

Nutrients

Long Ashton: The 50% Long Ashton treatment was shown (Table 3) to be effective in enhancing parameters of growth in *Leucadendron xanthoconus* seedlings relative to the native soil control, in terms of biomass production and plant height, but without affecting the root:shoot ratio or the leaf specific weight. While the LA_5 and LA_{15} treatments also enhanced some of these parameters, phosphorus and nitrogen on their own appear to have had little effect at the concentrations applied, except for an increase in total production over the experimental period.
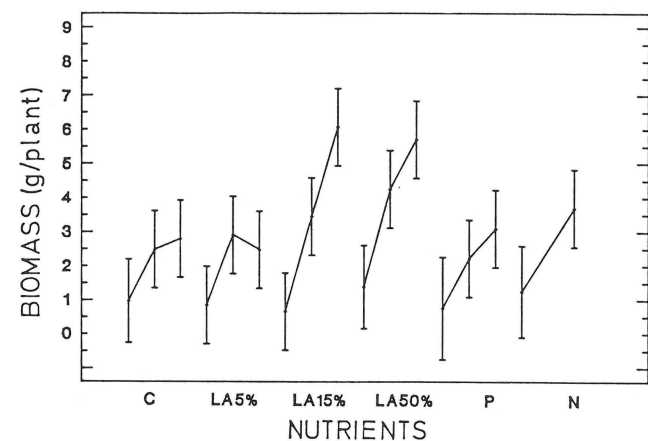
Table 2 Growth responses of *Leucadendron xanthoconus* seedlings to the applied experimental watering regimes, which ranged from near drought (Low) to maintained saturation (High). See Methods for details

Parameter	Low	Medium	High
Shoot mass (g)	0.80[a]	1.62[b]	1.93[c]
Root mass (g)	0.57[a]	1.47[b]	2.08[c]
Total leaf mass (g)	0.60[a]	1.29[b]	1.46[b]
Root:shoot ratio	0.684[a]	0.893[b]	1.014[b]
Mean leaf area (cm^2/leaf)	1.02[d]	1.26[d]	1.40[d]
Mean leaf specific weight (g/cm^2)	0.0098[a]	0.011[b]	0.011[b]
Plant height (mm)	216[a]	284[b]	327[c]
Sample size	25	33	41

[a,b,c] Homogeneous groups; Student-Neuman-Keul test ($p < 0.05$).
[d] Main effects inseparable owing to interaction of factors.

Figure 1 Interaction between the water and nutrient treatments and their influence on total biomass production by *Leucadendron xanthoconus* seedlings over the six-month experimental period. Each cluster represents increasing water levels (left to right) for each nutrient treatment labelled on the horizontal axis. Vertical bars indicate 95% confidence intervals of the central mean value. Sample sizes are presented in Tables 2 and 3.

Table 3 Response of *Leucadendron xanthoconus* seedlings to nutrient enhancement, where $LA_5 - LA_{50}$ are the Long Ashton supplements, and N and P the nitrogen and phosphorus supplements as described in Methods

Parameter	Control	LA_5	LA_{15}	LA_{50}	P	N
Shoot mass (g)	1.18[a]	1.24[a]	1.82[bc]	2.24[c]	1.41[ab]	1.37[ab]
Root mass (g)	0.98[a]	1.16[ab]	2.01[bc]	2.26[c]	1.17[ab]	1.44[ab]
Total leaf mass (g)	0.92[a]	0.96[a]	1.47[b]	1.72[b]	0.99[a]	1.10[a]
Root:shoot ratio	0.83[a]	0.90[a]	0.97[a]	0.90[a]	0.83[a]	0.90[a]
Mean leaf area (cm^2/leaf)	1.12[d]	1.18[d]	1.19[d]	1.55[d]	1.39[d]	1.13[d]
Mean leaf specific weight (g/cm^2)	0.0097[a]	0.0100[ab]	0.011[b]	0.010[ab]	0.010[ab]	0.010[ab]
Plant height (mm)	266[a]	260[a]	286[a]	339[b]	287[a]	261[a]
Sample size	20	18	18	17	14	12

[a,b,c] Homogeneous groups; Student-Neuman-Keul test ($p < 0.05$).
[d] Main effects inseparable due to interaction of factors.

Photosynthetic capacity and water use efficiency

Measurement of CO_2-uptake and transpiration of plants in the selected subset of experimental plants revealed no significant differences in performance between treatments with respect to the following parameters described in the methods section: A_{max}, WUE_{max} and 'light harvesting response'. However, using one-way ANOVA, a significant difference ($p < 0.01$) was found between treatments for the set of $(C_a - C_i)_{max}$ values, with the low-water treatment representing a group of plants capable of developing a steeper gradient in $[CO_2]$ than others. That result is implicit in the regressions which are plotted in Figure 2. Stomatal closure, as indicated by the water vapour conductance values derived from transpiration characteristics, did not
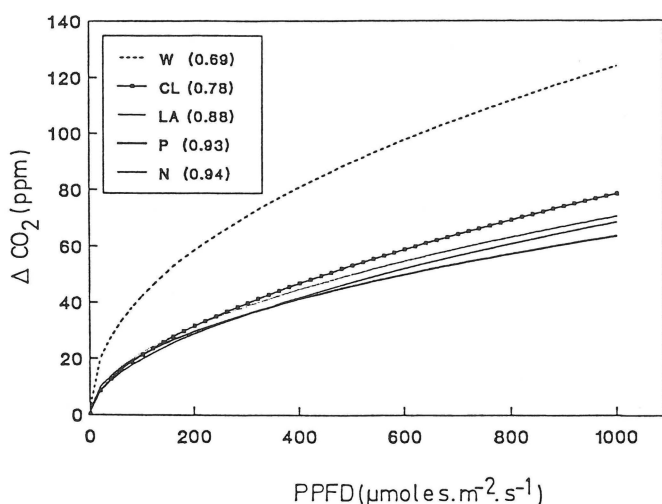
occur in the dark, and for most plants there was little or no irradiance-related response over the full range of PPFD tested. A one-way ANOVA and multiple-range test of the set of mean conductance values, of which the coefficient of variation was usually less than 10% and always less than 20%, showed that overall stomatal conductance of the low water (W_1) treatment was significantly less than the nitrogen (N) treatment ($p < 0.05$), while the remaining treatments (CL, LA_{50} and P) were intermediate.

Foliar nutrients

Results of the nutrient analyses performed on leaf material of this subset of plants are summarized in Table 4, where it can be seen that with the exception of copper, zinc and iron, there is a tendency for plants of the low-water treatment (W_1/CL) to form a group different from those from the other treatments. Also included in Table 4 is a summary of results obtained in the gas exchange work to provide a comparison of the response ranges encountered.

Principle components analysis (PCA)

Productivity, gas exchange and foliar nutrient data from plants used in the gas exchange work are summarized by the ordination in Figure 3. Groupings of samples are evident for the W_1/CL, W_3/CL and W_3/LA$_{50}$ treatments, whereas plants given exclusively phosphorus (W_3/P) or nitrogen (W_3/N) solutions displayed no such affinities. Groupings are juxtaposed to the measured parameter weights (WEIGHTS) and indicate a positive correlation between most of the growth parameters and the W_3/LA$_{50}$, while the low-water treatment (W_1/CL) is associated with higher levels of foliar sodium and potassium. (Because of the small amount of tissue accumulated by the low-water treatment plants, only one of that group could be analysed for foliar nitrogen by the Kjeldahl procedure, and hence N appears in parentheses in the plot.) Plants of the nitrogen and phosphorus treatments do not appear as such cohesive groups.

Figure 2 The $[CO_2]$ gradient between the atmosphere and the sub-stomatal cavity as a function of photosynthetic photon flux density (PPFD) in *Leucadendron xanthoconus* seedlings grown under different experimental conditions. Lines represent linear regressions of data transformed according to the function $y = ax^b$. Figures in parentheses in the legend represent the r^2 values for those regressions.

Table 4 Foliar nutrient levels and characteristics of photosynthetic capacity in the set of *Leucadendron xanthoconus* seedlings subjected to the analysis of gas exchange. Treatments are labelled as for plants in Tables 1 and 2

Parameter	Water: Nutrients:	Low Control	High Control	High LA_{50}	High P	High N
P (%)		0.03^c	0.02^c	0.19^b	0.41^a	0.02^c
K (%)		1.57^a	0.66^b	0.50^b	0.81^b	0.66^b
N (%)		1.18^d	0.76^b	0.69^b	0.70^b	0.80^b
Ca (%)		0.37^c	0.71^b	0.98^a	0.74^b	0.79^b
Mg (%)		0.21^b	0.29^{ab}	0.34^a	0.30^{ab}	0.28^{ab}
Na (%)		0.25^a	0.19^{ab}	0.13^b	0.20^{ab}	0.17^b
Cu ($\mu g.g^{-1}$)		0.20^a	0.27^a	2.16^a	0.36^a	1.36^a
Zn ($\mu g.g^{-1}$)		45.1^a	70.6^a	63.5^a	48.2^a	68.7^a
Mn ($\mu g.g^{-1}$)		144.4^b	260.0^a	292.9^a	206.4^{ab}	267.6^a
Fe ($\mu g.g^{-1}$)		31.9^a	29.1^a	57.0^a	23.5^a	40.0^a
B ($\mu g.g^{-1}$)		20.3^c	31.5^b	44.4^a	25.9^b	29.7^b
A_{max} ($\mu mol\ CO_2.m^{-2}.s^{-1}$)		8.3^a	10.6^a	10.3^a	10.0^a	11.4^a
$(C_a - C_i)_{max}$ (p.p.m.)		97.2^a	57.3^b	61.8^b	48.8^b	52.5^b
Stomatal conductance ($\mu mol\ H_2O.m^{-2}.s^{-1}$)		0.175^a	0.366^{ab}	0.331^{ab}	0.392^{ab}	0.408^b
Sample size		4	5	6	4	5

[a,b,c] Homogeneous groups; Student-Neuman-Keul test ($p < 0.05$).
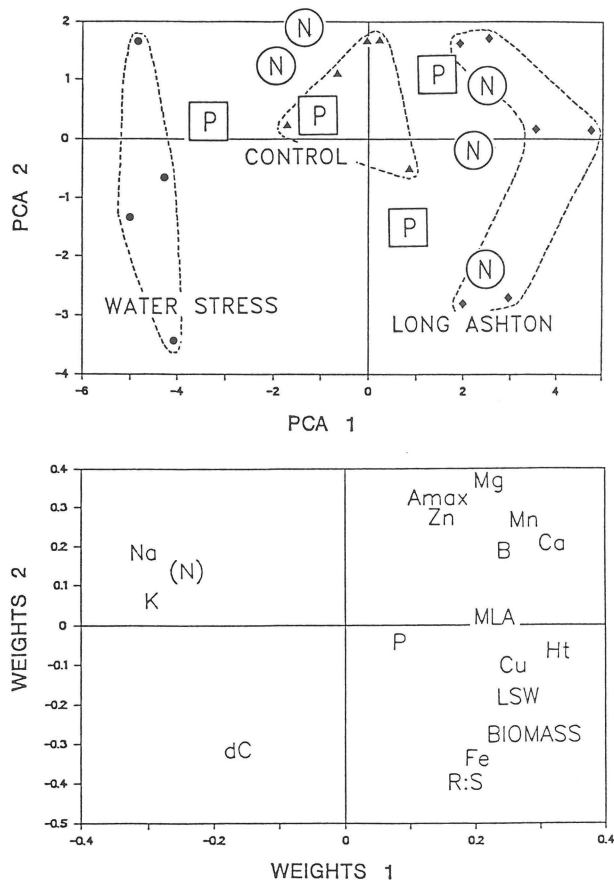[d] $n = 1$ owing to shortage of tissue.

Figure 3 Ordination by Principal Components Analysis (PCA) of growth, gas exchange, and foliar nutrient data derived from experimental plants. The top figure is a scatter plot of ordination values in the first two dimensions (accounting for 47% and 15% of the data variance, respectively), and the bottom figure gives the relative positions of selected parameters used as weighting in the PCA. Symbols used are as follows (unambiguous ones are omitted here): *Top*: WATER STRESS: plants of low water treatment and no nutrient supplement; CONTROL: high water, no nutrient supplement (control); LONG ASHTON: Long Ashton supplement (50% dilution); blocked P: phosphorus addition alone; circled N: nitrogen addition alone. *Bottom*: R:S: root:shoot ratio; LSW: leaf specific weight; MLA: mean leaf area; HT: plant height at harvest; Amax: calculated maximum photosynthetic rate; dC: maximum [CO_2] gradient between the atmosphere and the sub-stomatal cavity; chemical symbols: concentrations of foliar nutrients. The approximate position for nitrogen (N) is derived from a separate PCA on account of the number of missing data points incurred by this parameter (see text).

Discussion

The data obtained in this study are sufficient to demonstrate that both water and nutrients influence *Leucadendron xanthoconus* seedling growth within the first six months after germination. While the overall effect was for additional water and nutrients to promote productivity, the influence of the nitrogen and phosphorus treatments as applied did not clarify the nature of the limitations to growth of this species in native soil. In his work with sandplain lowland fynbos species, Witkowski (1989b) showed that in the field situation, the growth of evergreen sclerophyllous shrubs was limited by nitrogen and other nutrients, but not by phosphorus. Parallel work with potted *Protea repens* plants (Witkowski 1989c) indicated that under artificial propa-

gation conditions, growth was limited by phosphorus, while nitrogen had an inhibitory effect. Stock and Lewis (1984) found that seedlings of *Protea repens* did not benefit from an excess supply of nitrogen, whereas Lamb and Klaussner (1988) showed that supplements of nitrogen, and nitrogen plus phosphorus, affected vegetative growth in mature plants of the same species negatively. Our work on *L. xanthoconus* showed no marked inhibitory effect of nitrogen. It appears, therefore, that one or more nutrients other than nitrogen and phosphorus are influential for growth, either as nutrients *per se*, or as co-factors for the uptake and metabolism of nitrogen and phosphorus (Marschner 1986). Stock *et al.* (1990) showed that several proteaceous species selectively stored nitrogen and phosphorus in their seeds, and that during the first 80 – 120 days after germination, seedlings were less dependent on a soil supply for these two key nutrients than they were for the cations Ca^{2+}, Mg^{2+} and K^+. They (Stock *et al.* 1990) see this as an adaptation of plants to fire-driven systems with nutrient-poor soils, where nitrogen and phosphorus are likely to have limited availability for regenerating plants due to volatilization and immobilization, respectively, while cationic elements are relatively abundant from the debris in the post-fire environment.

Unlike reports from other studies which describe a decrease of root mass relative to shoots in plants growing in resource-rich environments (Chapin 1980; Barbour *et al.* 1987; Gower & Vitousek 1989), *L. xanthoconus* seedlings displayed no such switch to investment in shoot tissue under similar conditions. The relatively water-stressed plants showed a reverse response (Table 2). This latter observation may result from the maintenance of soft root tissue in the well-watered plants by the favourable environment, whereas much of that tissue would have died and sloughed off under drought conditions. In this respect the driest experimental treatment probably represented a stress situation not normally encountered by these plants in their natural mesic mountain fynbos environment, where foraging for water and other resources would not be restricted by a black plastic bag barrier. It should also be noted that the root:shoot ratios recorded here are high relative to those reported for mature proteaceous plants. Higgins *et al.* (1987) measured root:shoot ratios of 0.2 for the reseeding species *Protea neriifolia* and *P. repens*, and 0.6 for the resprouter *Leucadendron salignum*. Kruger (1987) on the other hand, in his work on shade tolerance in *Leucadendron xanthoconus* seedlings, found a similar range of root:shoot ratios to those that we report in this study.

Leucadendron xanthoconus, which regenerates as an obligate post-fire seeder in mountain fynbos vegetation, normally germinates and establishes itself during the first winter after the fire. To survive the first fynbos summer, with the high probability of extended dry periods, there is a need to establish a root system for securing a water supply from deeper and less drought-prone soil layers as quickly as possible. The ambient nutrient regime, which is likely to be favourable in the post-fire environment (Rundel 1983; Stock & Lewis 1986), is probably for adaptive reasons less influential than water on the distribution of biomass between above- and below-ground organs of re-establishing seedlings.

The gas exchange results, and especially the apparent lack

of stomatal sensitivity to light intensity, must be interpreted in the context of the artificial propagation employed, and the ambient conditions during the analyses. Previous work on this species (Davis & Midgley 1990) has shown that the diurnal pattern of stomatal conductance follows the intensity of ambient irradiance in 18-month-old plants growing under field conditions. The observed absence of this phenomenon in this study may be explained by one or more of a set of possible factors: (a) the capacity of this species to regulate gas exchange, possibly through stomatal sensitivity to irradiance, may increase with increasing age (see Davis & Midgley 1990); (b) growing conditions in the greenhouse, where both microclimatic (especially reduced irradiance) and plant competitive effects are different from field conditions, may have influenced stomatal response characteristics; (c) the effects of a predetermined diurnal rhythm on stomatal opening may have overridden the relatively asynchronous experimental light regime; and (d) the technique of progressively changing ambient conditions during construction of the response curves may be prone to lags in stomatal response. Such lags have been observed in response to stepwise increases in light intensity (Gross & Chabot 1979), and may be of the order of 50 min or more. These speculated influences on stomatal behaviour in *L. xanthoconus* need further investigation. The higher ($C_a - C_i$) values observed for the water-stressed plants, whether resulting from increased photosynthetic activity or merely from increased stomatal resistance, nevertheless indicates a treatment effect on physiological behaviour in this species.

Results of the ordination (Figure 3) indicate that the relatively water-stressed plants are associated with higher foliar levels of the mobile univalent cationic elements sodium and potassium (Marschner 1986), and possibly also with an increased level of nitrogen as suggested by the incomplete set of N data. The latter phenomenon may reflect aspects of nitrogen nutrition in the experimental system similar to mechanisms operative in natural systems. Although the lack of water in the low-water (W_1) treatment would have slowed microbial activity and the decomposition of detrital material in the soil (Read & Mitchell 1983), the leaching of applied and mineralized nitrogen would also have been minimized, thereby allowing nitrogen to be readily available at times when water was provided. Coupled with the retarded plant growth observed in W_1 plants, this may have provided the opportunity for nitrogen concentration in the foliar tissue.

The leaf nitrogen (N_{leaf}) and leaf specific weight (LSW) data of the experimental work concurred with those of Field and Mooney (1986), who showed that those two parameters were inversely related over a wide range of species. Comparison of the data describing A_{max} and N_{leaf} with Field and Mooney's (1986) relationship $A_{max} = -76.1 + 149N_{leaf}$ (where A_{max} is in nmol $CO_2.g^{-1}.s^{-1}$ and N_{leaf} is in mmol.g^{-1}), showed that the experimental plants were consistent with that model, although they were more productive and contained more foliar nitrogen than the fynbos shrubs investigated by those workers.

This study had as its starting point the response of natural fynbos vegetation, and *L. xanthoconus* in particular, to human-induced disturbances of its substrate. A knowledge of plant responses to environmental disturbance is probably becoming increasingly important for the management of

ecosystems, and the problems discussed above are relevant to activities such as land reclamation following mining or road and township development, and the cultivation of plants for the decorative wildflower industry. If *L. xanthoconus* is characteristic of a functional component of fynbos vegetation, the results suggest that for optimal growth in the seedling establishment phase, supplementation of both water and nutrients might be desirable for some revegetation projects. Addition of nitrogen and phosphorus alone were shown to be less influential than more complete fertilization, and the influence and interaction of other elements need to be considered in more detail. The advantages of a system which favours rapid plant growth by provision of luxury conditions may also be offset by secondary problems, such as the creation of a favourable environment for plant pathogens (Malajczuk & Glenn 1981), an undesired change in community structure (Davis 1990) or, relative to the target plant, possible inhibition of acclimation to environmental stresses.

Management of natural vegetation, either for the repair of damaged ecosystems, or for the protection and maintenance of threatened ones, will be assisted by a knowledge of broad ecophysiological patterns in functionally similar groups of plants. The task now is to define the response topographies of these groups to stresses within and beyond their ranges of adaptation, in order to learn something of the limits on sustainability.

Acknowledgements

References

BARBOUR, M.G., BURK, J.H. & PITTS, W.D. 1987. Terrestrial plant ecology, 2nd ed. Benjamin/Cummings, Menlo Park.

BARNES, R.M. (ed.) 1981. Developments in atomic plasma spectrochemical analysis. Heyden and Son, London.

CHAPIN, F.S. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11: 233 – 260.

DAVIS, G.W. 1990. Commercial wildflower production in the Fynbos Biome and its role in the management of land-use. Unpublished Ph.D. thesis, University of Cape Town.

DAVIS, G.W. & MIDGLEY, G.F. 1990. Effects of disturbance by fire and tillage on the water relations of selected mountain fynbos species. *S. Afr. J. Bot.* 56: 199 – 205.

FIELD, C. & MOONEY, H.A. 1986. The photosynthesis–nitrogen relationship in wild plants. In: On the economy of plant form and function, ed. T.J. Givnish. Cambridge University Press, Cambridge.

GOWER, S.T. & VITOUSEK, P.M., 1989. Effects of nutrient amendments on fine root biomass in a primary succession forest in Hawaii. *Oecologia* 81: 566 – 568.

GROSS, L.J. & CHABOT, B.F. 1979. Time course of photosynthetic response to changes in incident light energy. *Pl. Physiol.* 63: 1033 – 1038.

HEWITT, E.J. & SMITH, T.A. 1975. Plant mineral nutrition. The English Universities Press, London.

HIGGINS, K.B., LAMB, A.J. & VAN WILGEN B.W. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley, south-western Cape Province. *S. Afr. J. Bot.* 53: 249 – 257.

HILTON-TAYLOR, C. & LE ROUX, A., 1989. Conservation status of the fynbos and karoo biomes. In: Biotic diversity in Southern Africa: Concepts and conservation, ed. B.J. Huntley. Oxford University Press, Cape Town.

KRUGER, F.J. 1979. South African heathlands. In: Ecosystems of the world, Vol 9A, Heathlands and related shrublands, Descriptive studies, ed. R.L. Specht. Elsevier, Amsterdam.

KRUGER, F.J. 1987. Succession after fire in selected fynbos communities of the south-western Cape. Ph.D. thesis, University of the Witwatersrand, Johannesburg.

LAMB, A.J. & KLAUSSNER, E. 1988. Response of the fynbos shrubs *Protea repens* and *Erica plukenetii* to low levels of nitrogen and phosphorus applications. *S. Afr. J. Bot.* 54: 558 – 564.

LI-COR, 1987. LI-6200 Technical reference. LI-COR, Lincoln.

MACDONALD, I.A.W., KRUGER, F.J. & FERRAR, A.A. (eds.) 1986. The ecology and management of biological invasions in southern Africa. Oxford University Press, Cape Town.

MALAJCZUK, K. & GLENN, A.R. 1981. *Phytophthora cinnamomi* – a threat to the heathlands. In: Ecosystems of the world, Vol. 9B, Heathlands and related shrublands, ed. R.L. Specht. Elsevier, Amsterdam.

MARSCHNER, H. 1986. Mineral nutrition of higher plants. Academic Press, London.

MILLER, P.C., MILLER, J.M. & MILLER, P.M. 1983. Seasonal progression of plant water relations in fynbos in the western Cape Province, South Africa. *Oecologia* 56: 392 – 396.

MITCHELL, D.T., BROWN, G. & JONGENS-ROBERTS, S.M. 1984. Variation of forms of phosphorus in the sandy soils of coastal fynbos, south-western Cape. *J. Ecol.* 72: 575 – 584.

MOLL, E.J. & SOMMERVILLE, J.E.M. 1985. Seasonal xylem pressure potentials of two South African coastal fynbos species in three soil types. *S. Afr. J. Bot.* 51: 187 – 193.

READ, D.J. & MITCHELL, D.T. 1983. Decomposition and mineralization processes in mediterranean-type ecosystems and in heathlands of similar structure. In: Mediterranean-type ecosystems: The role of nutrients, eds. F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis. Springer-Verlag, Berlin.

RUNDEL, P.W. 1983. Impact of fire on nutrient cycles in mediterranean-type ecosystems with referrence to chaparral. In: Mediterranean-type ecosystems: The role of nutrients, eds. F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis. Springer-Verlag, Berlin.

SAS Institute Inc. 1985. SAS User's Guide: Statistics, version 5 edition. SAS Institute Inc., Cary, N.C.

STOCK, W.D. & LEWIS, O.A.M. 1984. Uptake and assimilation of nitrate and ammonium by an evergreen fynbos shrub species *Protea repens* L. (Proteaceae). *New Phytol.* 97: 261 – 268.

STOCK, W.D. & LEWIS, O.A.M. 1986. Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *J. Ecol.* 74: 317 – 328.

STOCK, W.D., PATE, J.S. & DELPHS, J. 1990. Influence of seed size on seedling development under low nutrient conditions in five Australian and South African members of the Proteaceae. *J. Ecol.* 78: 1005 – 1020.

THOMPSON, W.A., STOCKER, G.C. & KRIEDEMANN, P.E. 1988. Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell., a rainforest tree with broad tolerance to sun and shade. *Aust. J. Pl. Physiol.* 15: 299 – 315.

VAN DER HEYDEN, F. & LEWIS, O.A.M. 1989. Seasonal variation in photosynthetic capacity with respect to plant water status of five species of the mediterranean climate region of South Africa. *S. Afr. J. Bot.* 55: 509 – 515.

VON WILLERT, D.J., HERPPICH, M. & MILLER, J.M. 1989. Photosynthetic characteristics and leaf water relations of mountain fynbos vegetation in the Cedarberg area (South Africa). *S. Afr. J. Bot.* 55: 288 – 298.

WITKOWSKI, E.T.F. 1989a. Response to nutrient additions by the plant growth forms of sand-plain lowland fynbos, South Africa. *Vegetatio* 79: 89 – 97.

WITKOWSKI, E.T.F. 1989b. Effects of nutrient additions on litter production and nutrient return in a nutrient-poor Cape fynbos system. *Pl. Soil* 117: 227 – 235.

WITKOWSKI, E.T.F. 1989c. Effects of nutrients on the distribution of dry mass, nitrogen and phosphorus in seedlings of *Protea repens* (L.) L. (Proteaceae). *New Phytol.* 112: 481 – 487.

WITKOWSKI, E.T.F. & MITCHELL, D.T. 1987. Variations in soil phosphorus in the fynbos biome, South Africa. *J. Ecol.* 75: 1159 – 1171.