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 voedingstoetehandelings gekweek. Die voedingstoetehandelings het uit oplossings van stikstof, fosfor en Long Ashton makrovoedingstof (LA) bestaan. Drie verskillende watervlakke is gehandhaaf, wat gewissel het vanaf droogte tot volgehou gronddeurweekheid. Voordat die plantes op 'n ouderdom van ses maande geoes is, is die tempo van gaswisseling van 'n subreeks experimentele plante onder verskillende ligintensiteit ondersoek. Die bepaling van die biomassa en die verspreiding daarvan het toon 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 vermindere het. Algemeen het die hoogste water-toevoering, die laagste in die kontrole, terwyl forfor- en stikstoftoevoergings 'n intermedieere effek getoon het. Geeneen van die behandelingstoe in die gaswisselingstudies het een effek op fotosintetiese kapasiteit of waterverbruiksdieetreffendheid gehad nie. Saailinge vanaf droogte blootgestel het, die 'n verhoogde vermoe om koolstofdiksidie aan Stomata en verlaag, getoeno. Ligintensiteit het geen effek op blarekondutskansie uitgeoefen nie. Die verwantskappe was ondersoek is, is in die lig van fynbosbenutting en die bestuur van natuurlike fynboslandskappe vir die herwinning en die onderhoud van natuurlike ekosysteme 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 above-ground 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 (W₁); 300 ml once per week (W₂); and 75 ml daily (W₃). Treatment W₁ maintained plants at or close to field capacity, while occasionally additional water was administered to W₁ to minimize mortality through droughting.

Nutrient additions were based on the Long Ashton nutrient medium with 1 mM NH₄NO₃ 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 (LA₅) solution; (iii) 15% LA solution (LA₁₅); (iv) 50% LA solution (LA₅₀); (v) only the phosphorus component of the LA₅₀ solution (P); and (vi) only the nitrogen component of the LA₅₀ solution (N). Deviations from this regime included omission of the W₂/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 morphology 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 analyzer (Li-Cor 6200 with 4-l cuvette), configured as a closed system, was used to investigate CO₂ and H₂O 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, LA₅₀, P and N. A set of four plants from the low-water/control-nutrient 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 μmol.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 CO₂ 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 μmol.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 (N₉₅). 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 (Aₘₐₓ) was derived from the y-intercept of the plot of log₁₀(A)/A against (1/PPFD), where A is the net assimilation rate at the associated PPFD; (ii) maximum water use efficiency (WUEₘₐₓ) 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 ≤ PPFD ≤ 650 μmol.m⁻².s⁻¹; and (iv) for each plant's set of light response

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

| 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     |
| Ca²⁺ (me/100 g)    | 3.467  | 0.917     |
| Mg²⁺ (me/100 g)    | 1.010  | 0.132     |
| Al (me/100 g)      | 0.210  | 0.089     |
| pH (in 1M KCl)     | 5.3    | 0.35      |

*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.*

*Sample taken from sieved experimental soil.*
data, the largest difference between the measured CO₂ 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 \((C_a - C_i)_{\text{max}}\).

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 \(A_{\text{max}}\) 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 LA₅ and LA₅₀ 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.

![Figure 1](image_url)

**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)             | 0.80ₖ | 1.62ₖ | 1.9₃ₖ |
| Root mass (g)              | 0.57ₗ | 1.47ₗ | 2.0₈ₗ |
| Total leaf mass (g)        | 0.60ₗ | 1.2₉ₗ | 1.₄₆ₗ |
| Root:shoot ratio           | 0.684ₖ | 0.₈₉₃ₖ | 1.₇₁₄ₖ |
| Mean leaf area (cm²/leaf)  | 1.₀₂₅ | 1.₂₆₄ | 1.₄₂₄ |
| Mean leaf specific weight (g/cm²) | 0.₀₀₉ₘ | 0.₀₁₁ₘ | 0.₀₁₁ₘ |
| Plant height (mm)          | 2₁₆ₗ | 2₈₄ₗ | ₃₂₇ₗ |
| Sample size                | ₂₅ₗ  | ₃₄ₗ   | ₄₁ₗ   |

ₖₗ Homogeneous groups; Student-Neuman-Keul test \((p < 0.05)\).

₅ Main effects inseparable owing to interaction of factors.

**Table 3** Response of Leucadendron xanthoconus seedlings to nutrient enhancement, where LA₅ and LA₅₀ are the Long Ashton supplements, and P and N the nitrogen and phosphorus supplements as described in Methods

| Parameter                  | Control | LA₅ | LA₁₅ | LA₂₅ | P | N |
|----------------------------|---------|-----|------|------|---|---|
| Shoot mass (g)             | 1.₁₈ₖ  | 1.₂₄ₖ | 1.₈₂ₖ | 2.₂₄ₖ | 1.₄₁ₖ | 1.₃₇ₖ |
| Root mass (g)              | 0.₉₈ₖ  | 1.₇₆ₖ | ₂.₀₁₈ₖ | ₂.₂₆ₖ | ₁.₇₇ₖ | ₁.₄₄ₖ |
| Total leaf mass (g)        | 0.₉₂ₖ  | 0.₉₆ₖ | ₁.₄₇ₖ | 1.₇₂ₖ | ₀.₉₉ₖ | ₁.₈₉ₖ |
| Root:shoot ratio           | ₀.₈₃ₖ  | ₀.₉₀ₖ | ₀.₉₇ₖ | ₀.₉₀₆ | ₀.₈₃₆ | ₀.₉₀₆ |
| Mean leaf area (cm²/leaf)  | ₁.₁₂₅ | ₁.₁₈₅ | ₁.₁₉₅ | ₁.₅₅₅ | ₁.₃₉₅ | ₁.₁₃₅ |
| Mean leaf specific weight (g/cm²) | ₀.₀₀₉₇ₗ | ₀.₀₁₀₇ₖ | ₀.₀₁₁₇ₖ | ₀.₀₁₀₇ₖ | ₀.₀₁₁₇ₖ | ₀.₀₁₀₇ₖ |
| Plant height (mm)          | ₂₆₆ₗ | ₂₆₀ₗ | ₂₈₆ₗ | ₃₃₉ₗ | ₂₈₇ₗ | ₂₆₁ₗ |
| Sample size                | ₂₀     | ₁₈    | ₁₈    | ₁₇    | ₁₄    | ₁₂    |

ₖₗ Homogeneous groups; Student-Neuman-Keul test \((p < 0.05)\).

₅ Main effects inseparable due to interaction of factors.
Photosynthetic capacity and water use efficiency
Measurement of CO₂-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: Aₚₚₚₚ, WUEₚₚₚₚ and 'light harvesting re-
sponse'. However, using one-way ANOVA, a significant
difference (p < 0.01) was found between treatments for the
set of (Cᵢ - Cᵢ)ₚₚₚₚ values, with the low-water treatment
representing a group of plants capable of developing a
steeper gradient in [CO₂] 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 (Wₜ) treatment was significantly less than the nitrogen
(N) treatment (p < 0.05), while the remaining treatments
(CL, LAₚₚₚₚ 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
(Wₜ/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 Wₜ/CL, Wₜ/CL and Wₜ/LAₚₚₚₚ treatments, whereas plants
given exclusively phosphorus (Wₜ/P) or nitrogen (Wₜ/N)
solutions displayed no such affinities. Groupings are juxta-
posed to the measured parameter weights (WEIGHTS) and
indicate a positive correlation between most of the growth
parameters and the Wₚₚₚₚ/CL and Wₚₚₚₚ/CL

Figure 2 The [CO₂] 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 = aₓᵇ. Figures in parentheses in the legend represent the r² values for
those regressions.

Table 4 Foliar nutrient levels and characteristics of photosynthetic capacity in the set of Leuca-
dendron xanthoconus seedlings subjected to the analysis of gas exchange. Treatments are label-
led as for plants in Tables 1 and 2

| Parameter       | Water: Nutrients | Low Control | High Control | High LAₚₚₚₚ | High P | High N |
|-----------------|------------------|-------------|--------------|------------|--------|--------|
| P (%)           |                  | 0.0³        | 0.0²         | 0.1⁹⁺       | 0.4¹⁺  | 0.0²   |
| K (%)           |                  | 1.57⁺       | 0.66⁺        | 0.50⁻       | 0.8¹⁺  | 0.66⁻  |
| N (%)           |                  | 1.18⁺       | 0.76⁺        | 0.69⁺       | 0.7⁰⁻  | 0.8⁰⁻  |
| Ca (%)          |                  | 0.3⁰⁻       | 0.7¹⁺        | 0.9⁸⁻       | 0.7⁴⁻  | 0.7⁹⁻  |
| Mg (%)          |                  | 0.2¹⁺       | 0.2⁹⁺        | 0.3⁴⁻       | 0.3⁰⁻  | 0.2⁸⁻  |
| Na (%)          |                  | 0.2₅⁻       | 0.1⁹⁻        | 0.1³⁻       | 0.2⁰⁻  | 0.1⁷⁻  |
| Cu (µg.g⁻¹)     |                  | 0.2⁰⁻       | 0.2⁷⁻        | 2.1⁶⁻       | 0.3⁰⁻  | 1.3⁶⁻  |
| Zn (µg.g⁻¹)     |                  | 45.1⁴       | 70.6         | 63.⁵⁺       | 48.²⁺  | 68.⁷⁺  |
| Mn (µg.g⁻¹)     |                  | 144.⁴⁺      | 260.0⁺       | 292.9⁺      | 206.⁴⁺ | 267.⁶⁺ |
| Fe (µg.g⁻¹)     |                  | 31.⁹⁺       | 29.¹⁺        | 57.⁰⁺       | 23.⁵⁺  | 40.⁰⁺  |
| B (µg.g⁻¹)      |                  | 20.³⁺       | 31.⁵⁻        | 44.⁴⁺       | 25.⁹⁺  | 29.⁷⁺  |
| Aₚₚₚₚ (µmol CO₂.m⁻².s⁻¹) |          | 8.³⁺       | 10.⁶⁺       | 10.³⁺       | 10.⁰⁺  | 11.⁴⁺  |
| (Cᵢ - Cᵢ)ₚₚₚₚ (p.p.m.) |   | 97.2⁺       | 57.₃⁺        | 61.⁸⁺       | 48.⁸⁺  | 52.⁵⁺  |
| Stomatal conductance (µmol H₂O.m⁻².s⁻¹) |      | 0.175⁺      | 0.366⁺       | 0.331⁺      | 0.392⁺ | 0.4⁰⁺⁺  |

Homogeneous groups; Student-Neuman-Keul test (p < 0.05).
⁴ n = 1 owing to shortage of tissue.
Parallel work with potted *Protea repens* (Witkowski 1989c) indicated that under artificial propagation 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 seedler 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 macroclimatic (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 \( (W_l) \) 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 \( W_l \) plants, this may have provided the opportunity for nitrogen concentration in the foliar tissue.

The leaf nitrogen \( (N_{\text{leaf}}) \) 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 \( A_{\text{max}} \) and \( N_{\text{leaf}} \) with Field and Mooney's (1986) relationship \( A_{\text{max}} = -76.1 + 149N_{\text{leaf}} \) (where \( A_{\text{max}} \) is in nmol CO\(_2\).g\(^{-1}\).s\(^{-1}\) and \( N_{\text{leaf}} \) 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.

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