Effects of Increased Fire Frequency on Life History Traits of Protea lorifolia

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Contents

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ABSTRACT

Fynbos managers use fire as one of their principle tools for ecosystem management. They are required to burn at a frequency that maintains biodiversity while maximising sustainable water yield. They base their burn frequency on the maturation period of the slowest maturing species, assuming that this is a constant species characteristic.

Protea lorifolia, a serotenous, obligate seeder, was seen to adapt it's life history traits according to fire regime. With an increase in fire regime, the proteas of both the present and the parent populations, were found to grow faster and reproduce earlier, indicating that maturation period is not a constant species characteristic. The increase in growth rates resulted in increased water consumption by the proteas.

The increase in growth rates is achieved by a quantitative change in leaves, although a qualitative change in physiological attributes was seen to be developing.

The implications of the switch in life history traits are twofold: a compromise in short- and long-term survival of the proteas and a decrease in water availability lower down in the catchment.

INTRODUCTION

Recurrent fires in vegetation are a general feature of mediterranean-type ecosystems and the profound effect of fire regimes on these ecosystems is generally acknowledged (Kruger, 1983). Fire has been identified as one of the major selective force in the evolution of fynbos plant reproductive ecology (le Maitre & Midgley, 1992). As a consequence, it has been strongly implicated in the in the maintenance of community richness (Cowling, 1987; Kruger, 1987). Fire is thus an essential prerequisite for ecosystem functioning in the in fynbos (Kruger, 1983).

Indeed, fynbos managers, who seek to maintain ecosystem stability and function ie. retain it in a relatively pristine state, rely on fire as one of their principle management tools (Specht et al, 1983). Management strategies are concerned with two factors in particular: maintenance of species diversity and maximising sustainable water yield (Bosch & von Gadow, 1990). These, however, are conflicting ideals. Biodiversity, especially of slow growing proteas, is favoured by low to intermediate fire frequency (Kruger, 1983, 1987; Kruger & Bigalke, 1984; Specht et al, 1983). Water yields, on the other hand are increased by decreased biomass ie. from frequently burnt veld (Bosch & von Gadow, 1990). Thus managers must find compromise in fire frequency that optimises the balance between the biodiversity and maximum sustainable water yield.

Managers base the frequency of their burns on the maturation period of the slowest maturing species, timing their burns in order to ensure that they reproduce. This however, assumes that maturation time is a constant species characteristic (Bond, pers. comm.). However, in direct contrast to this assumption, current theories of optimal life history traits in relation to disturbance regimes (Clark, 1991), predict that plants shift their life history characteristics to suit the ambient disturbance regime. Thus if disturbance (eg. fire) frequency is high, the theory predicts that the plants will evolve to fit this regime by decreasing time to maturation. Here I report evidence for such shifts in life history in the fynbos.

Two populations of Protea lorifolia, located on the southern slopes of the Central Swartberg, were seen to display distinct differences in life history patterns (Vlok, 1994). The individuals of the population occurring at the high fire frequency site seemed to grow faster and reach reproductive maturity earlier. I aim to quantitatively test these differences, to determine whether there is a shift in life history traits of P.lorifolia in response to increased fire frequency.

Since maintenance of water availability is one of the priorities of managers, the fact that the frequently burnt stands might have a higher growth and maturation rate, would be of concern. Carbon assimilation rate is directly proportional to transpirational water loss (Passioura, 1982; Schultz & Hall, 1982; Bloom et al, 1985). Therefore, the faster a plant grows, the greater it's water consumption and consequently a resultant reduction in water runoff from the catchment system. Thus, the manner in which the plants achieve faster growth, and the effects thereof are of prime importance to managers.

In the study the following four questions were addressed:

1. Has shorter fire frequencies led to a selection for faster growing, earlier reproducing genotypes in Protea lorifolia?
2. If there is a selection for faster growing genotypes, does this occur at the expense of increased water use?
3. What constitutes this difference in growth rate ie. how does the plant grow faster?
4. What are the implications of changes in life history patterns?

Rationale for the study:

"Effective management needs the means to predict the effects of measures applied to vegetation on dynamic aspects of resources, species diversity and the potential for fire in the vegetation (Kruger, 1987)". With this in mind, the study is aimed at providing a better understanding of the consequences of more frequent burning, so as to add to the managers' store of available knowledge in order to aid in practical management strategies.

METHODS

Study site

Protea lorifolia is a serotenous, obligate seeding protea that is killed by fire. The two populations of P.lorifolia are found at sites on the southern slopes of the Central Swartberg in the vicinity of the Swartberg Pass, near Oudtshoorn (Fig. 1). The sites, which are 1.87 km apart, are of similar altitude, aspect and slope. They are close enough, and without large physical barriers between them, to assume that they receive the same annual rainfall. Thus the sites share a similar macroclimate. There is, however, a considerable difference in their fire history:

Weerstasie (high frequency) has been burnt four times since 1956 (mean = 12 yrs).

Skelmdraai (low frequency) had three fires since the 1949 (mean = 21.2 yrs) (Table 1). The mean fire frequency for the Groot Swartberg region is 18 years (Kruger, 1983).

Table 1: Fire history of two populations of Protea lorifolia on the southern slopes of the central Swartberg.

Weerstasie		Skelmdraai	
Date of fire	Vegetation Age (years)	Date of Fire	Vegetation Age (years)
		19/11/1949	?
23/01/1956	?		
25/07/1977	21.5		
		04/04/1980	30.5
29/04/1984	6.75		
22/02/1992	7.8	22/02/1992	11.8
	2.75		2.75

(after Vlok, 1994)

Both sites were burnt in January 1992 thus the current vegetation at each would be of approximately 2.75 years old.

The vegetation age of the previous generation, calculated as the period between fires, was 7.8 years at Weerstasie and 11.8 years

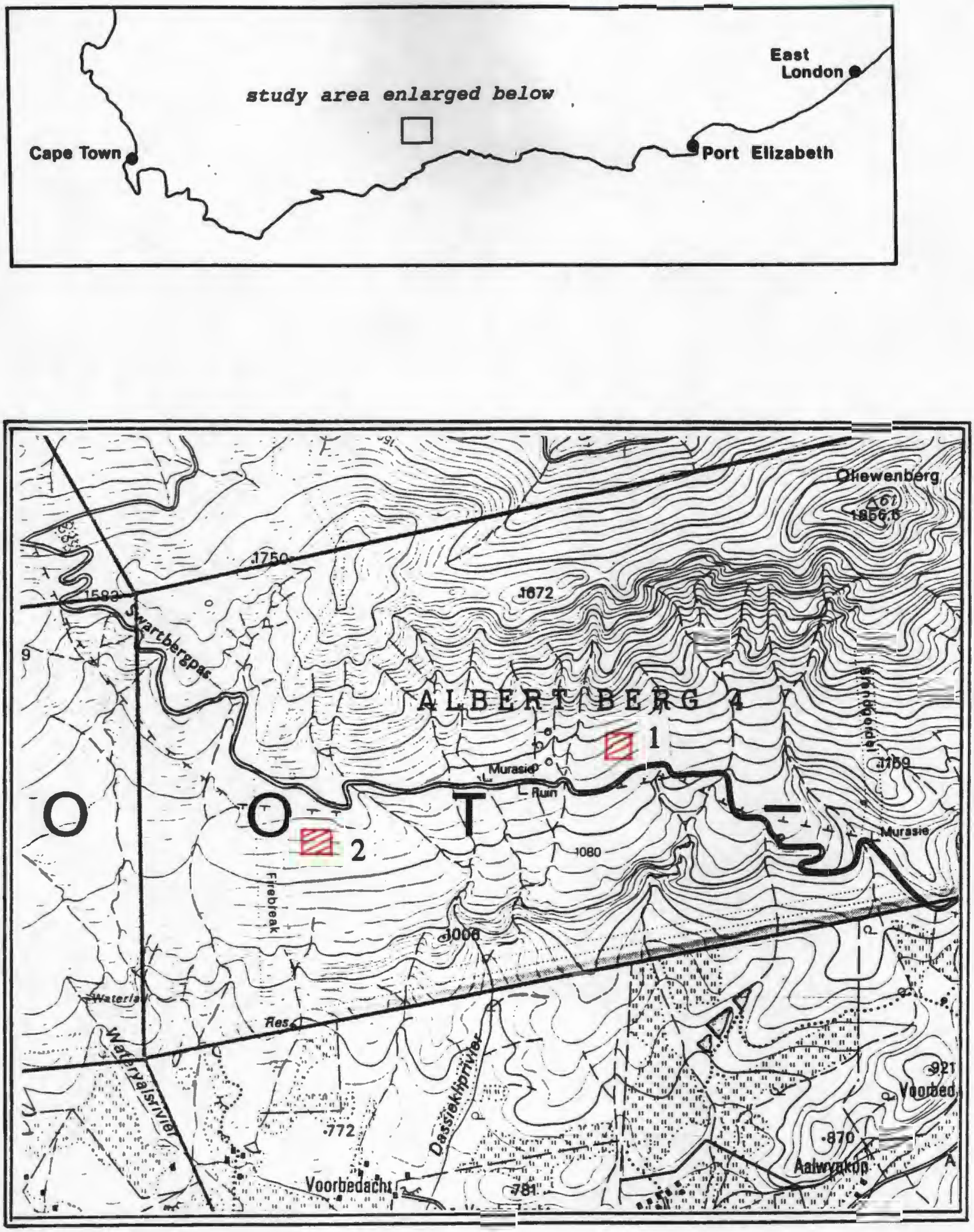


Figure 1. Map showing the location of the study sites on the southern slopes of the Central Swartberg.
Study sites are: 1 Weerstasie; 2 Skelmdraai.

at Skelmdraai. Most importantly, Weerstasie has been subjected to two consecutive short interval burns, while Skelmdraai has been subjected to much longer intervals.

Study approach:

Populations of the P.lorifolia from the high and low fire frequency sites were compared to determine whether there was any evidence for differences in their growth and maturation rates. Furthermore, physiological differences between the population that might account for the differences this difference, especially when relating to water use, were also investigated.

Controls:

Variation in relative growth rate in natural populations has been attributed to variation in a number of biotic and abiotic factors (Rocher et al, 1989). In order to isolate the effects of fire frequency, it is necessary control for the any other factors, such as nutrient levels and competition.

Nutrient levels were controlled for using biological controls. Two species Elegia filacea (a restio) and Pteronia stricta(Aiton) found ubiquitously throughout the area, were selected as these biological controls. Pteronia flowers within two to three years of the burn, so it has a lifespan shorter than lowest average fire frequency and would thus remain unaffected by the fire frequency. The restio, being a sprouter, is also unaffected fire frequency. Any difference in the mean height of the species between the two sites would indicate that there is a difference in nutrient levels of the sites.

In the case of the restio; ten height measurements per individual were recorded, and the mean of these was taken as representative of the individual height. Twenty "individuals" were randomly sampled per site.

For Pteronia, only flowering individuals were measured. The height of each flowering stem was measured. In this manner an average value was assigned to each selected individual. Twenty plants were sampled at each site to determine an overall mean for the site.

Of the biotic factors, density effects were controlled for by the nature of the sampling techniques. Only those P.lorifolia growing individually within a radius of 30cm were sampled. This arbitrary radius was determined by digging up the root system of three large individuals to determine the extent of their subterranean sphere of influence. This was never found to be greater than 20cm from the base of the individual. The seedlings were still fairly short, so they were unlikely to compete for light outside of this radius. To avoid the possible effects of increased water supply, sampling did not take place near stream beds or obvious runoff gullies. The potential problem caused by overlapping generations was not relevant because of the serotenous nature of P.lorifolia reproduction. The parents are killed by the fire and recruitment is restricted to the period immediately after the fire. The seeds are short lived after release (van Wilgen et al, 1992) and so little chance of generation overlap exists.

Sampling methods:

Life History Traits

Twenty seedlings and ten skeletons (of the previous generation) of P.lorifolia were randomly selected at each site during the first field excursion. A further twenty seedlings were selected at each site during the next field trip. To ensure that the sampling was random and representative of the population, only every third (solitary) seedling was selected. The populations at each site were small (between 150 and 200 individuals), so extensive subsampling was not feasible.

Height: Proteas can be aged from node counts along the stem and branches. The height of each year's growth was taken as the distance between two successive nodes (cm). Measurement started at the point at which the seedling emerged from the soil, and ended at the tip of the apical bud. However, one should note that "double growth spurts" were encountered on occasion, where two nodes were formed in a year. In this case the measurements were combined for that year.

Leaf Area: Leaves were removed from each year's growth. Leaf area (cm^2) was measured using a LICOR leaf area meter.

Age of First Flowering: The age and height at which the plants flowered first, were measured in 100 plants of the previous generation before the burn. This gives an indication of the plants' juvenile period (Kruger & Bigalke, 1984; Vlok, 1994). Since P.lorifolia is not a sprouter and is therefore killed by fire, populations/genotypes will be eliminated if they burn before reproductive maturity has been reached. Juvenile period is an indication of reproductive maturity. These data were collected by Jan Vlok.

Plant Characteristics:

Plant-Water Relations: potometry experiments.

If there is a difference in growth and maturation rates, by determining the mean transpiration rates of the two populations, the extent to which the faster growing individuals use more water can be determined. Transpiration rate and the total quantities of water transpired by each plant were measured using the cut-shoot method. Fifteen seedlings were sampled at each site (the same plants used in determining the growth parameters). Each seedling was removed from the ground and immediately placed in a bucket of water. The stems were cut at the point at which they emerged from the soil. Care was taken to avoid wetting the leaves which would have resulted in stomatal closure. A 20ml test tube was then submerged in the bucket and the seedling was placed into the test tube. Both were then removed from the water and replaced in the original growth site, in a similar position to the original one. The top of the test-tubes were covered with "Prestik", in order to minimise any water loss due to evaporation. The apparatus was supported by a wooden peg.

Water usage was recorded by refilling the test tube with a known volume of water. Measurements were taken every 2 to 3 hours, for a period of two days (48 hours).

The absolute transpirational water loss (ml) was recorded. This technique has an advantage over porometry for two reasons: It is a measure of whole-plant/integrated response (as opposed to a single leaf response) as well a measurement over a length of time rather than an instantaneous measure. Instantaneous measurements are too easily affected by temporary changes in microclimate.

Stem Density:

The density of the stems were measured to get an indication of allocation patterns in these seedlings. If the plant grows faster, we would expect the stems to be less dense, since a plant that grows faster allocates more to the organs actively involved in nutrient assimilation, at the expense of allocation to structural components (Loelhe, 1987).

The first 2cm (ie. the portion of the stem that emerges from the soil) of the stem was removed and the volume and dry weight of that section was determined. Density was determined as volume/ dry weight ($cm^3.mg$)

Specific Leaf Area (SLA) and Leaf pigment content:

These were measured at each site to determine if there is a difference in leaf characteristics between the sites. These measurements would be an indication of the manner in which the faster growing individuals achieve enhanced growth rate.

SLA: Five leaves from 1994's growth were sampled from identical positions on each protea. Individual leaf areas (cm^2) and dry weights (g) (leaves were dried at 65°C for 24 hrs) were determined. SLA was determined as leaf area/leaf weight ($cm^2.g^{-1}$).

Leaf Pigment Concentrations: Carotenoids, chlorophyll a and chlorophyll b were extracted and measure spectrophotometrically. Twenty seedlings from both sites were used.

The following protocol was used:

A known mass of leaf material was homogenised in 5mls of Ammoniacal acetone (81.8% $(CH_3)_2CO$; 18% H_2O; 0.2% NH_4OH v/v). The extraction was repeated four times, in order to ensure that all chlorophyll was extracted.

The homogenase was centrifuged at 3000 **g** for 10 min and absorbances (at wavelengths of 470, 647, 663 and 710nm) were measured.

Calculations were as follows:

a) Chlorophyll a:
  i. (12.25 x (A663 - A710) - (2.79 x (A647 - A710)) [A]
   units: mg.l^{-1}
  ii. convert to mg.g^{-1}:
   ([A] / 20) / mass of leaf material [B]

  iii. convert to umol.g^{-1}: [B] x 1.119 [C]

b) Chlorophyll b:
  i. (21.5 x (A647 - A710) - 5.1 x (A663 - A710)) [Ai]
   units: mg.l^{-1}
  ii. convert to mg.g$_{-1}$:
   ([Ai] / 20) / mass of leaf material [Bi]

  iii. convert to umol.g^{-1}: [Bi] x 1.102 [Ci]

c) Chlorophyll a + Chlorophyll b: [C] + [Ci]

d) Carotenoids:
  i. (1000 x (A470 - A710) - 1.82 x [A] - 85.02 x [Ai]) / 198
   [Aii]
  ii. convert to mg.g^{-1}:
   ([Aii] / 20) / mass of leaf material

(after Lichtenthaler, 1987)

Statistical Analyses:

Statistical and data analysis and graphic display were performed using the STATGRAPHICS and QUATTRO PRO software packages.

Linear regressions were used to determine whether relationships existed between the growth parameters and the various plant characteristics eg. transpiration rate, SLA, leaf chlorophyll contents, and stem densities.

These were performed to determine whether growth rate influences particular plant characteristics or vice versa. These regression analyses would also elucidate the manner in which the slower growing plants differed physiologically from faster growing individuals.

To determine whether there was any difference in growth and reproductive patterns of the seedlings at the two sites, T-Tests were used for parametric, homoscedastic data, and Mann Whitney U tests for nonparametric, heteroscedastic data.

RESULTS

Controls:

No significant difference was observed between the mean height of the populations of either the restio (T_{38} = -0.8456, $p > 0.4$) or annual (Mann Whitney U stat = 0.5817, z = 0.5607) at the two sites (Fig. 2). We can thus make the assumption that there was no significant difference in the nutrient status or other edaphic features of the two sites.

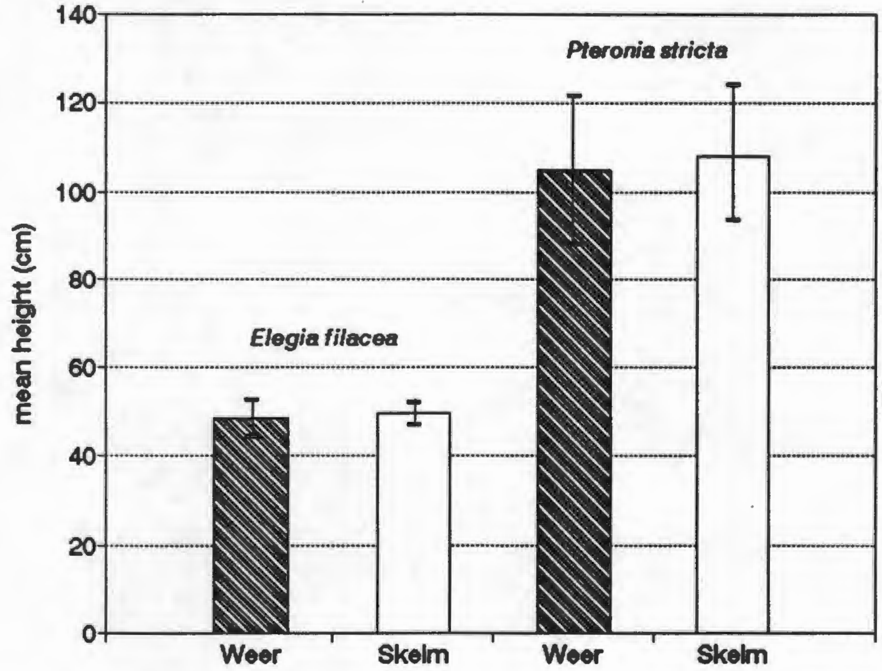


Figure 2. Mean height of two populations of Eligia filacia and Pteronia stricta found at Weerstasie and Skelmdraai, two sites on the southern slopes of the Central Swartberg.

Life History Traits

Seedlings:

The proteas at Weerstasie grew at a rate of 5.8 $cm.yr^{-1}$ as opposed to the Skelmdraai population which had a mean growth rate of $4.75cm.yr^{-1}$. This was reflected in the significant difference in heights in 1994 (T_{79} = 3.0216, $p < 0.05$) (Fig. 3). Similarly, the total seedling leaf area of the Weerstasie population was significantly greater than the Skelmdraai population (Mann Whitney U stat = -3.415, z = 9.01×10^{-4}, n = 81) (Fig. 4).

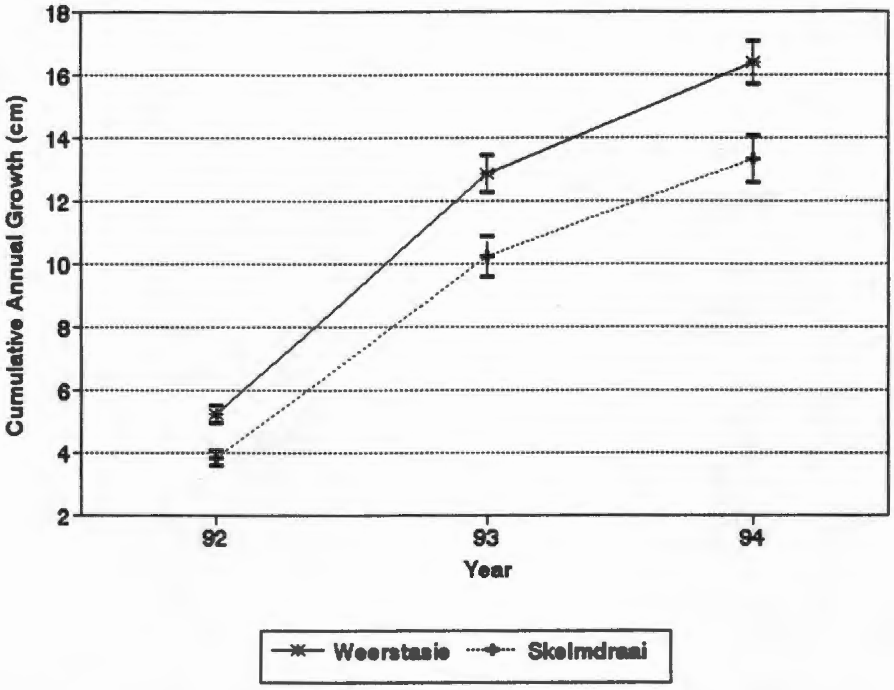


Figure 3. Cumulative annual growth of the P.lorifolia seedlings at two sites on the southern slope of the Central Swartberg. The mean seedling height of the two populations differed significantly (T_{79} = 3.0216, $p < 0.05$).

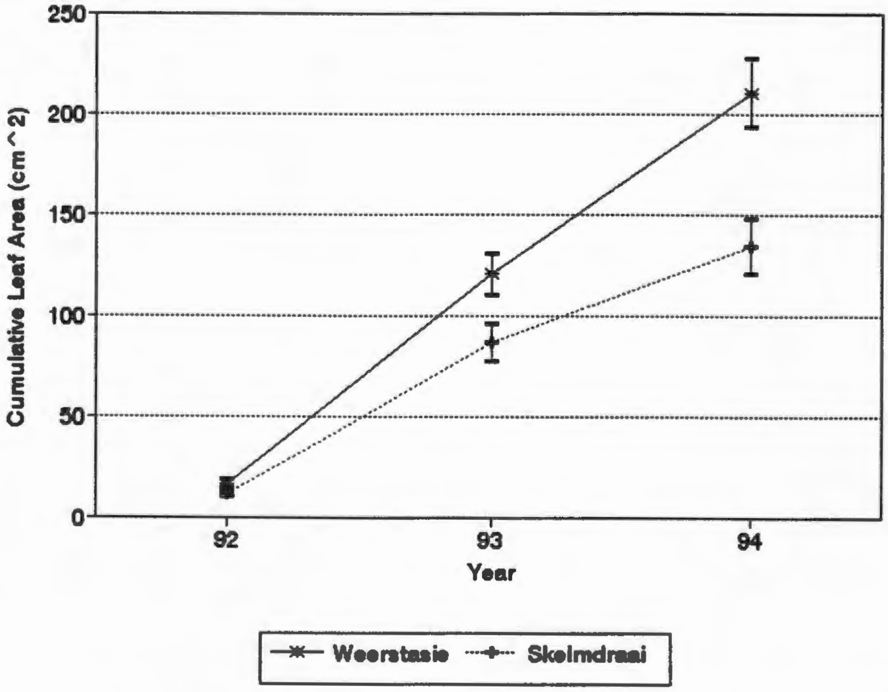


Figure 4. Cumulative annual leaf area of two populations of P.lorifolia seedlings found at two sites on the southern slopes of Central Swartberg. The mean total leaf area of the seedlings at Weerstasie is significantly greater than those at Skelmdraai (Mann Whitney U stat = -3.415, $z = 9.01 \times 10^{-4}$, n = 81).

Parent population (previous generation)

The skeletons of 7.8 year old proteas at the Weerstasie site were slightly taller than the 11.8 year old proteas at Skelmdraai. Furthermore, growth rates can be inferred from the slope of the regression relationship between age and cumulative annual growth. The slope of regression line of the population exposed to high fire frequencies [Weerstasie: $\log Y = 0.766 + 1.284 \log X$; $r^2 = 0.937$; $p < 0.001$] was significantly greater than the population at the low fire frequency site [Skelmdraai: $\log Y = 0.6087 + 1.1985 \log X$; $r^2 = 0.95634$; $p < 0.001$] ($T_{196} = -2.267756$; $p < 0.05$) (Fig. 5). The absolute growth rates were 11.28 $cm.yr^{-1}$ at Weerstasie and 7.3 $cm.yr^{-1}$ at Skelmdraai.

The aboveground biomass of the proteas, represented by mean height, width, height of first branching, number of terminal branches in 1992, and total number of cones per individual, was greater at Weerstasie than at Skelmdraai (Fig. 6).

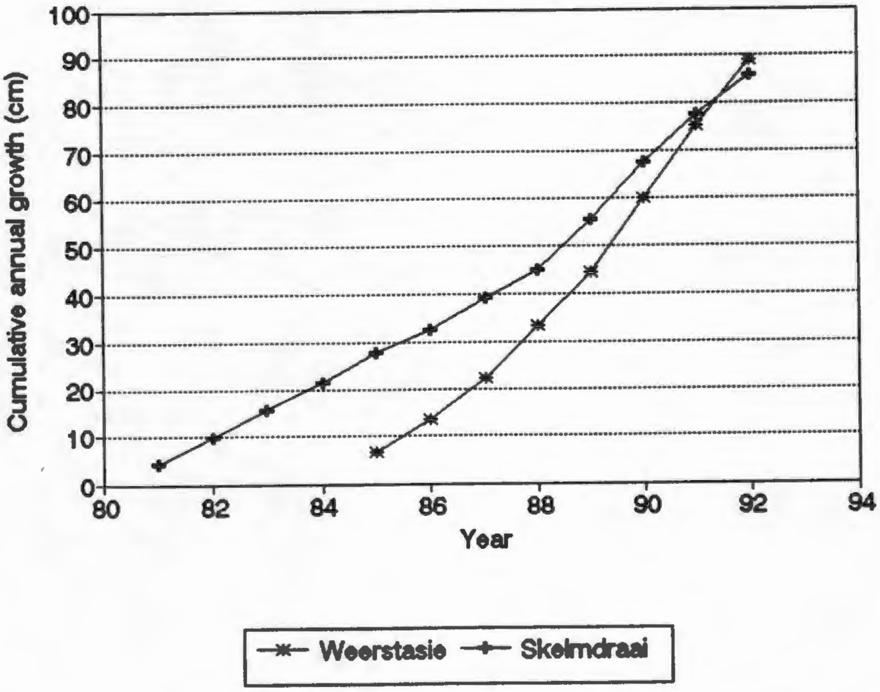


Figure 5. Mean cumulative annual growth of P.lorifolia from the last generation (pre 1992) at two sites in the southern Swartberg, near Oudtshoorn. The Weerstasie population grew at a greater rate, indicated by the significant difference in slopes of the log transformed regression line ($t_{196} = -2.267756$; $p < 0.05$). The Weerstasie population grew at 11.28 $cm.yr^{-1}$ at and the Skelmdraai population at 7.3 $cm.yr^{-1}$.

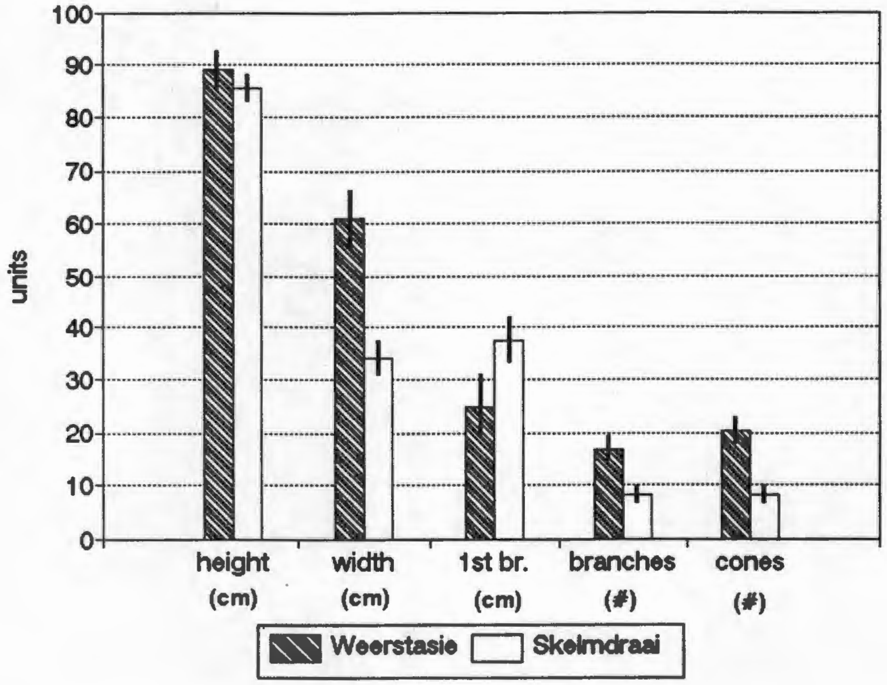


Figure 6. Growth characteristics of two populations of P. lorifolia from the last generation (pre 1992) at two sites in the southern Swartberg, near Oudtshoorn.

Age of First Flowering

At the Weerstasie site, 81% of the plants had flowered by the time that they reached the age 7.8 [mean: 6.43 (0.348)], as opposed to the 53% that had flowered by the age of 11.8 years [mean 10.45 (0.67)] at Skelmdraai (Fig. 7). There was a significant difference in the age of first flowering (Fig.8).

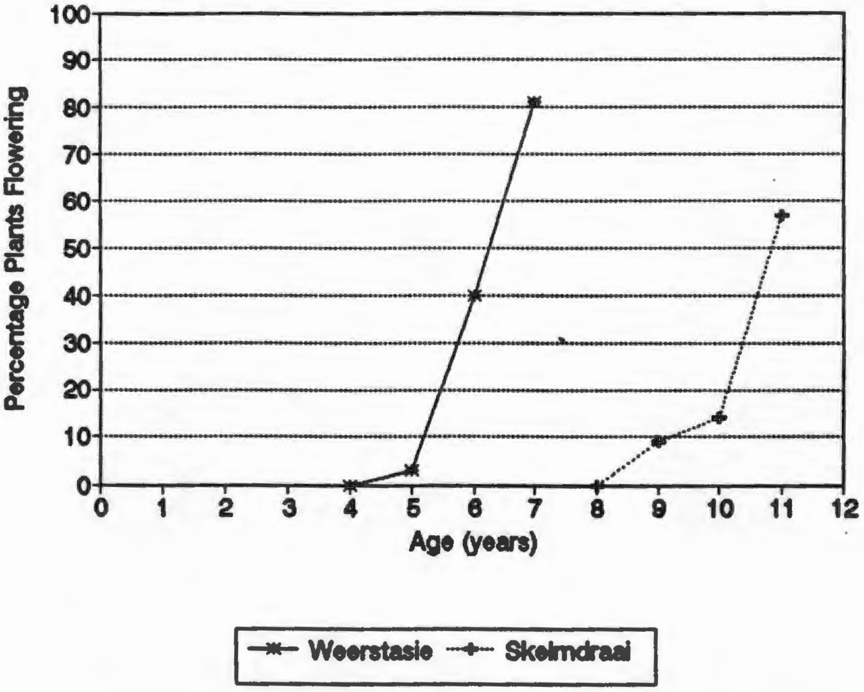


Figure 7. Differences in age of first flowering between two populations of P. lorifolia on the southern slopes of the Swartberg. (after Vlok, 1994)

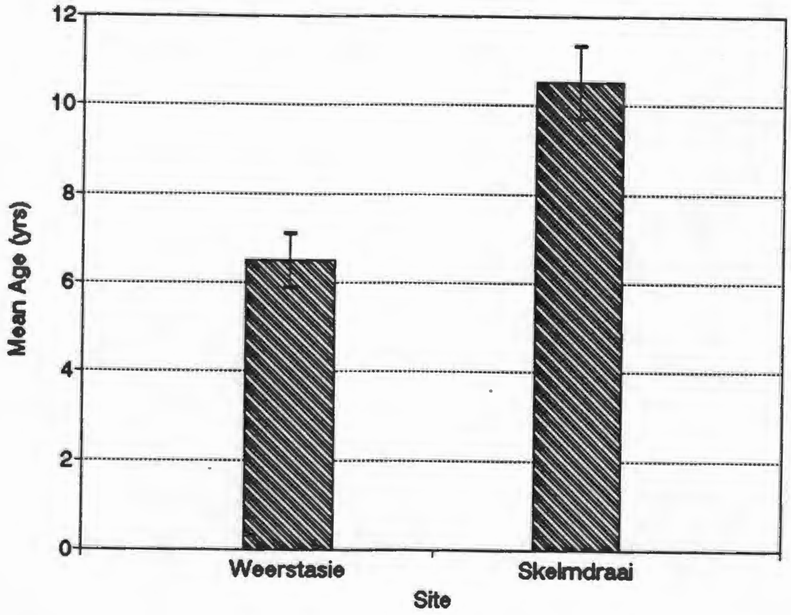
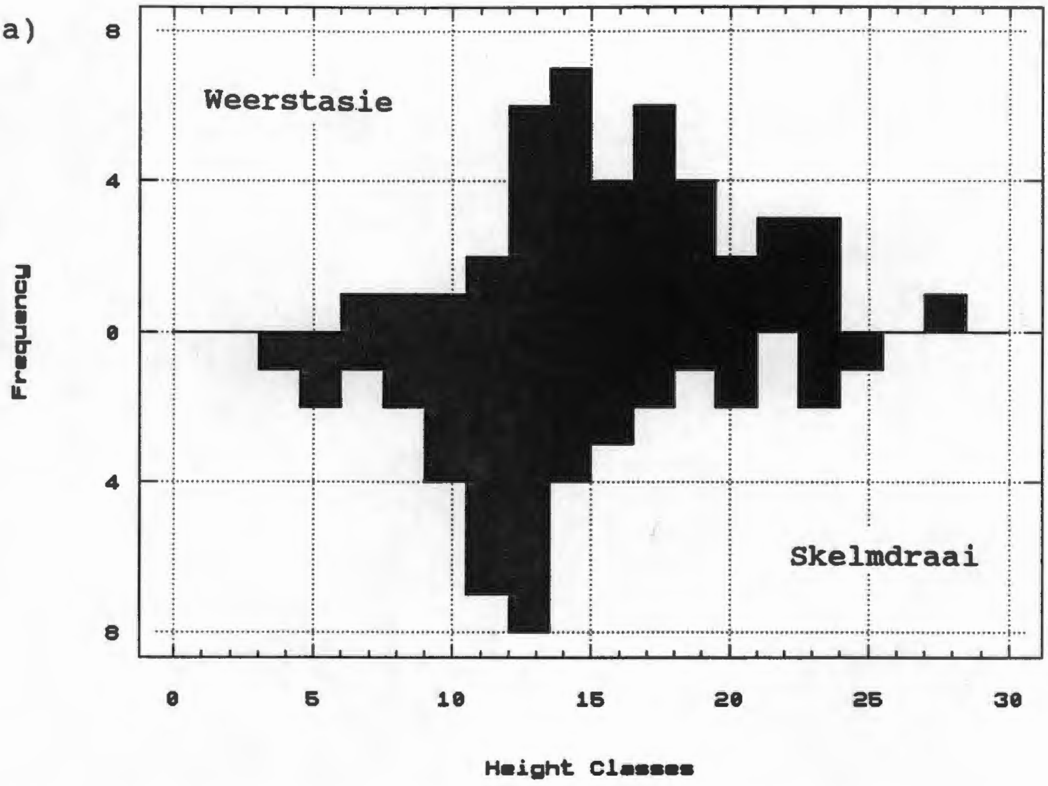


Figure 8. Mean age of first flowering of two populations of P.lorifolia on the southern slopes of the Central Swartberg. There was a significant difference in age of first flowering of the two populations (Mann Whitney U stat = 10.3852, p = 0.0000).

a)



b)

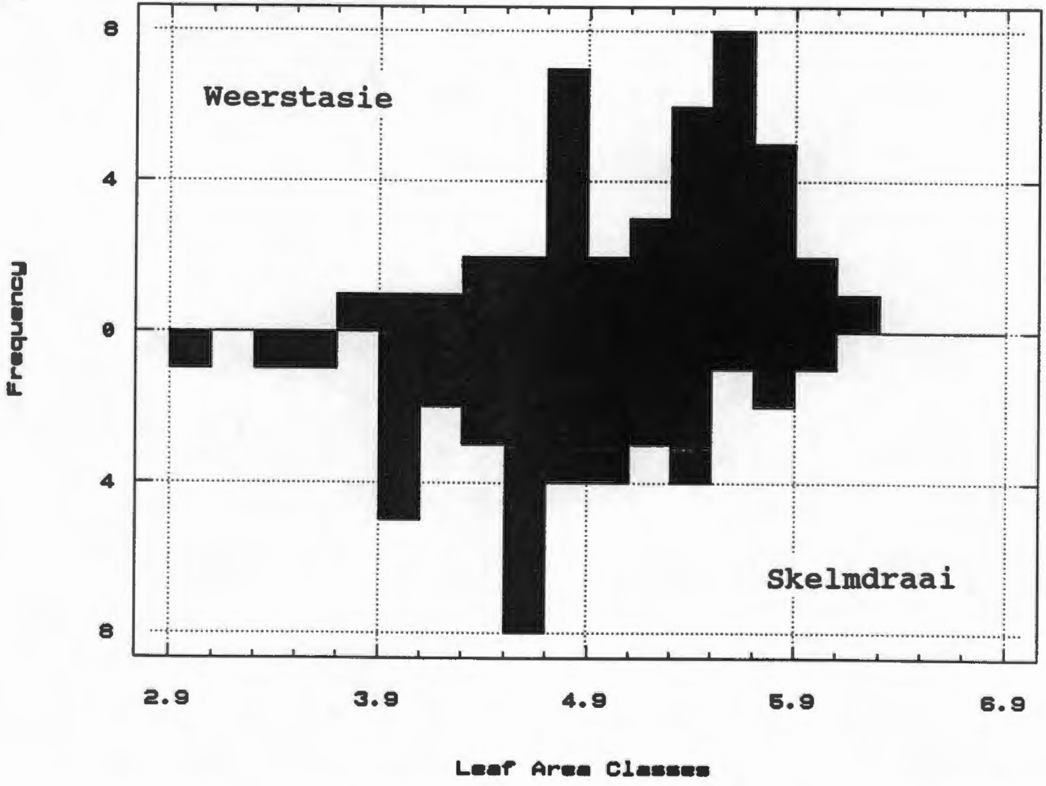


Figure 9. Frequency distribution of the Heights (a) and Leaf Area (b) of two populations of P.lorifolia found on the southern slopes of the Central Swartberg.

Plant Characteristics

Water Relations

Potometry experiment: Mean transpiration rates were higher at Weerstasie, but the difference was not statistically significant (Mann Whitney U stat = -1.3067, z = 0.19, n = 30). (Fig. 10)
A clear relationship between mean seedling leaf area (cm^2) and transpiration rate (ml) was observed at both sites (Weerstasie: $r^2 = 0.5334$, $p < 002$; and Skelmdraai: $r^2 = 0.6372$, $p < 001$). There was a difference in slope of the regression lines, but the difference was not significant (T_{26}, 2.056, $p > 0.05$) (Fig. 11).

total water Use ?

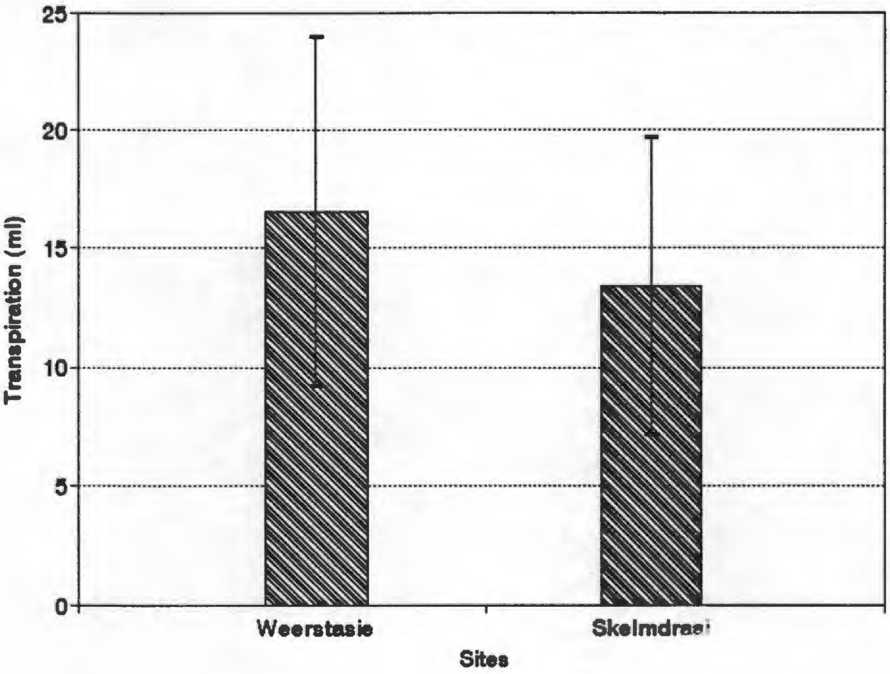


Figure 10. Mean transpiration of two populations of <u>P.lorifolia</u> on the southern slopes of the Central Swartberg. The Weerstasie population transpired at a greater rate, but the difference in rates between sites was not statistically significant (Mann Whitney U stat = -1.3067, z = 0.19).

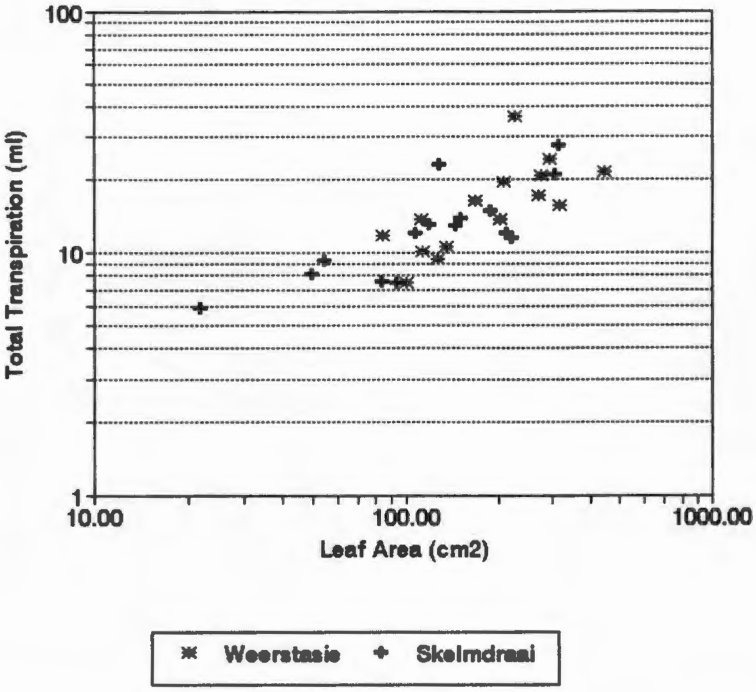


Figure 11. Leaf area (cm^2) in relation to total transpiration (ml, measured over 48 hrs).
Weerstasie: $\log Y = -0.2115 + 0.617 \log X$, $r^2 = 0.5334$
Skelmdraai: $\log Y = 0.0835 + 0.4835 \log X$, $r^2 = 0.6377$

Stem density:

There was a slight, but statistically insignificant difference in mean stem densities of the two populations: Weerstasie: 1.80 [0.22] cm^3.mg^{-1} vs Skelmdraai: 1.83 [0.26] cm^3.mg^{-1} (Fig. 12). The regression analysis between stem density and total leaf area showed a significant relationship (Weerstasie: $r^2 = 0.32$; $p < 0.01$; Skelmdraai: $r^2 = 0.639$; $p < 0.005$, overall: $r^2 = 0.4016$, $p < 0.01$) (Fig.13).

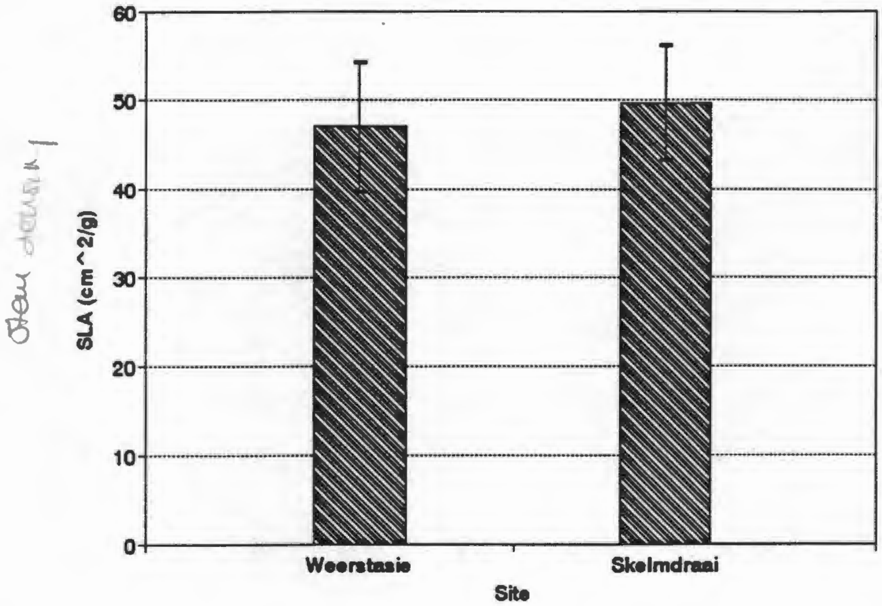


Figure 12. Mean stem density ($cm^3.mg^{-1}$) of two populations of P. lorifolia on the southern slopes of the Swartberg. There was no statistically significant difference between the two population ($T_{38} = -0.417$, $p > 0.5$)

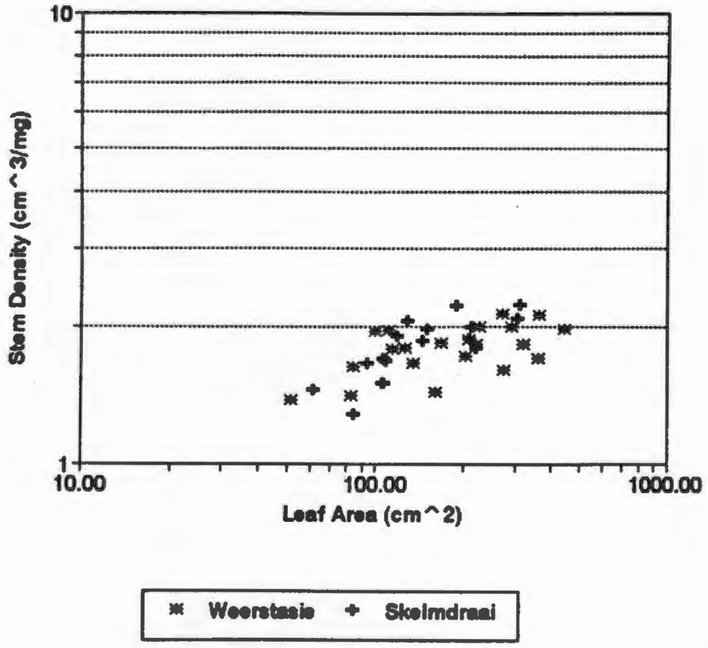


Figure 13. Total seedling leaf area (cm^2) in relation to stem density ($cm^3.mg^{-1}$) for two populations of P. lorifolia on the southern slopes of the Central Swartberg.
a) Weerstasie: $r^2 = 0.32$, $p < 0.01$, $b = 0.125$
b) Skelmdraai: $r^2 = 0.639$, $p < 0.005$, $b = 0.276$
c) Overall: $r^2 = 0.4016$, $p < 0.01$, $b = 0.17$

Specific Leaf Area: No significant difference is observed between the mean SLA of the seedlings at the two sites ($T_{79} = -1.670$, $p > 0.05$) (Fig 14).

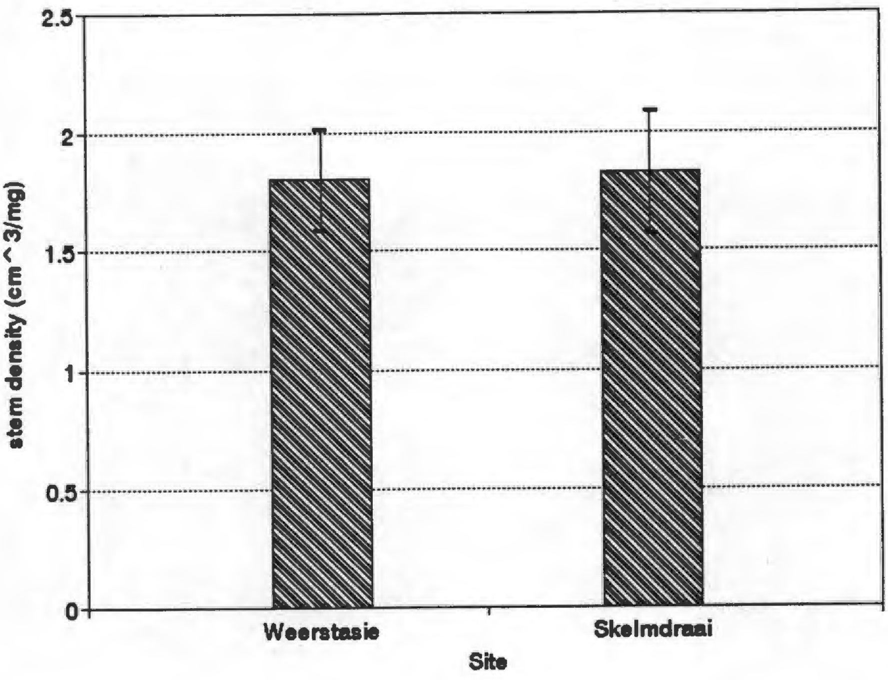


Figure 14. Mean SLA of P.lorifolia seedlings at two sites on the southern slope of the Central Swartberg. No significant difference between the means was observed ($T_{79}= -1.670$, $p > 0.05$).

Leaf Pigment Concentrations

A significant difference was observed between the leaf carotenoid content of the seedlings at the two sites ($T_{34} = 2.407$, $P < 0.05$). Both chlorophyll a & b content was higher at the Weerstasie site, but the difference was not significantly different (Chl a: $T_{34} = 1.718$, $P > 0.05$; Chl b: $T_{34} = 1.777$, $P > 0.05$) (Fig. 15).

No significant relationships were observed between leaf chlorophyll content and leaf area (Fig. 16).

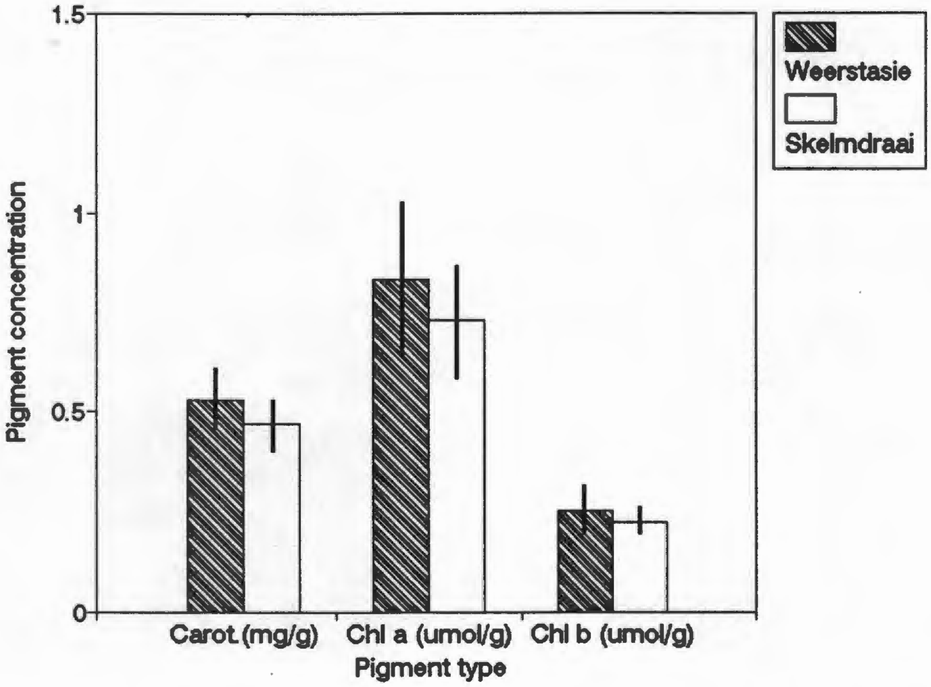


Figure 15. Leaf pigment concentration of P.lorifolia seedlings at two sites on the southern slopes of the Central Swartberg.
Carotenoid: Sign. diff. $T_{34} = 2.407$, $p < 0.05$;
Chlorophyll a: no Sign. diff. $T_{34} = 1.718$, $p > 0.05$;
Chlorophyll b: no Sign. diff. $T_{34} = 1.1.777$, $p > 0.05$.

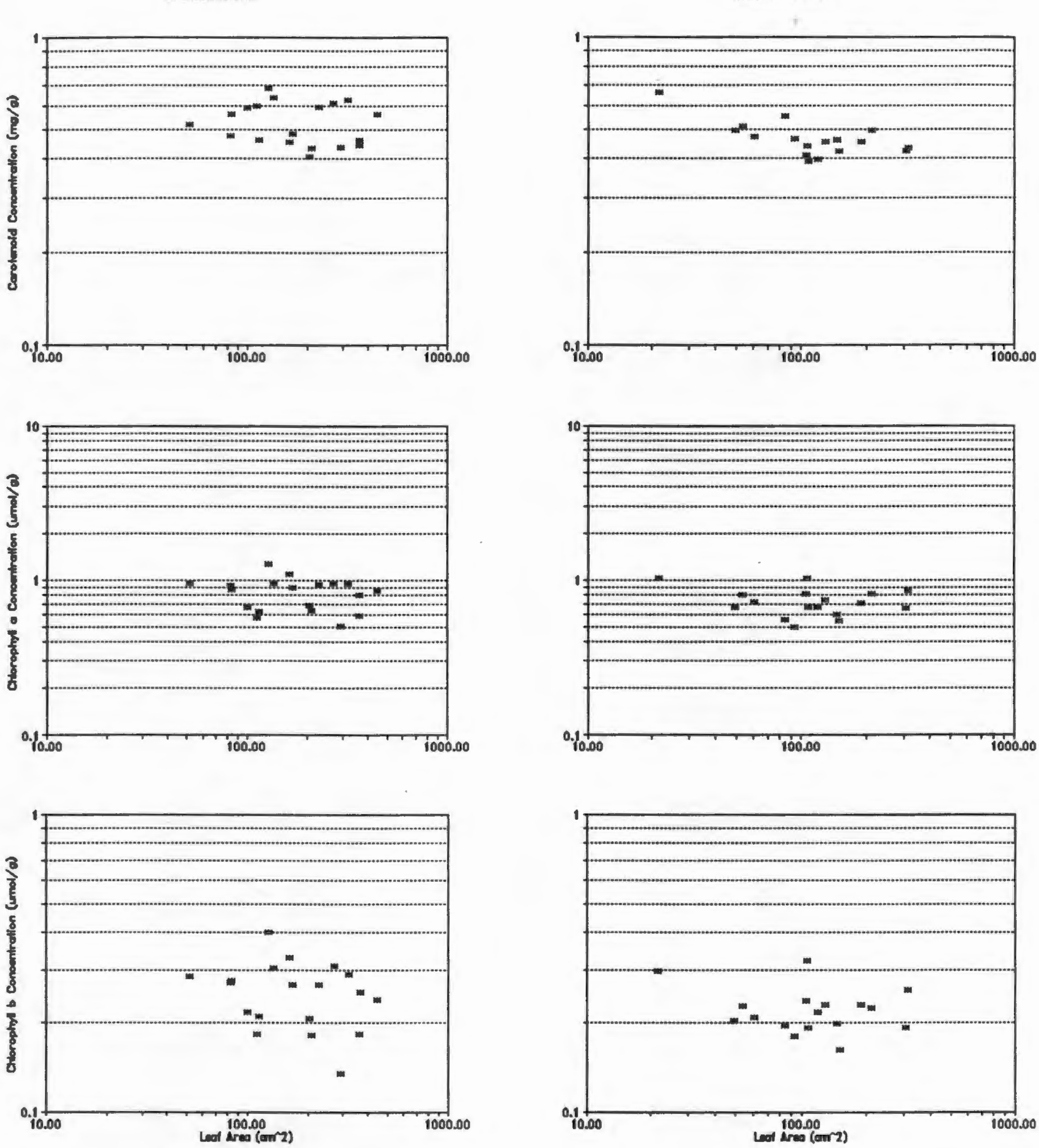


Figure 16. Leaf area (cm^2) in relation to leaf pigment concentrations (mg.g^{-1}/umol.g^{-1}) of two populations of <u>P.lorifolia</u> on the southern slope of the Central Swartberg.
No significant relationships were observed:
A: Weerstasie.
a) Log leaf area (cm^2) vs Log carotenoid (mg.g fresh matter^{-1})
b) Log leaf area (cm^2) vs Log chlorophyll a (umol.g fresh matter^{-1})
c) Log leaf area (cm^2) vs Log chlorophyll b (umol.g fresh matter^{-1})
B: Skelmdraai
d) Log leaf area (cm^2) vs Log carotenoid (mg.g fresh matter^{-1})
e) Log leaf area (cm^2) vs Log chlorophyll a (umol.g fresh matter^{-1})
f) Log leaf area (cm^2) vs Log chlorophyll b (umol.g fresh matter^{-1})

DISCUSSION

1. Has shorter fire frequencies led to a selection for faster growing, earlier reproducing proteas?

There is compelling evidence for changes in growth rate of both the seedlings (Figs 3 & 4) and the parents (Figs 5 & 6), and juvenile period (Figs 7 & 8) of the proteas of the Weerstasie population. According to the results of the control experiments (Fig. 2), there is no difference in nutrients between the sites, and density is not a factor, so the changes in life history patterns had to be due to the increase in fire frequency. This provides strong evidence for Clark's (1991) theory that plants shift their life histories to suit disturbance regime. The only other reported evidence for this, is the change to serotiny in Pinus contorta with increased fire frequency (Muir and Lotan, 1985).

Fire is a potent selective force, in that all above-ground living matter is killed during a fire (van Wilgen et al, 1992), and hence would provide compelling stimulus for adaptive change, resulting in rapid evolution. Therefore fire frequency would play a large role in determining the survival of obligate seeders in the fynbos. A prolonged absence of fire may lead to vegetation stagnation and senescence (Kruger & Bigalke, 1984; Kruger, 1987) and possibly a change in community structure. Too frequent fires, on the other hand, result in the elimination of slow maturing, obligate seeders, in that they cannot reproduce in time, and favour sprouters because their propagation is stimulated by high fire frequencies (Haynes as cited by Kruger, 1983). The fire frequency recorded at Weerstasie, was most likely not short enough to completely eradicate P.lorifolia, but certainly short enough to kill those not reproducing in time. Since flowering is considered to be related to height rather than age (Clark, 1991; Vlok, 1994), only those individuals with a high growth rate, and hence earlier reproductive maturity (Vlok, 1994), were able to reproduce before the burn, in effect selecting for faster growing individuals. The frequency distribution of plant height and leaf area values recorded at each site (Fig. 9) graphically indicate the selection for faster growing individuals at the Weerstasie site. There has been a shift in the distribution from slower growing individuals at the Skelmdraai site, to faster growing individuals at Weerstasie. The fact that this change is so rapid is remarkable: the shift in life history strategy took place after just two short fire cycles.

2. Has the increase in growth rate occurred at the expense of increased water use?

Mean transpiration was higher at the Weerstasie site (Fig. 10), although the difference was not statistically significant. This is substantiated further by the strong relationship between leaf area and transpiration rate (Fig. 11) and the large (35%) difference in mean leaf area of the P.lorifolia seedlings between the two sites (Fig. 4), which , by inference suggest that there would be a significant difference increase in water consumption by the Weerstasie population. The lack of statistical significance might be due to the small sample size coupled with the large variances. Thus the faster growing genotypes at Weerstasie consume greater quantities of water.

3. How do the Weerstasie seedlings achieve faster growth?

A number of theories regarding plant growth strategies have emerged in the past decade (Bloom et al, 1985; Hunt and Lloyd, 1987; Korner, 1991; Reich et al, 1991) many of which refer to the following basic theory. For a plant to grow faster, more resources must be allocated to it’s functional tissues. In woody plants, this allocation is in particular to leaf area available to intercept solar radiation (as described in le Roux, 1993).

Most of these theories are based on interspecific studies (eg. Reich et al, 1991) wherein they discuss how differences in leaf characteristics result in faster growth. For example, faster growing species would have a greater SLA, higher leaf N content and lower leaf conductance (g). However, in this study, the comparison in growth rates is intraspecific.

There was no significant difference in mean stem density between the sites (Fig.12), but stem density was related to leaf area (Fig.13) i.e. the greater the leaf area, the less dense the stems. The decrease of stem density with plant height is an indication of increased allocation to the leaves (Loehle, 1987). Thus the overall patterns are the same: the faster growing plants allocate more resources to the canopy. Indeed, when considering the aboveground biomass of the seedlings and the skeletons of the proteas from the parent generation, a large difference in growth characteristics between sites is apparent. The Weerstasie proteas, both the seedlings (Figs 3 & 4) and parent generation (Fig. 7), display a greater above-ground biomass that those at Skelmdraai. However, it is the nature of this allocation, in an intraspecific comparison, that is in question. A number of studies have dealt with within species variation of relative growth rates (RGR) (Lambers et al, 1989; Friejsen & Veen, 1989), where they found that the plants of the same species enhance growth rates by changing their leaf morphologies and allocation patterns rather than their physiologies. But their focus was on the difference in RGR associated with differences in nutrient levels. Here, however, the nutrient status of each site is presumed to be equal, so the difference in growth rates is due rather to disturbance regime. Is the manner in which the proteas at Weerstasie grow faster, any different to the strategies described by Lambers et al (1989) i.e. do the plants change the physiological characteristics of their leaves so as to increase the carbon assimilation per leaf area or they simply increase the number of leaves?

By examining various characteristics of the leaves, the following was determined. There was no significant difference in SLA of the proteas at the two sites (Fig. 14). SLA is a good indicator of a number of important characteristics of leaves, which in turn, relate to important life history traits.

SLA is strongly related to leaf lifespan, which in turn is strongly correlated with leaf conductance (Reich et al, 1991; Reich, 1993), and therefore, by inference, leaf conductance is likely to correlate strongly with SLA. Thus because there is no difference in SLA of the seedlings from the two sites, it is also likely that there is no difference in leaf conductance (g) and hence leaf specific transpiration rate. Additionally, since SLA is strongly related to leaf N content and net photosynthesis (Reich et al, 1991), it is unlikely that these would differ between sites. This indicates that there is no difference in the photosynthetic characteristics of the leaves. Also, since leaf specific N concentration, a good indicator of relative growth rate, does not differ between sites, and the fact that there is a marked difference in growth rates (Fig. 2 & 3), indicates that the difference in growth rates must have been achieved by producing more leaves. There was also no statistical difference in chlorophyll a & b concentrations between the sites.

Furthermore, because there is a significant difference in total leaf area between the sites, by testing whether there is a relationship between any of the measured characteristics and leaf area, we can see if the difference or similarity between sites is real. For example, if there is no difference in the mean values of a given parameter between sites, but there is a significant relationship between this parameter and leaf area, the lack of difference in means could be explained (for instance, due to high variation). Conversely, if a difference is seen between the means, a relationship between the parameter and leaf area could serve to verify this result. Thus, when relating leaf pigment concentrations to leaf area, no significant relationships were observed (Fig.14), confirming that there is no significant difference in leaf chlorophyll a & b concentrations.

Judging from the results, the increase in growth rate of the <u>P.lorifolia</u> at the Weerstasie site is due to a quantitative rather than a qualitative change in leaves, in contrast to interspecific theories. This stands to reason, since leaf characteristics are likely to be conservative in plants growing in low nutrient environments (Bloom et al, 1985). A similar strategy was observed in maize plants of differing growth rates (Rocher et al, 1989).

However, one cannot ignore the trends that are emerging. The significant difference in leaf carotenoid concentration and the slight, but statistically insignificant, increase in leaf chlorophyll a & b concentrations and transpiration rates per leaf area (as indicated by the slight difference in slope) of the Weerstasie population, indicate that a difference in physiological characteristics may in fact be developing. Leaf chlorophyll content is known to be fairly plastic with regard to changes in environmental conditions (Austin, 1992) eg. the reduction of non-limiting enzymes and the increase in leaf chlorophyll content following shading of plants. It follows that leaf chlorophyll concentrations could well be the initial change in leaf characteristics. With regard to the difference in transpiration per leaf area, depicted by the difference in slopes of the regression lines (Fig.11), the following calculation would serve to highlight this difference:

When comparing the water consumption of individuals with a leaf area of 300 cm^2, from both sites, the Weerstasie proteas were found to consume 20.75 ml as compared to 19.05 ml of the Skelmdraai proteas. Similarly, for a leaf area of 400 cm^2, the Weerstasie proteas consume 24.77 ml compared to 22.02 ml at Skelmdraai. Thus, if this trend continues, as the growth patterns of the parent population suggest (Fig.6), then it is likely that it will result in even greater differences in water consumption per leaf area as they mature. However, this requires further testing.

This indicates that the selection for faster growing genotypes by increased fire frequency may well influence their physiological characteristics. However, the increase in carotenoids and could partly be attributed to the plants response to stress (Austin, 1992). Nonetheless, if the fundamental characteristics of the plants' leaves are changing due to increased fire frequency, the condition would be hard to reverse.

4.Implications of a increased growth rates and early maturation:

With the change in time to reproductive maturity, the plant must balance the costs and benefits of this change (Clark, 1991). So with the benefit of the decrease in maturation time, continued short term survival, comes the increase in the costs in terms of long term survival. The following section deals with the costs of increased growth rates and early maturation, in terms of both individual and species fitness.

4.1. Increased Water Consumption

The ecological value of fynbos is well recognised, but perhaps most importantly for an area that is short of water, fynbos acts as a stable vegetation cover in the mountain catchments of the most important sources of water for agricultural and industrial economies of the region (Kruger, 1987). As has been demonstrated, P.lorifolia grows faster under a high fire frequency regimes, and as a result, consume more water per individual. If this fire regime is implemented on a large scale, it would diminish water availability lower down in the catchment systems, to the detriment of those reliant on this water supply.

4.2. Loss of ability to response to changes in environmental conditions

Genetic variability: The loss of population genetic variability with the eradication of the slower growing genotypes would severely compromise the protea's survival on an evolutionary time scale. However, due to the rapid nature of this change (2 generations), the evolutionary time scale, may well be condensed into ecological time scales, thus threatening the short-term survival of the species.

Increased Water consumption: the intrinsic increase in water consumption would impair the plants' ability to survive drought. In a water stress situation, the faster growing plants are less likely to survive because of their increased relative water requirements. Thus their ability to survive and respond to environmental stress would be hindered. Also, as compared to the an unstressed situation, the relative costs of both carbon and water acquisition during drought, increase with enhanced growth rate (Bloom et al, 1985). The acquisition of carbon increases because of higher mesophyll resistance and lower quantum yields in the leaves, and similarly water "costs" more because of root death associated with drought. Therefore, on top of the higher intrinsic need for water that accompanies higher growth rate, the increased cost of resource acquisition, relative to the unstressed state (and slower growing individuals), means a decreased ability to survive a drought.

Change in Allocation Patterns: Mortality in proteas is largely a result of structural collapse (Kruger, 1987). The increased allocation to the leaves, and the consequent decrease in allocation to support organs decrease plant longevity (Loehle, 1987). The stem density of the proteas from the high fire frequency site, implies earlier mechanical collapse. Compounding this, the fact that the proteas reach reproductive maturity earlier (Fig.9), thus incurring further resource costs, resulting ultimately in earlier mortality. This would in turn compromise the plants' long term survival. As has been mentioned, if a long interval between fires is experienced, the proteas now more likely to senesce before the next burn, and since they require fire to reproduce, the plants would die before reproducing.
The plant would also be more susceptible to pathogenic attack, as allocation to defences are disregarded in favour of faster growth.

4.3. Possible increases in probability of fire

The point at which a patch of fynbos first burns, is in part determined by fuel availability (Kruger and Bigalke, 1984). Thus with the increase in growth rates and consequently aboveground biomass, this point would be reached sooner, thus making that patch more susceptible to fire.

CONCLUSION

The Protea lorifolia seedlings at the Weerstasie site, do in fact have an increased growth rate and water consumption relative to those at the Skelmdraai site. Their parent population, also with a higher growth rate, reach reproductive maturity earlier. So in answering the first question, an increase in fire frequency does result in an increase in growth rate and reaching reproductive maturity earlier.

The plants achieve this increase in growth rate by increasing allocation to their leaves, at the expense of increased water consumption. This allocation results in a quantitative rather than a qualitative change in the leaves i.e. to grow faster the plants make more leaves, although a physiological change might be happening. The implications of these findings are that a) it is likely to compromise the long term survival of the proteas in this area b) a possible loss of the species and c) increased water consumption at the upper catchment level, resulting in reducing runoff and hence a decrease in water availability further down.

Further research would include planting out of the seedlings of the proteas from both sites under similar conditions, to conclusively test whether these traits are inherited. Furthermore, if more sites such as those at Weerstasie and Skelmdraai can be found, the effects of increased fire frequency can be tested on other species.

Implications for managers.

The findings of this study serve to highlight the importance of the effects of increased fire frequency. Since the change in life history is closely linked disturbance regime history, managers can no longer base their burn times on the juvenile periods of the local proteas. Thus determining the age at which a stand can be burnt, should incorperate both age of peak biodiversity and maximum sustainable water yield, but also take into the account the dynamic nature of the proteas' life history attributes and their possible effects on water consumption.

Although this study was conducted on *Protea lorifolia* only, it is likely that this study might be applicable to many other species. For instance, Vlok (1994) found similar life history patterns in *P.eximia* and *P.punctata*. Also, the increase in fire frequency is particularly likely to affect the obligate seeders, especially the Proteoid shrubs, which are prominent in the fynbos (le Maitre and Midgley, 1992). Furthermore, 49 out of the 82 *Leucadendron* species found in the fynbos are serotenous (Kruger and Bigalke, 1984), indicating that they may also be affected. Kruger and Bigalke (1984) remarked that a number of proteas found in sites of high fire frequency display precocious flowering (eg. *P.repens* and *P.neriifolia*). This could quite easily be a symptom of the fire-induced reduction of juvenile periods. The increased growth rates may also have profound trickle-down effects on the other species in the community. Competition dynamics are likely to be altered, thus impacting on the other non-seeding individuals, although this still has to be tested.

The rapid change in life history with increased fire frequency, would be difficult to reverse, especially if it is accompanied by a physiological change in leaf characteristics. This change would take a number of generations before the reverting back to normal. Therefore, if high fire frequency burns become a feature of management strategies, the impacts of the above mentioned phenomenon has the potential to become extensive throughout the fynbos.

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