The competitive dynamics of two *Protea* shrubs growing in a mixed fynbos stand.

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ABSTRACT

Patterns of segregation among *Protea* species were investigated. Interspecific competition was studied as a cause of these patterns. Two different methods were used for measuring competition in a mixed stand of *P. lepidocarpodendron* and *P. coronata* growing on the Cape Peninsula. These were the plot-based averaging method, which considers stand density, and the nearest neighbour approach, which considers competitive impacts as a function of the immediate neighbouring plant. Both methods demonstrated negligible interspecific, and strong intraspecific competitive effects on fecundity. However strong interspecific competition appears to be occurring at earlier stages of the life cycle and may account for habitat segregation of *P. coronata* and *P. lepidocarpodendron*. *P. lepidocarpodendron* juveniles appear to outgrow and suppress *P. coronata* plants. Survivors of this interaction grow to full maturity, giving an apparent lack of species interactions when measured in terms of fecundity. The same results were demonstrated in a mixed stand of *P. lepidocarpodendron* and *H. suaveolens*, where *H. suaveolens* suppresses *P. lepidocarpodendron*. The study indicates the importance of shrub architecture in reducing species interactions, and juvenile phase properties in determining competitive displacement. Soil preferences and variable fire responses between the species were studied in an attempt to explain the restricted distribution of the stronger competitor, *P. lepidocarpodendron* at the study site. No conclusions were reached, but the restriction of this species from certain sites appears to be a fire response.

INTRODUCTION

One of the dominating themes in plant ecology has been the question of what determines species richness in plant communities (Shmida & Ellner 1984). Much time has been devoted to increasing our understanding of what determines plant community composition, and yet this question still poses one of the greatest challenges to biologists (Auerbach & Shmida 1987).

Gondwanan shrublands are renowned for their diversity, and the fynbos biome is no exception, having an immense diversity of species over a small geographical area (Bond *et al.* 1992). Even more startling in these communities is the coexistence of many morphologically similar, or trophically equivalent species (Cowling 1987; Shmida & Ellner 1984). These high levels of species diversity, combined with an apparent paucity of functional diversity have stimulated a great deal of interest in the rules which govern community composition and pattern (Bond & van Wilgen 1996).

Studies in the past have focused largely on abiotic and exogenous determinants of community composition, where species' physiologies and abiotic environmental factors were used to explain species locations (Bond *et al.* 1992). While these elements are all important, and still form a component of any distributional study, they fail to fully explain the high alpha diversity found on a local scale in fynbos (Cowling *et al.* 1994). Plant interactions and competitive dynamics have, until recently, been largely overlooked. This is particularly true of many fire-prone environments, where previously these communities were believed to be shaped predominantly by disturbance (Bond & van Wilgen 1996). Cody (1986) was the first to challenge these ideas, and suggested that distribution patterns among the Proteaceae were a function of the relative abundance of the various species, rather than abiotic factors.

Several authors have considered the dynamics of single-species plant populations, and this is equally true of the Proteaceae, where many of the demographic studies in the past have considered only single species (Esler & Cowling 1990; Mustart & Cowling 1993; Maze & Bond 1996). This is not reflective of the community structure of the fynbos biome, where many proteas exist in mixed stands. The aim of this study is to explore the implications for the fecundity and demography of *Protea* species growing in mixed populations.

Besides being of ecological interest, there are applied aspects to competition studies in mixed species stands in fynbos. They have relevance to *Protea* flower harvesting, where the implications of harvesting only one species in a mixed stand are unknown, studies in the past having focused on the interactions of single species (Maze & Bond 1996). Studies taking into account the effects of other functionally similar species will allow for the development of appropriate management principles. Another area of application is alien plant invasion. Models developed to predict the invasibility of introduced species (Tucker & Richardson 1995; Richardson *et al.* 1992), have focused largely on the reproductive attributes of invasive species, relying on lottery models to predict invasive success. What competition studies in fynbos can contribute, is an understanding of the vegetative and growth attributes of this flora, which would provide a more effective tool for predicting which communities are sensitive to invasion, allowing for more focused control programmes. Effective competition studies have both an applied aspect, and would serve to provide a better understanding of the dynamics of coexistence behind the high diversity, and apparently low functional diversity, of fynbos (Cowling et al. 1994).

The challenge to biologists is to show whether competition in plant communities does indeed exist, and if so, how it is acting to shape populations and communities. Some of the difficulties in addressing these questions, are how to effectively measure competition, and its degree of impact. One approach is to quantify the outcomes of immediate neighbour competition, such as relative growth rates, and reproductive output (Law & Watkinson 1989). The demographic effects have been explored by Silander and Pacala (1985) where competition is the result of the immediate neighbouring plant. The proximity of the neighbour will determine the degree of competitive impact, which can affect survival, and, given the plasticity of the plant, general fecundity. In using this method an assumption has to be made as to which neighbours fall within the competitive arena.

In their review on past competition studies among plant communities, Law and Watkinson (1989) concluded that there is no firm foundation on which to quantifiably measure interaction strengths, and develop a basis on which to build an analysis to make predictions about subsequent community structure. The controversies surrounding the importance of competition as a factor determining community structure are symptomatic of this lack of a secure empirical foundation in competition studies (Law & Watkinson 1989).

An alternative approach, is to average the competitive effects of neighbours by looking at mean performance at different population densities (Rees *et al.* 1996). The effects of a competing species are modelled by an extension of the single species population growth model, but where a competitive coefficient, alpha, incorporates the impact of the contraspecific species into the population growth rate, lambda. Rees *et al.* (1996) used this approach on annual plants, but it is also appropriate for serotinous *Protea* shrubs, which have been shown to be density-dependent in terms of reproductive output (Bond *et al.* 1995). Among these species this method should serve to model the reproductive output of densely packed plants, and demonstrate how the density of one species affects the other. Plot-based methods take no account of the spatial structure of the stand, but looks only at the relative densities of each species.

The two central questions this project sets out to answer are;
1) Does competition between *Protea* species occur?
2) What is the best way to measure for competition?

In order to answer these two questions, several subsidiary questions, which form the logic of the study are asked. These are as follows:

- Is there evidence of macro- and micro-scale segregation among fynbos proteas, and does competition account for these patterns?
- How exactly does competition manifest itself on a local scale, is it a function of stand density, or the immediate neighbour of each individual?
- At what stage in the life history of a stand are competitive interactions evident?

- Are *Protea* species "competitive equivalents", or is there some degree of niche separation among coexisting *Protea* species?
- In light of these findings, how is competition best tested for?

These questions are addressed by looking at the dynamics of two *Protea* shrubs, *P. lepidocarpodendron* and *P. coronata,* growing in a mixed stand in fynbos.

METHODS

Study Area

The Cape Peninsula formed the general study area of this project. Most of the project was based on a site below Constantiaberg Peak (34° 03′S, 18° 23′E), which forms part of the Table Mountain series. The Cape Peninsula, situated at the south-western edge of southern Africa, experiences a Mediterranean-type climate, with typically hot dry summers, and cool wet winters (Richardson *et al.* 1995). These climatic conditions apply to the Constantiaberg site. The aspect of the slope on which the populations were growing was north-easterly, and was at an altitude of approximately 400 - 450m. The species were growing on Table Mountain Sand Stone of the Peninsula Formation, immediately above a shale band of the Graafwater Formation (see fig 1).

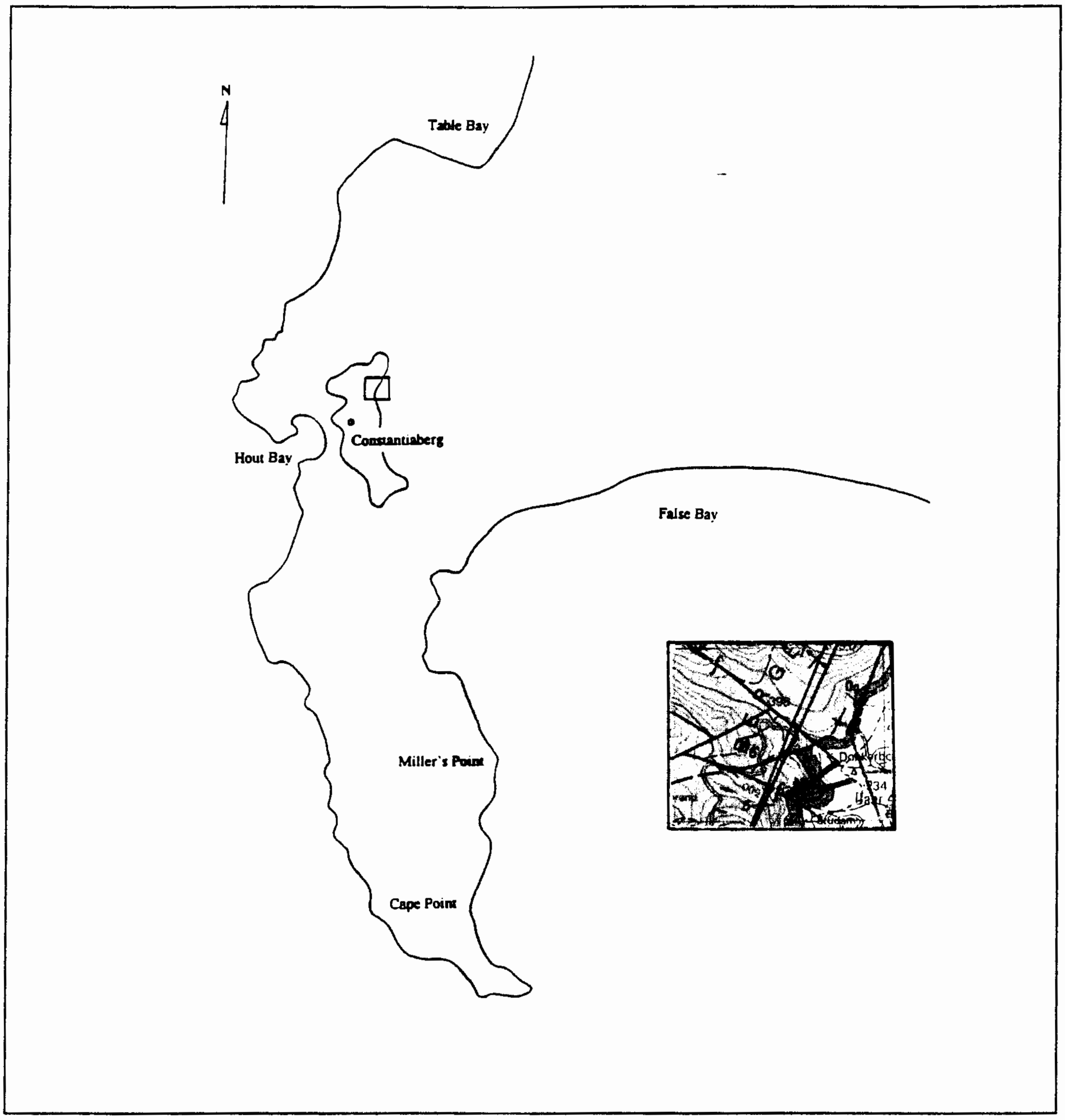
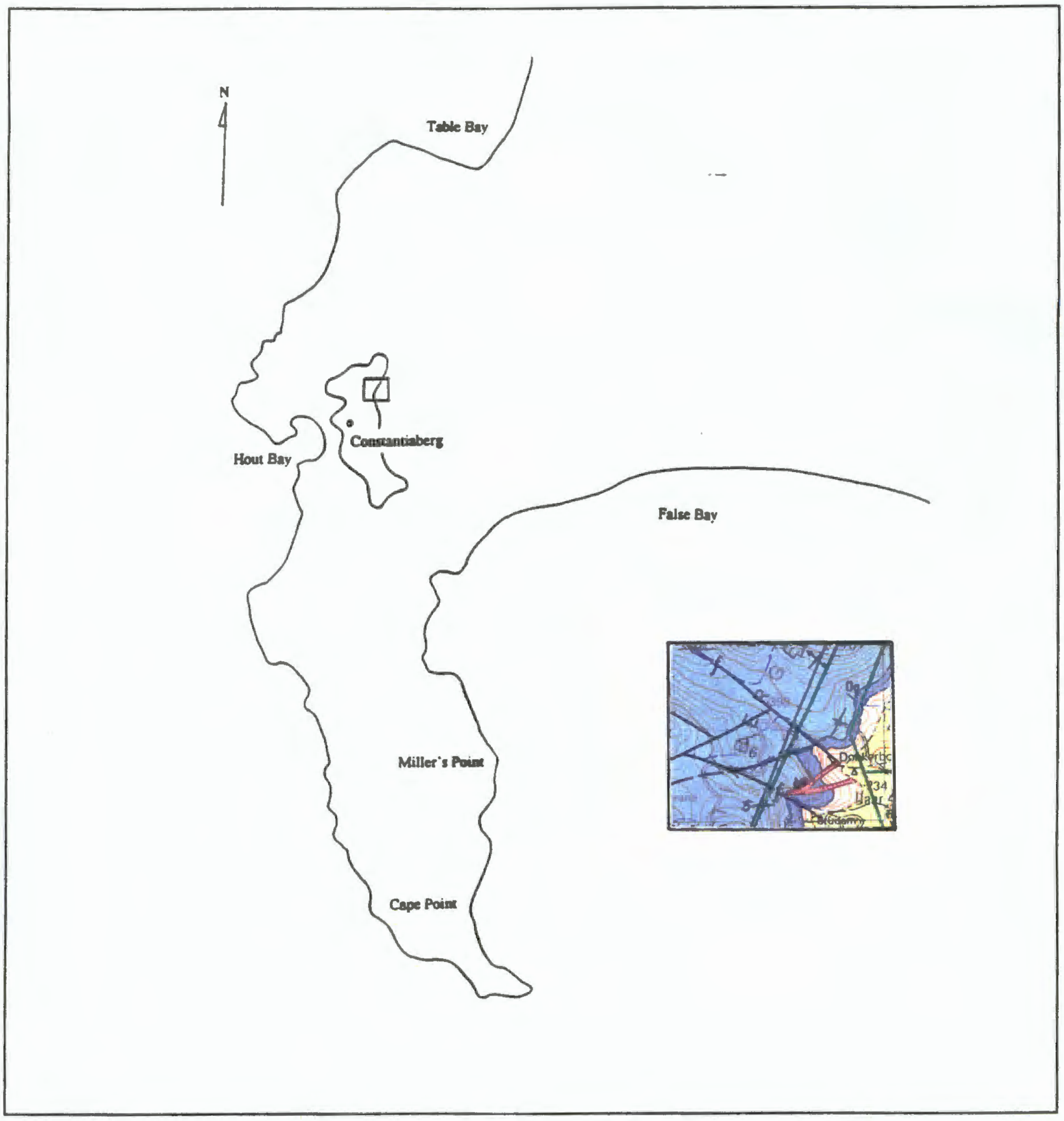


Fig 1 A map of the Cape Peninsula showing the Constantiaberg site where the population of *Protea lepidocarpodendron* and *Protea coronata* were studied (indicated by box). Inset is a geological map of the immediate study area indicated by the box. Peninsula formation soil is indicated by light blue, and the Graafwater formation by dark blue. On the eastern side of the Peninsula is Millers Point , where a study on *P. lepidocarpodendron* and *Hakea suaveolens* was carried out.



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Material Studied

This project was based in the mountain fynbos flora of the Cape Peninsula. A preliminary aspect of this study looked at patterns of species segregation of the proteoid elements of the fynbos of the Peninsula at large. Two serotinous Leucadendron species, *L. xanthoconus* and *L. laureolum*, were studied, as well as the two *Protea* species, *Protea lepidocarpodendron* and *Protea coronata*, studied subsequently at the Constantiaberg site.

At the Constantiaberg site, which formed the main focus of the study, two co-occurring *Protea* species were studied: *P. coronata* and *P. lepidocarpodendron.* These proteas are both tall, erect shrubs, forming part of the dominant overstorey of the fynbos community. Both species are killed by fire, having non-overlapping generations and recruiting in the first rains subsequent to the fire. They both flower in the Cape winter, from around April to August. According to Rourke (1980), both species show a preference for clay soils, such as those found on the exposed shale bands of Table Mountain.

P. coronata occurs from the Cape Peninsula, to as far east as Port Elisabeth. At maturity it grows to a height of 3.5 m, sometimes more, and is typically sparsely branched (see plate 1) (Rourke 1980). *P. lepidocarpodendron* is a coastal species, found within 20 km of the sea. Its range is less extensive than *P. coronata*, with an eastern boundary at Stanford. While *P. lepidocarpodendron* reaches similar heights to *P. coronata*, of approximately 3m at maturity, it has a far denser canopy (see plate 2).

Plate 1 A *P. coronata* individual.

Plate 2 A *P. lepidocarpodendron* individual.

A mixed stand of *Hakea suaveolens* and *P. lepidocarpodendron* was also studied. *H. suaveolens*, also a member of the Proteaceae, is a woody shrub that reaches approximately 3 m in height. This Australian member of the Proteaceae was introduced to South Africa in the 1830s, since when it has become a problematic invasive plant. Unlike *P. coronata* and *P. lepidocarpodendron*, which have terminally borne inflorescence, *H. suaveolens* has clusters of inflorescence borne laterally in the axil of its leaves (Wrigley & Fagg 1989). The vegetation at this site was 8 years old (Yeaton & Bond 1991).

At the Constantiaberg site *P. lepidocarpodendron* and *P. coronata* were present across the study area in three different age classes, as the result of varied fire history. They displayed a "checkerboard" distribution, growing both as mixed and single species stands (see plate 3). Figure 2 displays the positioning of the populations across the study area (see fig 2 and plate 3). The vegetation in the firebreak was aged as 5 years (5 y) old, the break having been burnt in the spring of 1991 (Zeeman pers. comm.). No fire records could be obtained for the vegetation immediately surrounding the firebreak, and plant ages were estimated as 10 years (10 y) old in the intermediate aged stand, and of 15 years (15 y) old in the oldest stand.

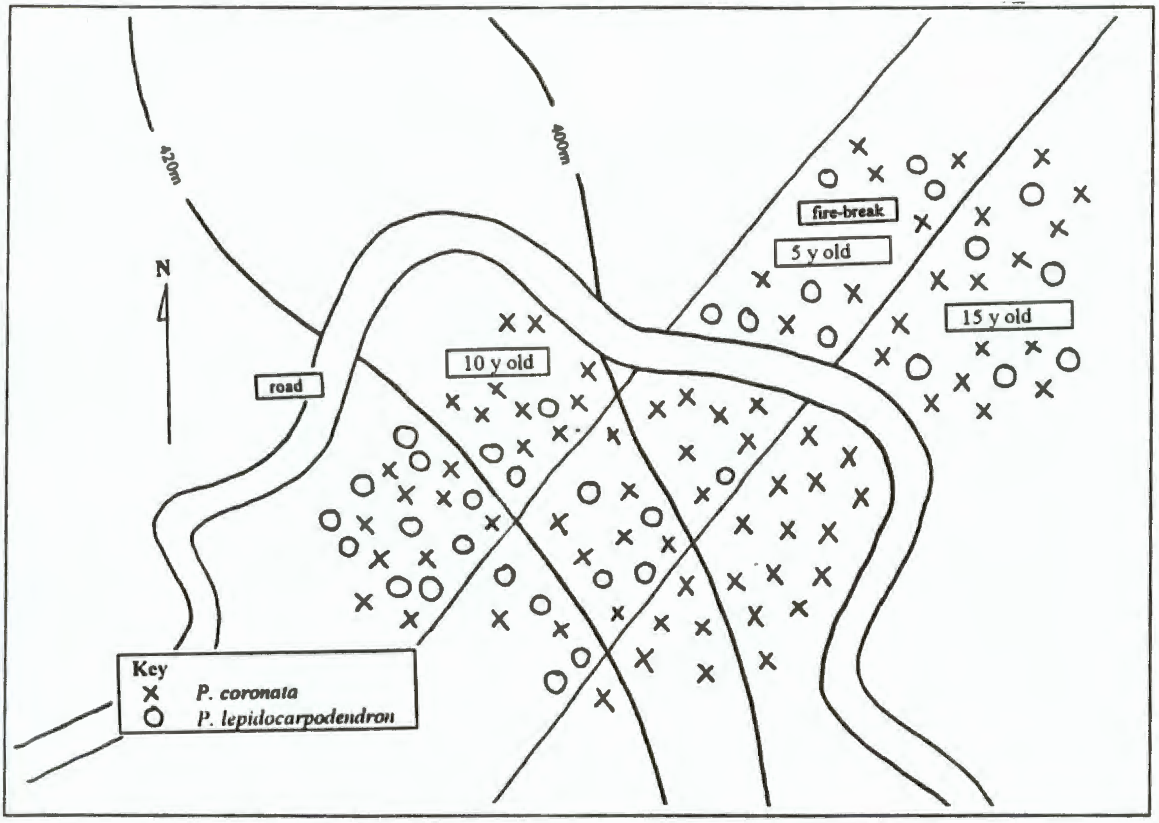


Fig 2 Map of the study site showing the spatial distribution and species combinations of the three different aged populations.

Plate 3 Photograph of the study site showing the firebreak (A), with mixed vegetation of *P. coronata* and *P. lepidocarpodendron*, and the adjacent old vegetation (B), comprised solely of *P. coronata*.

Methods

Are there patterns of segregation among *Protea* species?

Previously compiled data of fynbos community composition, taken from 300, 5 x 10m plots from across the Cape Peninsula (Simmons, unpublished data), was analysed to test for distribution patterns of proteoid shrub species. This was done using the method described by Laurie and Mustart (1992), whereby the expected frequency of plots where species may coexist is calculated, and compared to the observed frequencies of coexistence. This was carried out for sites containing *P. coronata* and *P. lepidocarpodendron*, and *L. laureolum* and *L. xanthoconus*. All four species share similar growth forms, similar non-sprouting life histories, and all are serotinous. From among these four species both congeneric and contrageneric coexistence was analysed. This was in order to assess whether distribution patterns are random, or whether certain combinations of *Protea* species are segregated. This data was then tested statistically using a chi-squared test.

The same exercise was performed at the Constantiaberg study site, where community composition was recorded in 4 x 4m plots along a transect, at 9m intervals. Expected and observed frequencies of single and mixed species combinations were analysed in the same way. In this case only *P. lepidocarpodendron* and *P. coronata* were noted as they form the dominant species at the site, and the focus of this project.

In addition to this, percent contribution of *P. lepidocarpodendron* and *P. coronata* to the proteoid cover in 15 plots of 4 x 4 m taken along the same transect, was calculated. The percent cover of the two species was then correlated, in order to assess the importance of the relative abundance of each species on distribution patterns.

Is there evidence for competition among *Protea* species?

Testing for competition using plot-based averaging.

In the 10 y old mixed stand (see fig 2) the effects of intraspecific and interspecific density on fecundity was tested. Twelve dense, mixed plots of 7 x 7m were measured out, and numbers of each species, and their respective cone numbers were recorded.

Cone numbers were used as a measure of fecundity. Non-linear regression equations were used to test for the relative effects of intraspecific and interspecific competition. The following non-linear equations were fitted to the collected data (Rees *et al.* 1996).

a) $f = \lambda / (1 + Nt_A + (\alpha \times Nt_B))^b$ (interspecific and intraspecific effects)

b) $f = \lambda / (1 + Nt_A)^b$ (intraspecific effects)

Where: f = expected fecundity per plant; Nt_A and Nt_B are the number of adult plants of each species; λ = lambda max., the fecundity on an isolated plant; α = the competitive coefficient; and b = steepness of the density dependent relationship.

The plot-based method of measuring competition, was repeated at Miller's Point on the Cape Peninsula (see fig 1). The species at this site were *P. lepidocarpodendron* and *H. suaveolens*. H. suaveolens in known to be an aggressive invader, over-topping and suppressing *Protea* species (Richardson *et al* 1992). This analysis of mixed stands of *Protea* and *Hakea* were used to test the power of the method in detecting known competitive effects.

Testing for competition using the nearest neighbour measures.

In the 15 y old stand, nearest neighbour interactions between *P. lepidocarpodendron* on *P. coronata* were measured. Neighbours were assumed to be those plants with their trunk bases within 0.5 m of one another. The spatial arrangement in the stand was such that there were insufficient individuals of *P. lepidocarpodendron* neighbouring each other to test for intraspecific competition within this species. The impacts of interspecific and intraspecific effects were compared, and in turn compared to free-standing plants for *P. coronata*. Competitive impacts were tested by measuring the height, basal trunk diameter and cone numbers of 25 *P. coronata* neighbouring *P. lepidocarpodendron*. These measurements were repeated on free-standing *P. coronata*, and pairs of neighbouring *P. coronata*. Samples were randomised using the Wandering Quarter Method (Catana 1963).

The relationship between basal diameter and cone production was graphed to view the effects of different neighbour combinations.

The results of this nearest neighbour analysis were reviewed in relation to the findings of the plot-based method, in order to assess the effectiveness of each.

At what stage are competitive effects evident?

Effects of different neighbour combinations were measured in the 5 y old, 10 y old, and 15 y old stands. Moving along a transect, canopy heights, and canopy diameters were measured of both *P. coronata* and *P. lepidocarpodendron* neighbour combinations. Intraspecific combinations were also measured, including those of *P. lepidocarpodendron* in the 5 y old stand. The same measures were carried out on free-standing individuals of each species. From these measures canopy volumes were calculated. These data sets were tested for internal variance, using a one way ANOVA. The findings of all three age classes were then compared, in order to establish when competitive effects come into play.

Are juvenile plants of the two species segregated at a micro-spatial scales?

In the youngest stand in the firebreak, distribution patterns were analysed to determine whether juvenile plants are spatially separated. This was done by taking three 50m transects through the firebreak and recording presence of each plant, and when applicable, its neighbour (neighbours again were assumed to be those plants growing within 0.5m of each other). The expected frequencies of different neighbour combinations were calculated, and compared to the observed. This was done using a chi-squared test.

Do these species occur on different soil types?

Fourteen systematic soil samples were taken along a transect through the study site. Soil depth and colour were noted in relation to the species composition in 4 x 4m plots. Soil colour was broken in to four categories; soils with an E-horizon, red coloured soils, yellow coloured soils, and loamy soils. Depth was divided into two categories; soil of less than 50 cm, and soil of more than 50 cm deep. The frequencies of sites with different species combinations at different soil depths, and growing on different soil colour types were graphed to test for any patterns relating community composition to soil type.

Proteoid species composition in a 2m area to each immediate side of the fire break was recorded on a 35m transect up the left hand side of the firebreak. This was done in order to describe changes in proteoid composition clearly not related to soil.

Do these species have different fire responses?

Possible differences in fire frequency responses were tested by comparing mean cone production of each species at the three different ages. In addition to this, parent to seedling ratios were calculated by counting skeletons and juvenile plants of each species in 18, 5 x 5m plots in the fire break. An attempt was made to find out the fire history of the area, in order to relate possible species patterns to variable fire season. To address this possibility, the 5 y plants growing in the firebreak were examined for phenological differences.

Seed viability in relation to fire intensity was tested. Ninety cones of each species were picked. Temperatures from 100°C to 800°C, at 100°C increments were used to simulate different fire intensities, following Midgley and Viviers (1990). Ten cones of each species were exposed to each temperature in a muffle furnace for one minute. The seeds were then removed from their cones, and 20 were picked at random out a bag and placed in 20 ml of pure water. Conductivity was then measured at 5 minute intervals for 20 minutes and the mean conductivity for twenty seeds per five minute interval was calculated. The basis for using this as a measure of seed viability is that once the membrane of a seed is damaged, in this case through heat, solutes will leak across it and dissolve into the water, and subsequently serve to increase the conductivity (Simons 1974). The rates of leakage were compared between the two species at the various temperatures. Seeds were then placed in petri-dishes and placed in a germination chamber, at 20° C, for 16 hours of light, and at 10° C for 8 hours of darkness. At the time of submission these germination results were not available.

RESULTS

Are there patterns of segregation among *Protea* species?

Table 1 shows that *L. laureolum* and *L. xanthoconus* are found co-occurring significantly less frequently than expected. Patterns of co-occurrence of *P. coronata* and *P. lepidocarpodendron* appear to be random, as no significant differences between the observed and the expected. There were too few occurrences of *P. coronata* though to place much reliability on the results. At a contrageneric level mixed populations are more likely to be encountered than expected, with both genera growing together significantly more often than expected (see table 1).

Table 1 Observed versus expected community composition calculated according to Laurie and Mustart (1992) of *L. xanthoconus* and *L. laureolum,* and *P. coronata* and *P. lepidocarpodendron* for sites across the Cape Peninsula.(NS = not significant)

Community composition	Observed	Expected
Leucadendrons		
L. laureolum alone	50	36.2
L. xanthoconus alone	83	69.2
both species together	2	13.8
neither species present	165	180.8
3 degrees of freedom, $x^2 = 77.7$, $p < 0.001$		
Proteas		
P. coronata alone	6	5.1
P. lepidocarpodendron alone	45	44.1
both species together	2	0.9
neither species present	247	249.9
3 degrees of freedom, $x^2 = 0.79$, $p > 0.1$, NS		
Proteas and Leucadendrons		
Leucadendron only	114	104.5
Protea only	25	15.5
both genera together	142	9.5
neither present	19	170.5
3 degrees of freedom, $x^2 = 1336$, $p < 0.0001$		

At the Constantiaberg site where only *P. coronata* and *P. lepidocarpodendron* were analysed, distribution patterns were not found to be significantly different to that of a random distribution (see table 2). In this case no patterns of segregation are evident.

Table 2 Observed versus expected number of sites with the possible community combinations of *P. coronata* and *P. lepidocarpodendron* at Constantiaberg. (NS = not significant)

Community composition	Observed	Expected
P. lepidocarpodendron alone	9	10.1
P. coronata alone	17	18.1
both species together	6	4.9
neither species	38	36.9
3 degrees of freedom, $\chi^2 = 0.42$, $p > 0.1$, NS		

The relationship between the percentage cover of each species at a site, unlike the presence absence data, shows a strong relationship of avoidance. Given a dense enough cover of *P. lepidocarpodendron*, *P. coronata* is absent (see fig 3).

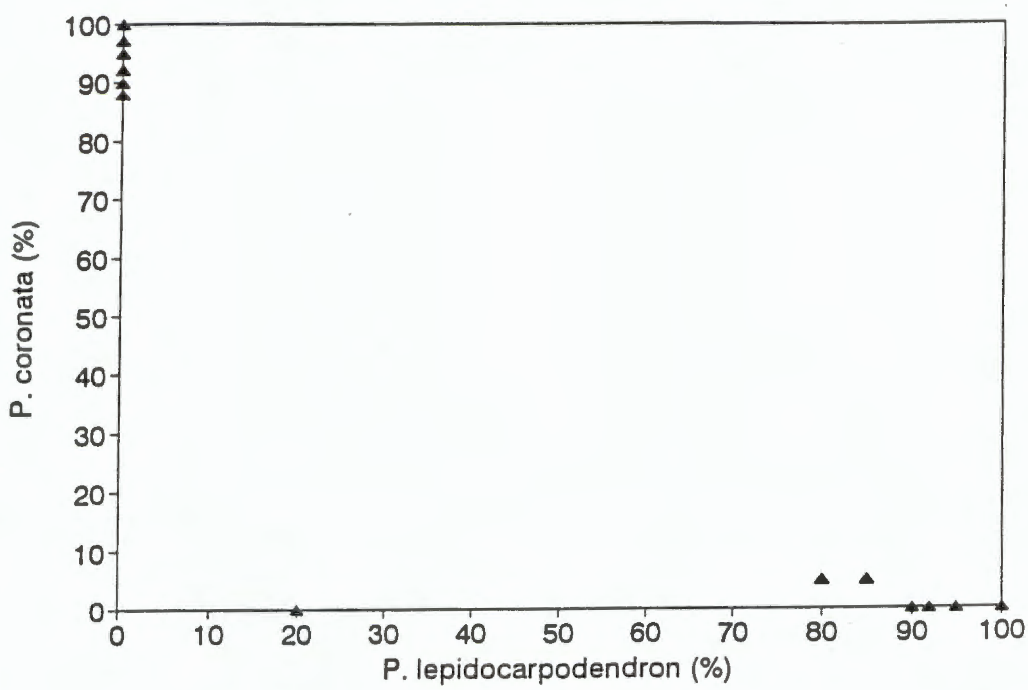


Fig 3 The relationship between percentage cover of *P. lepidocarpodendron* and *P. coronata*, each contributes to the total proteoid cover in 4 x 4 m plots at the Constantiaberg site (n = 15).

Is there evidence for competition among these *Protea* species?

Testing for competition using plot-based averaging.

For both *Protea* species, observed cone production per plant is reduced at higher intraspecific densities. Figs 4 & 5 indicate the results of the non-linear regression for the intraspecific competitive impacts (equation b, the solid line). Density effects in both species follows the same trend, intraspecific impacts apparently accounting for a large portion of variance in cone production. The addition of interspecific effects to the regression (equation a, indicated by the open squares, see figs 4 & 5), fails to account for residual variation. In both cases there is evidence of intraspecific competition, but no interspecific competition. These results are evident in table 3 in the low alpha (α) calculated for interspecific effects, where an $\alpha = 1$ would indicated these two species to be trophic equivalents, and $\alpha = 0$ would indicated total niche separation. According to this analysis, these two species appear to occupy separate niches!

Table 3 Non-linear estimation results for intraspecific and interspecific interactions between *P. coronata* and *P. lepidocarpodendron* (see equations a & b for explanation of symbols).

Species combination	λ	**b**	α	r^2
Intraspecific: *P. coronata*	324.25	1.26	-	0.78
Intraspecific and interspecific: *P. coronata* with *P. lepidocarpodendron*	226.8	1.16	-0.045	0.75
Intraspecific: *P. lepidocarpodendron*	190.4	0.95	-	0.84
Intraspecific and interspecific: *P. lepidocarpodendron* with *P. coronata*	233.18	0.97	0.06	0.81

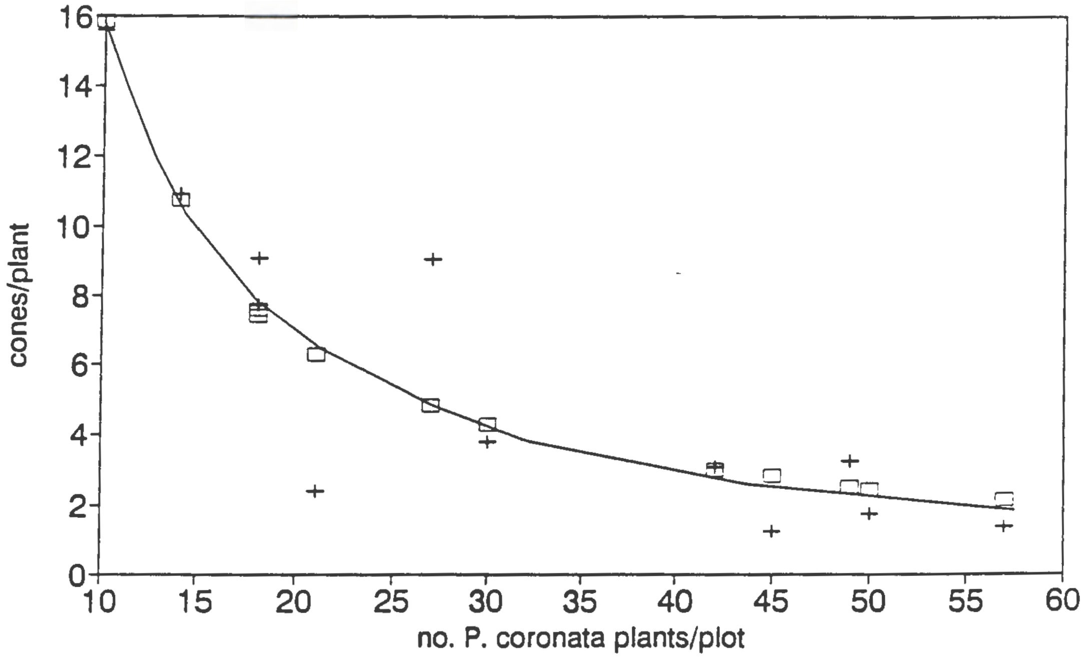


Fig 4 Density impacts on mean cone production per plant for *P. coronata* per 7 x 7m plot in a 10 y stand. Plus sign = observed cones produced, the solid line = predicted cone production with intraspecific effects, and the open square = predicted cone production with intraspecific and interspecific effects included (n = 12).

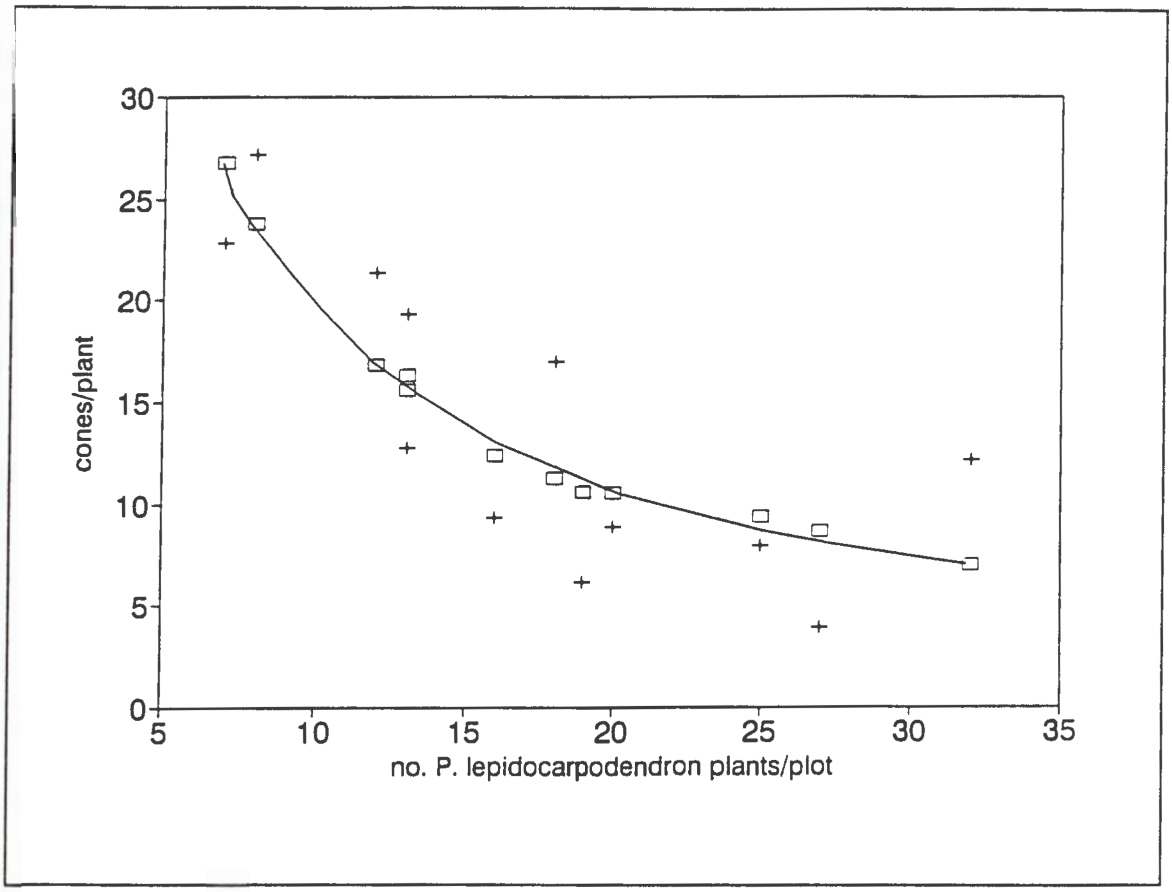
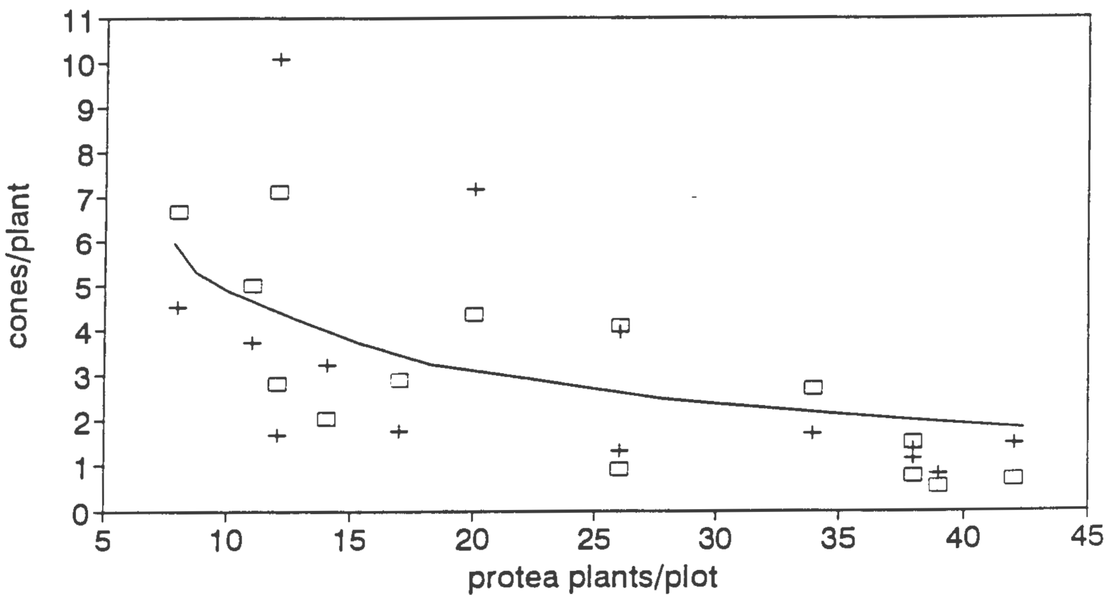


Fig 5 Density impacts on mean cone production per plant for *P. lepidocarpodendron* per 7 x 7m plot in a 10 y stand. Plus sign = observed cones produced, solid line = the predicted cone production with intraspecific effects, and the open square = predicted cone production with intraspecific and interspecific effects included (n = 12).

Figure 6 shows the relationship between stand density and cone production of *P. lepidocarpodendron* mixed with *H. suaveolens*. Intraspecific variation in stand density accounts for most of the variation in *P. lepidocarpodendron* cone production. Table 4 shows the predicted competitive impact of *H. suaveolens* on *P. lepidocarpodednron* is evident, but the calculated alpha low, and interspecific competition does not totally account for the observed trend.

Table 4 Non-linear estimation results for both intraspecific and interspecific interactions between *P. lepidocarpodendron* and *H. suaveolens* (see equations a & b for explanation of symbols).

Species combination	λ	b	α	r^2
Intraspecific: *P. lepidocarpodendron*	27.56	0.718	-	0.9
Intraspecific and interspecific: *P. lepidocarpodendron* with *H. suaveolens*	253048	3.07	0.668	0.58



ig 6 Density impacts on mean cone production per plant for *P. lepidocarpodendron* er 7 x 7m plot. Plus sign = observed cones produced, solid line = the predicted cone roduction with intraspecific effects, and the open square = predicted cone production vith intraspecific and the interspecific effects of *H. suaveolens* (n = 15).

Testing for competition using nearest-neighbour measures

In the 5 y old stand, nearest neighbour measurements show volumes of intraspecific *P. coronata* neighbour combinations to be significantly smaller than both those of free-standing individuals and those with *P. lepidocarpodendron* neighbours (see table 5). For *P. lepidocarpodendron* the volumes of free-standing plants were only marginally significantly larger than those with neighbours. In both species intraspecific neighbour combinations were flowering less frequently than those with interspecific neighbours and free-standing plants. More *P. lepidocarpodendron* plants were flowering than *P. coronata* plants in this young stand (see table 5).

Table 5 Measures of various nearest neighbour combinations in the 5 y old stand in the firebreak. (n = 25)

Neighbouring combination	**Mean logged volume** (cm^3)	**Percentage flowering** (%)
Intraspecific: *P. coronata*	0.019*	15
Interspecific: *P. coronata* with *P. lepidocarpodendron*	0.04	25
Free-standing *P. coronata*	0.05	45
ANOVA	$p = 0.0004$	
Intraspecific: *P. lepidocarpodendron*	0.047	25
Interspecific: *P. lepidocarpodendron* with *P. coronata*	0.049	70
Free-standing *P. lepidocarpodendron*	0.054*	80
ANOVA	$p = 0.021$	

* indicates the most significantly different figure from a Least Significant Difference (LSD) post hoc comparison.

In the 10 y old stand, the Kruskal-Wallis analysis of variance test showed both the heights and cones produced per plant to be significantly different between the three neighbour combinations (see table 6). Post hoc comparisons (LSD) showed nearest neighbour measurements from free-standing *P. coronata* plants to be the most significantly different, especially in relation to those plants with intraspecific neighbours. In the case of basal trunk diameter post hoc comparisons (LSD) also indicate some difference between free-standing plants and those with *P. lepidocarpodendron* neighbours, the greatest differences were between plants with intraspecific neighbours and free-standing individuals. Plants with intraspecific neighbours suffer the greatest competitive impacts, particularly in terms of reduced cone production (see table 6). This marked difference in cone production is demonstrated in figure 7, where the majority of those individuals with intraspecific neighbours, have less than 20 cones (see fig 7).

Table 6 Measures of nearest neighbour interactions in the 10 y old stand. (n = 25, M = mean, Md = median)

Neighbour combinations	**Height (m)**		**Base diameter (cm)**		**Cones / plant**	
	M	Md	M	Md	M	Md
Intraspecific: *P. coronata*	1.27	1.3	3.13	3	5.6	5
Interspecific: *P. coronata* with *P. lepidocarpodendron*	1.4	1.5	3.76	3.5	7.9	6
Free-standing *P. coronata*	1.48^{*}	1.4	4.96^{*}	5	14.3^{*}	13
Kruskal-Wallis ANOVA	$p = 0.009$		$p = 0.07$		$p = 0.004$	

*indicates the most significantly different figure from a post hoc comparison (LSD). df = 1

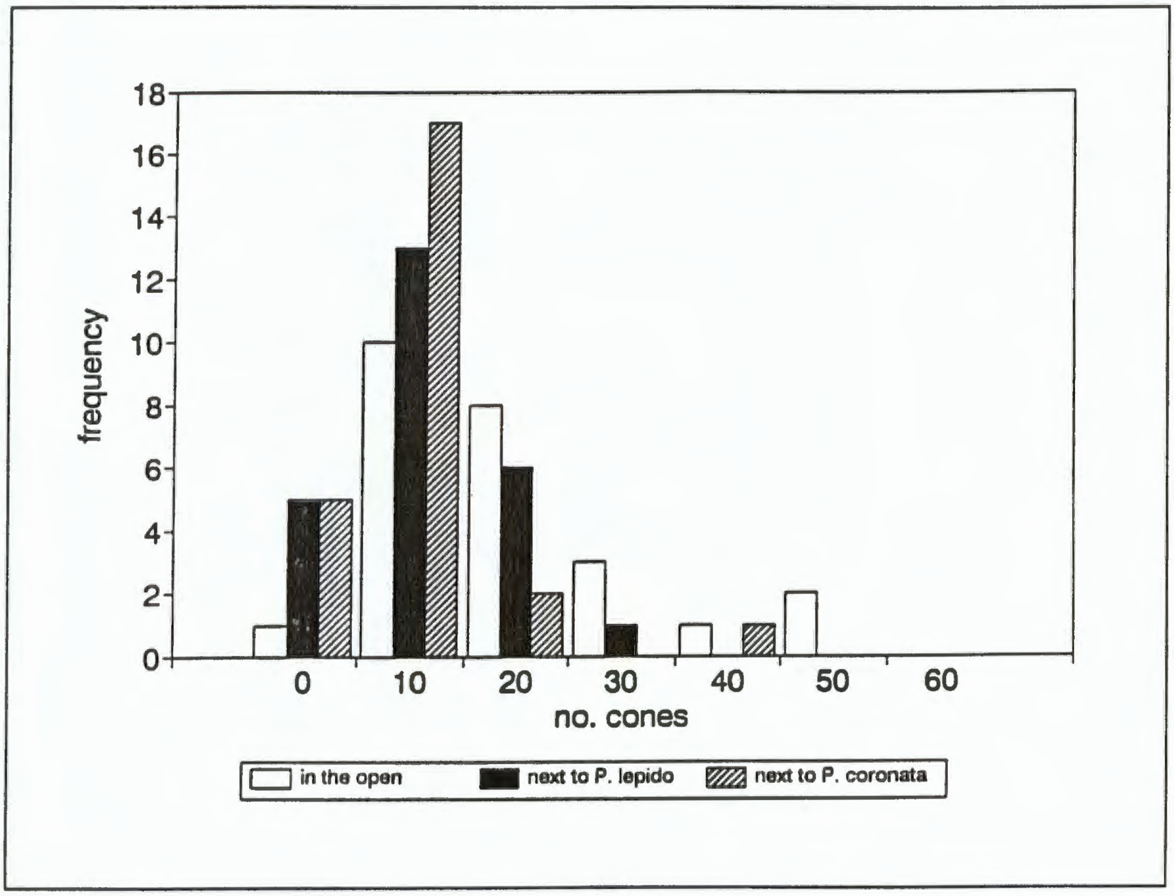


Fig 7 Frequency distribution of the number of cones produced per plant for *P. coronata* with different neighbouring combinations in the 10 y stand.

In the 15 y old stand, the Kruskal-Wallis analysis of variance test shows all three nearest neighbour measures, that of cone production, height and basal trunk diameter, to be highly significantly different (see table 7). Post hoc comparisons (LSD) indicate free-standing individuals to be significantly different in both cone production and height to those of individuals with neighbours. Basal diameter is smallest in those with *P. lepidocarpodendron* neighbours, this figure differing significantly to both free-standing plants and those with intraspecific neighbours. In both the 10 y old and 15 y old stands free-standing plants are considerably larger, and have greater reproductive output than those with neighbours (see table 7). The greatest impacts are of an intraspecific nature, particularly on cone production, taken as a measure of fecundity. In the oldest stand, there is evidence for interspecifc impacts, some *P. coronata* plants with *P. lepidocarpodendron* neighbours, were smaller than those with intraspecific or no neighbours. Variation in cone production is shown in figure 7, where, as in the 10 y old stand, the majority of those individuals with intraspecific neighbours have less than 20 cones. In this age group this pattern is more extreme (see fig 8).

Table 7 Measures of nearest neighbour interactions in a 15 y old stand. (n = 25, M = mean, Md = median)

Neighbour combinations	**Height** (m)		**Base diameter** (cm)		**Cones / plant**	
	M	Md	M	Md	M	Md
Intraspecific: *P. coronata*	2.17	2.1	5.03	4	4.52	3.5
Interspecific: *P. coronata* with *P. lepidocarpodendron*	2.18	2.1	2.62^*	2	4.45	2
Free-standing *P. coronata*	2.7^*	2.7	4.66	4.5	26.0^*	20
Kruskal-Wallis ANOVA	*p* =0.0001		*p* = 0.009		*p* = 0.000	

*indicates the most significantly different figure from a post hoc (LSD) comparison. df = 1

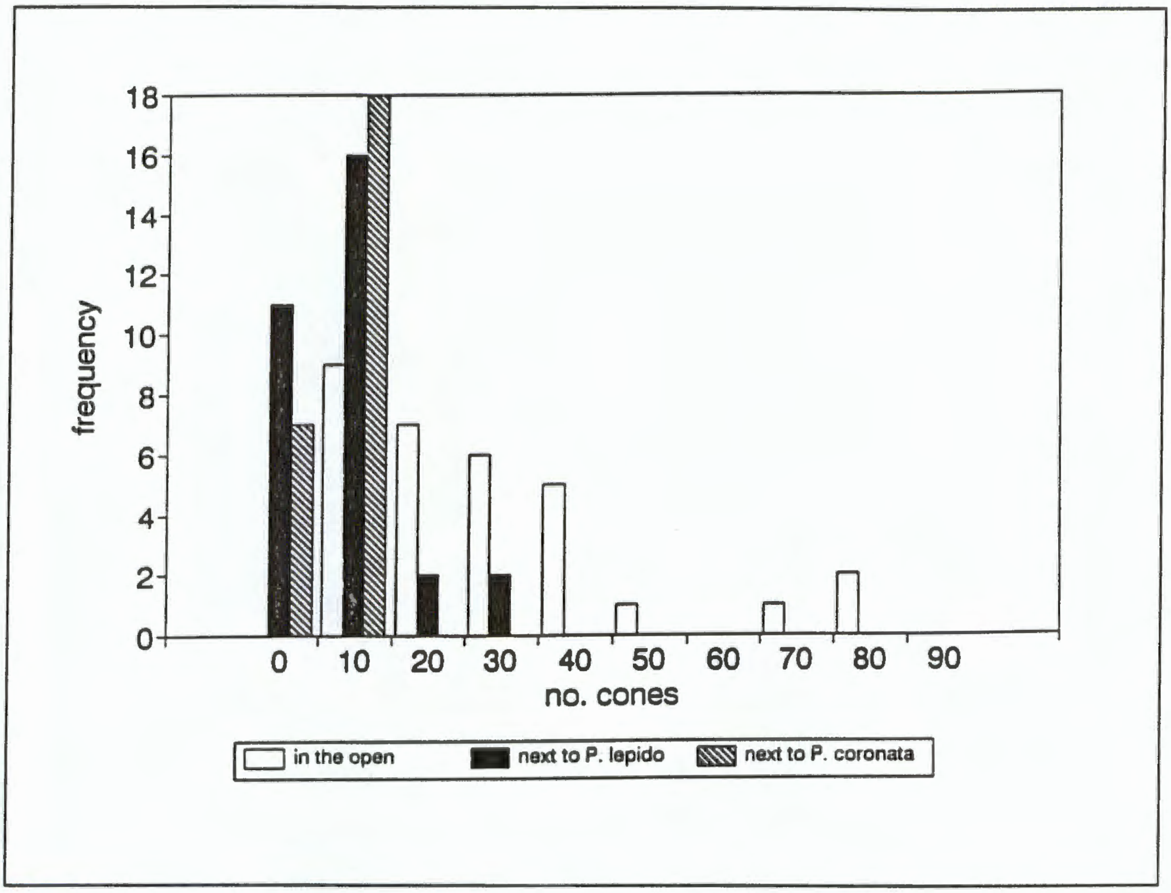


Fig 8 Frequency distribution of cones per plant for *P. coronata* plants with different neighbours in the 15 y old stand.

Cone production increased with plant size (based on basal trunk diameter) in *P. coronata* plants. The relationship between cone production and plant size was very similar in non-neighboured plants and plants with *P. lepidocarpodendron* neighbours (fig 9). However, plants with intraspecific neighbours showed markedly reduced cone production for larger plants sizes (fig 10). The same patterns were demonstrated in the intermediate aged stand.

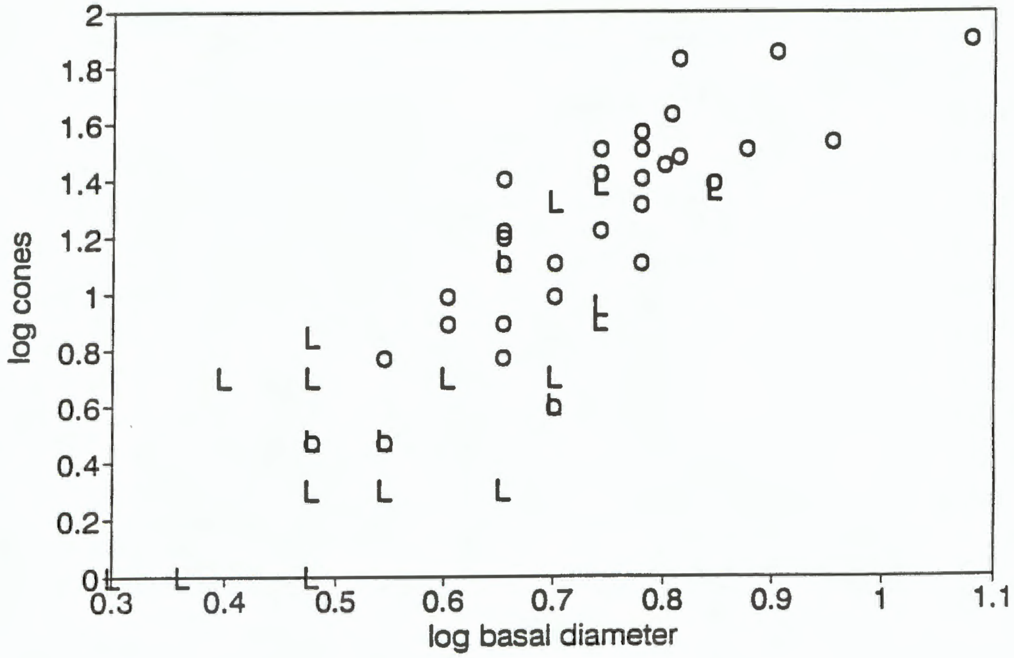


Fig 9 The relationship between basal trunk diameter and cone production for *P. coronata* plants with *P. lepidocarpodendron* neighbours and those without neighbours (L = *P. lepidocarpodendron* neighbours, O = those in the open without neighbours).

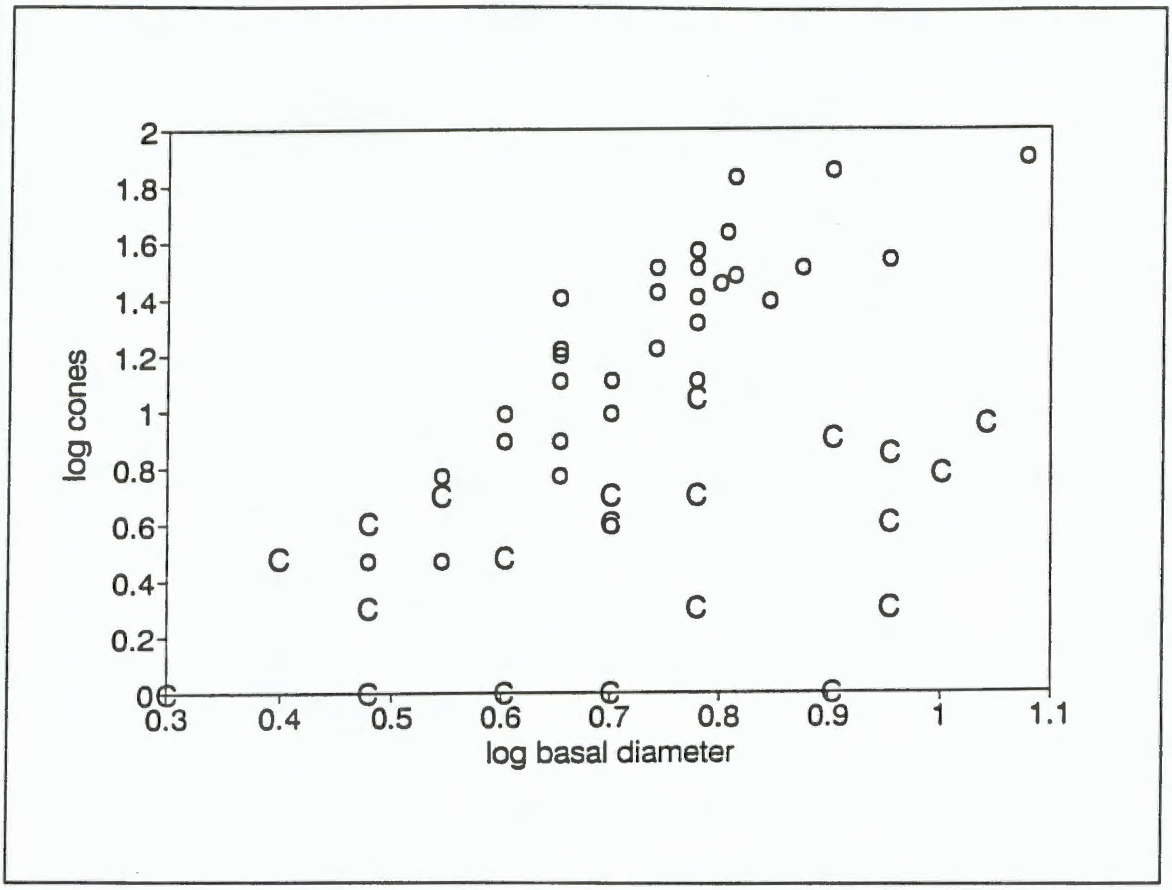


Fig 10 The relationship between basal trunk diameter and cone production for *P. coronata* plants with *P. coronata* neighbours and those without neighbours (C = *P. coronata* neighbours, O = those in the open without neighbours)

At what stage are competitive effects evident?

In this study no absolute answer could be obtained as to when these competitive interactions take place. The fact that the same patterns, or strong intraspecific and weak interspecific competition, are evident in both the 10 y old and 15 y old stands, implies the interspecific competitive interactions take place in the first 10 years.

Are juvenile plants segregated at a micro-spatial scale?

A sample of neighbour combinations in the 5 y old stand showed no particular patterns of aggregation as differing from the expected (table 8).

Table 8 Expected and observed frequencies of interspecific versus intraspecific neighbours in the 5 y old stand (n = 106).

Species composition	Expected	Observed
P. coronata	17	12
P. lepidocarpodendron	39	37
both species together	25	30
neither species present	25	27
3 degrees freedom, $x^2 = 0.434$, $p > 0.1$, NS		

Do these species occur on different soil types?

Of all the sites observed, only *P. coronata* occurred on loamy type soils. This species was found in sites on all the different soil types, though most commonly on yellow coloured soils (see fig 11). *P. lepidocarpodendron,* also found on yellow coloured soil, was most commonly found on soils with an E-horizon. No clear pattern relating to soil colour is apparent. Both species were found growing in both the soil depths, neither species showing a preference for shallower or deeper soil (see fig 12).

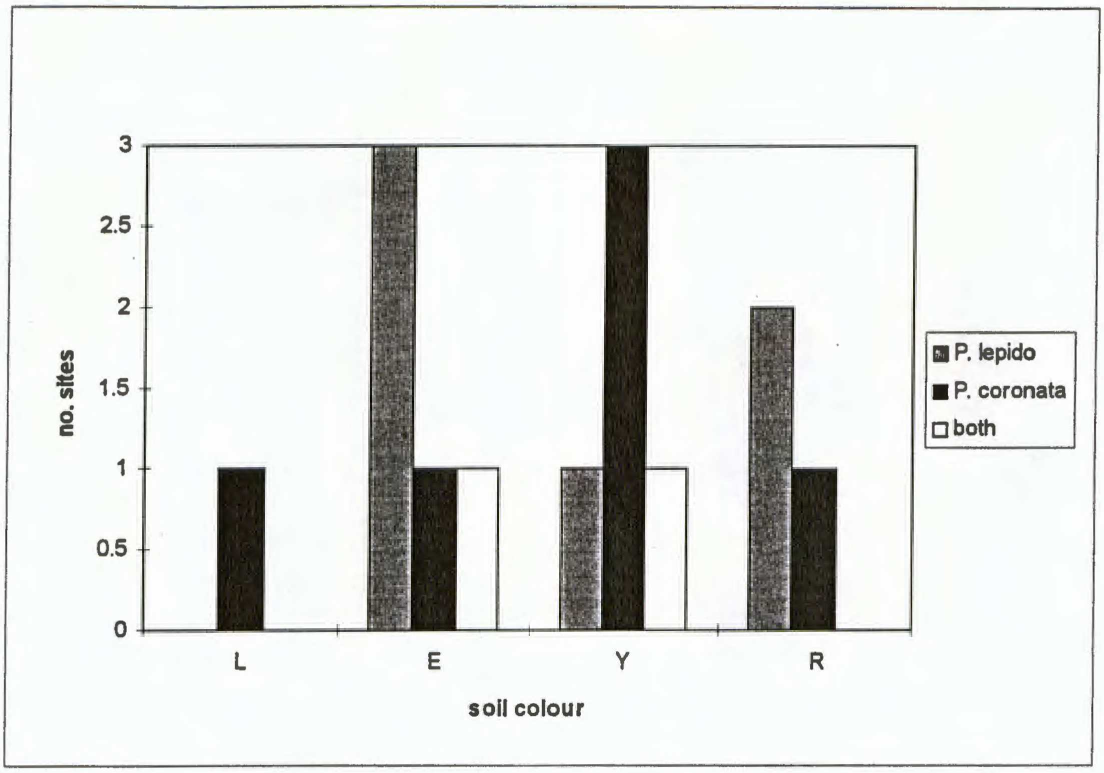


Fig 11 Frequency of sites of different community composition on varying soil colour. L = loamy soil, E = soil with an E-horizon, Y = yellow soil, R = red coloured soil. (n = 14)

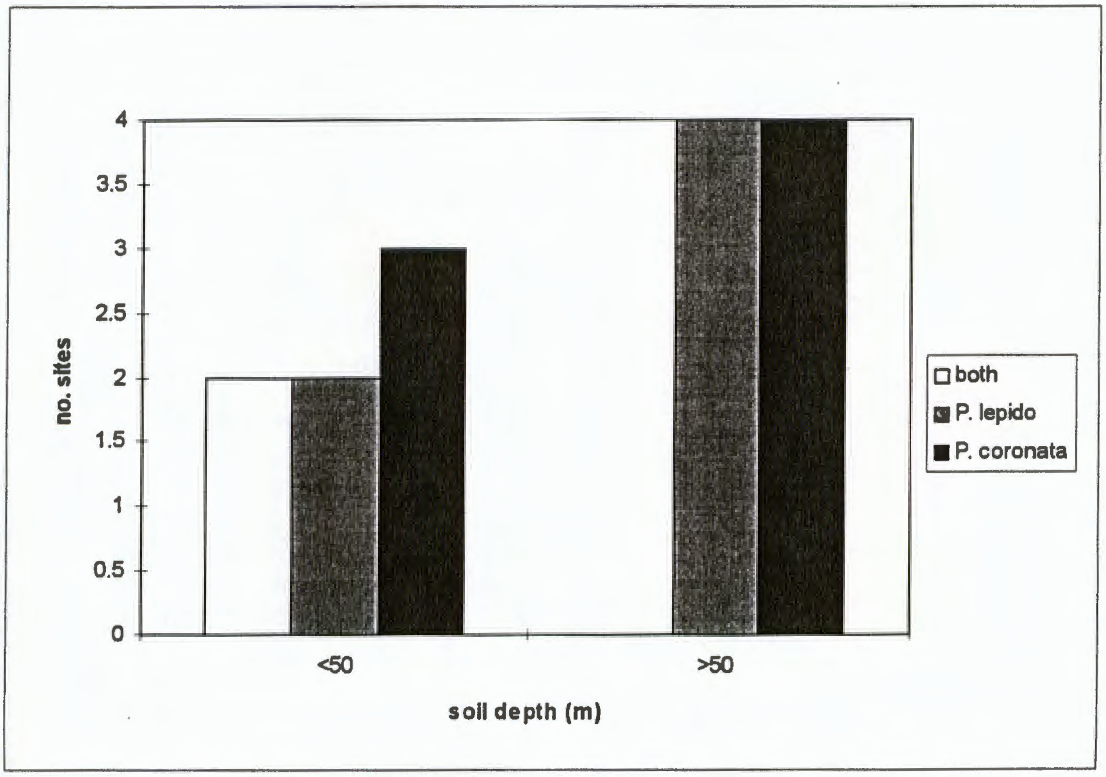


Fig 12 Frequency of sites of variable community compositions on different soil depths.

Do these species have different fire responses?

No certain knowledge of the fire frequency, or season of burn of the area could be obtained from the SAFCOL forestry records, except for the firebreak, which had been burnt five years prior to the study, and previously on a nine year rotation (Zeeman pers. comm.). The age of the fire break could not be ascertained, and unintentional fires may mean that the fire break was not strictly burnt on the stipulated nine year rotation.

A graph of the different cone production at each age group for each species shows that *P. lepidocarpodendron* produces considerably more cones with time than *P. coronata.* At no age in this study was *P. coronata* found to produce more cones per plant than *P. lepidocarpodendron* (see fig 13). This is reflected in mean parent to young plant ratios (with standard deviation in brackets) counted in the firebreak where a *P. coronata* adult produced 8.6 (±17.22) young, while a *P. lepidocarpodendron* adult produced 13.2 (±24.43) young.

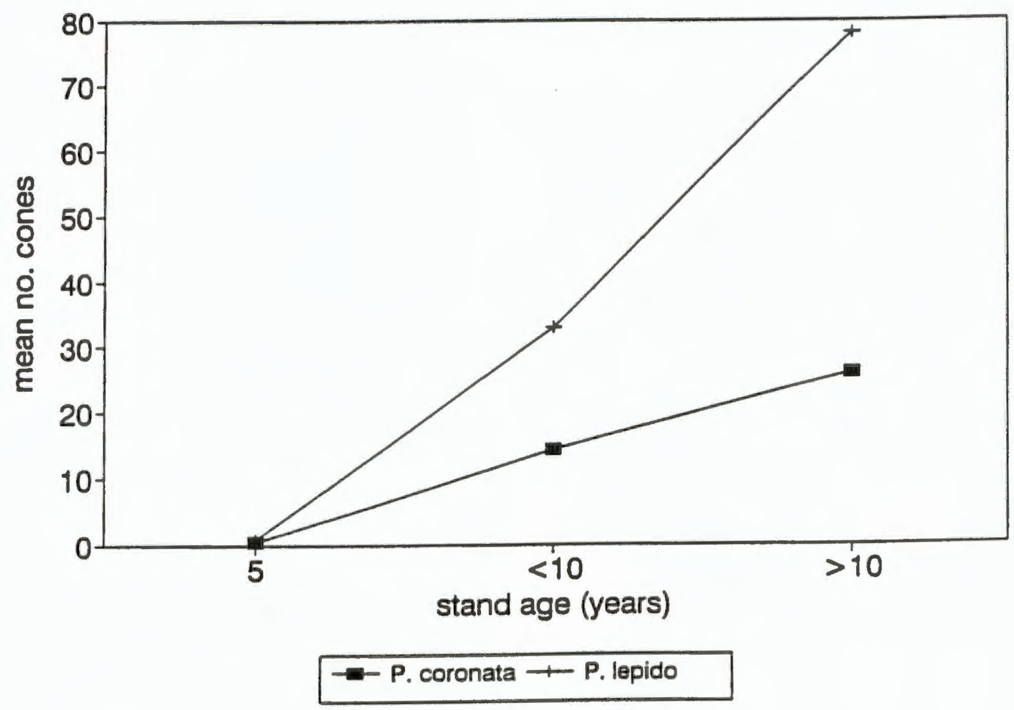


Fig 13 Mean cone production per plant for *P. lepidocarpodendron* and *P. coronata* in the three age classes studied.

No differences were found in seed viability responses to heating up to 700°C, in either species (table 9). At 800°C, which is the highest recorded temperature for a fynbos fire (Midgley & Watson 1992) *P. coronata* showed an increase in membrane leakage.

Table 9 Mean conductivity (µSm^{-2}) of solution from seed membranes over five minute intervals per twenty seeds, for seeds of *P. coronata* and *P. lepidocarpodendron* treated at different heat intensities.

Temperature of treatment (°C)	***P. lepidocarpodendron* seed leakage (µSm^{-2})**	***P. coronata* seed leakage (µSm^{-2})**
	Mean (SD)	Mean (SD)
0	5.12 (±2.8)	5 (±4.1)
100	3.66 (±2.4)	5.15 (±3.7)
200	4.88 (±4.8)	2.48 (±1.6)
300	3.35 (±2.4)	4.75 (±2.6)
400	3.1 (±0.9)	4.05 (±2.7)
500	2.23 (±1.7)	5.28 (±3.6)
600	4.08 (±1.8)	3.45 (±3.0)
700	3.4 (±2.2)	5.6 (±4.9)
800	4.28 (±2.0)	11.35 (±4.4)

DISCUSSION

Are there patterns of segregation among *Protea* species?

The distributions of the two genera in relation to each other, and that of Leucadendron to itself, demonstrate non-random patterns of proteoid segregation across the Cape Peninsula (Laurie & Mustart 1992) (see table 1). From these findings there appear to be some assembly rules determining the patterns of distribution among these Proteaceae (Bond & van Wilgen 1996). This distribution anomaly points to the validity of studying the effects of interspecific interactions among proteoid species. The sparse occurrence of *P. coronata* in this study reduces the validity of the findings for the two *Protea* species across the Cape Peninsula (see table 2).

At the Constantiaberg study site the "checkerboard" distribution of *P. lepidocarpodendron* and *P. coronata* indicates some possible interaction. This distribution pattern is not observed in the presence and absence study, where distributions appear to be random (see table 2). The "checkerboard" pattern is very much apparent in the correlation between the percent cover of each species (see fig 3). It would appear that the scale of the 4 x 4 m plots used in the presence absence study, is coarse, and that percent cover gives a better reflection of the pattern at the site, which is one predominantly of segregation. This is in agreement with Cody's (1986) original suggestion that distribution patterns among the Proteaceae are a function of the relative abundances of various species. One striking aspect of this distribution was a pure stand of *P. coronata* east of the fire break, and a near pure stand of *P. lepidocarpodendron* to the west of the firebreak, while in the firebreak itself mixed stands of both *P. coronata* and *P. lepidocarpodendron* occurred (see fig 2). Visible at the study site is a pattern of conspecific avoidance, despite an apparent shared fundamental niche (Begon *et al.* 1990). This project investigates interspecific competition as a possible cause for these patterns.

Is there evidence for competition among these *Protea* species?

Testing for competition using the plot-based averaging.

In the first attempt at locating competition, plot-based averaging was used, and showed strong intraspecific competition. The addition of the second species in the non-linear regression (see equation b) failed to demonstrate any interspecific interactions (see figs 4 & 5, table 3), suggesting instead almost complete niche separation! This is in complete contradiction to previous studies of proteas, and to suggestions that proteas are trophic equivalents (Shmida & Ellner 1984; Bond *et al.* 1992). Indeed the assumption of trophic equivalence, underlies recent attempts to use lottery models to explain *Protea* coexistence (Laurie & Cowling 1994). These findings are also in discordance with the notion that competition may account for the segregated distribution patterns of these two species at the site.

When testing this plot-based method in a stand of invasive *H. suaveolens* growing with *P. lepidocarpodendron* at Millers Point (see fig 1), only weak interspecific competitive interactions were evident (see table 4). The degree of interaction is far less intense than expected, given the reputation of *H. suaveolens* as a problematic invasive (Richardson *et al.* 1992). Once again, strong intraspecific interactions were evident among the *P. lepidocarpodendron* individuals (see fig 6). These findings, of no apparent interaction among the species, at both sites, is startling and unexpected.

Observations at the Miller's Point site showed that the surviving *Protea* plants are growing in the spaces between the *Hakea* plants, with very few plants beneath the hakeas. Apparently those that establish beneath hakeas do not survive. These observations in the mixed stand of *P. lepidocarpodendron* and *H. suaveolens*, in a case of known competition, suggest that in this case the competitive struggle is over, and the stand has been altered spatially as a result of interspecific competition. Apparently coexistence is merely local avoidance of the stronger competitor, by the weaker. This also explains the relatively strong intraspecific competition, where, as a result of interspecific interactions in the past, conspecific neighbour pairs are more common. Rees *et al.* (1996) reported similar results in their analysis of sand-dune annuals. They too found strong intraspecific, but negligible interspecific competition. They suggested several possible explanations, including micro-scale spatial segregation, due either to dispersal differences, or past competition. Midgley and Watson (1992), in contrast, suggested that strong intraspecific interactions should result in contraspecific neighbour pairs being more common. The apparent coexistence between *H. suaveolens* and *P. lepidocarpodendron*, is most likely temporary. As the *H. suaveolens* individuals grow bigger, the spaces between them, which currently serve as refuges to the *P. lepidocarpodendron* individuals, will close, suppressing the remaining proteas. This may explain the weak competition registered by the plot-based averaging method, where this once-off measure at this stage in the life history of the stand, only catches a glimpse of the ghost of competition past (Law & Watkinson 1989). These weak findings in such an obviously strong case of competition encourage us to reassess the analysis of competition between the species at the Constantiaberg site. They also indicate the importance of the proximity and nature of the immediate neighbour.

Testing for competition using nearest neighbour measures.

Examination of the effects of various immediate neighbours on fecundity, confirm the findings of the plot-based averaging approach, where the dominant competitive interactions are among conspecifics (see table 6 & 7, and figs 7 & 8). The results thus far, for both methods, indicate these species to be far from trophic equivalents, but rather totally niche separated. This is evident in the relationship between cone production and basal diameter of free-standing *P. coronata* plants and those with *P. lepidocarpodendron* neighbours, where the slopes of the curves relating to cone production are very similar (see fig 9). Apparently, a *P. lepidocarpodendron* neighbour has as little effect on the cone production of *P. coronata,* as no neighbours at all. This pattern supports the lack of interspecific effects found in the plot-based analysis. It also supports the strong intraspecific competition found in the plot-based averaging method, as those *P. coronata* plants with intraspecific neighbours have reduced fecundity (see fig 10). While these findings are in agreement with Law and Watkinson's (1989) review on competition studies, where they found the majority of studies showed intraspecific competition to be stronger than interspecific competition, they are in discordance with the idea that many fynbos *Protea* species are trophic equivalents (Shmida & Ellner 1986; Bond *et al.* 1992), and should thus be competing heavily. The findings in the study thus far, lead us to believe that these two species readily coexist, even in very dense stands.

However, what is evident from these curves, is that those *P. coronata* individuals with *P. lepidocarpodendron* neighbours are smaller in stature, indicated by a significantly smaller basal diameter (see table 7). Most of the *P. coronata* individuals neighbouring *P. lepidocarpodendron* individuals have been suppressed, except for a few that have broken past the canopy of their *P. lepidocarpodendron* neighbours, and do not suffer reduced fecundity. This suppression has occurred at some earlier stage in the life history of these two species. For a *P. coronata* individual to survive in a mixed stand with *P. lepidocarpodendron,* it must avoid this juvenile suppression. The competitive impact of *P. lepidocarpodendron* appears to be severe. If the *P. lepidocarpodendron* population were to get sufficiently dense, this suppression could lead to the eventual exclusion of *P. coronata.*

Two types of competition are apparent. The first is the interspecific suppression of juveniles, most likely due to competition for light, of which suppression of *P. lepidocarpodendron* by *H. suaveolens,* is an example. The second is the reduction of flower production due to neighbour suppression of branching, caused by intraspecific, but not interspecific neighbours. These findings are in agreement with Kenkel *et al.* (1989), who found in their study of competitive interactions in a naturally established jack pine stand, that the reproductive yield of an individual was influenced more by its immediate neighbour than overall stand density. Since plants interact with their immediate neighbours, the spatial lay out of a community will determine the scope for competitive interactions. There does not appear to be any evidence of micro-scale segregation among the juvenile plants that may account for competitive interactions measured (see table 8).

In this study we were unable to pin point the timing of competitive exclusion by suppression, as the same pattern is evident in both the 10 y old and 15 y old stands. This suppression must take place in the first 10 years of these plant's lives. In the case of the *H. suaveolens* and *P. lepidocarpodendron* interaction, the same impact is evident. In this case the vegetation is younger, and already at 8 years old, the competitive interaction seems largely over (Yeaton & Bond 1991).

The importance of shrub architecture in reducing species interactions.

Studies in the past have shown variable architecture, such as root architecture, to be an important factor in allowing coexistence (Yeaton *et al.* 1977). The results of the nearest neighbour measures show variable shrub architecture to be significant in reducing species interactions. In this case, should a *P. coronata* individual, neighbouring a *P. lepidocarpodendron,* avoid juvenile suppression, it will not suffer reduced fecundity as an adult. With sympodial branching and terminal inflorescence, space is all important to the reproductive performance of these *Protea* species (Bond *et al.* 1995). *P. coronata* (see plate 1) is sparsely branched and can grow past the dense canopy of *P. lepidocarpodendron* (see plate 2). In this case we see intraspecific density effects on reproductive output, where intraspecific crowding of *P. coronata* acts to reduce the fecundity of this species. These findings are similar to those of Yeaton and Bond (1991), who found variable seed dispersal to reduce the competitive interactions between asymmetrically competing fynbos shrubs.

What limits the distribution of P. lepidocarpodendron?

Given the evidence thus far for the competitive dominance of *P. lepidocarpodendron,* it is apparent that *P. coronata* would be rare where *P. lepidocarpodendron* is abundant. The question remains as to why there are stands in this study site where *P. coronata* is abundant, and *P. lepidocarpodendron* rare. In some cases *P. lepidocarpodendron* is totally absent. What restricts *P. lepidocarpodendron* from certain areas? Soil requirements and variable fire responses were investigated as possible factors restricting the distribution of the stronger competitor, *P. lepidocarpodendron.*

In a brief study, no patterns were found relating species composition to soil type or depth (see fig 11 & 12). The geological map also fails to indicate any change in soil type across the study site (see fig 1). The occurrence of pure stands of mature *P.*

coronata immediately adjacent to juvenile *P. lepidocarpodendron* plants in the firebreak, eliminate soil as a factor excluding *P. lepidocarpodendron* from this stand.

Different fire responses may also account for non-overlapping distribution patterns. However, at no stage does *P. coronata* display greater fecundity than *P. lepidocarpodendron* (see fig 13), indicating that short fire intervals would favour *P. lepidocarpodendron.* Longer fire intervals may differentially affect *P. lepidocarpodendron* if it senesces earlier than *P. coronata,* but this could not be tested due to the lack of old stands, or any well recorded fire history for the area.

Esler and Cowling (1990) found season of burn to be the overriding determinant of post fire recruitment in *P. lepidocarpodendron.* While both species flower in winter, variable times to seed maturity may differentially affect recruitment of the two species after different seasons of burn. Once again, the lack of any fire records for the site meant that this could not be tested.

Finally, an experiment looking at variable seed viability in response to different heat intensities failed to show any different responses to fire intensity between the two species (see table 9). Midgley & Viviers (1990), and reported different responses to fire intensity of several Proteaceae. The experiment may not have worked because conductivity was measured on more than one seed at a time (due to restricted facilities at the time of study), so that one seed with a damaged membrane can increase the conductivity measures. The germination trials presently being run on the same seeds should give better results. Until these results are obtained, variable responses to fire intensity cannot be ruled out as a possible factor explaining the absence of *P. lepidocarpodendron* from some areas.

No answer was reached to explain the abundance of *P. lepidocarpodendron* in some sites, and its total absence from others. Given the dramatic contrast in proteoid community composition over the firebreak, some form of variable fire response seems the most likely cause.

CONCLUSION

This study found no apparent competition between non-sprouting *Protea* species measured in terms of fecundity effects. Apparently, variable architectures can serve to reduce species interactions. However there was evidence for suppression of one species by another during the juvenile phase of growth. The study clearly indicates the risk of measuring only the outcome of competition, and not other processes producing neighbourhood patterns. The findings of this study call for a re-assessment of the processes influencing coexistence among *Protea* species, previously put down to lotteries, or competition for light and nutrients.

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