

VARIATION IN THE SEEDLING RECRUITMENT OF LEUCADENDRON LAUREOLUM
AND DIATELLA DIVARICATA SPECIES AFTER FIRE : A MANIFESTATION OF
SPECIES COEXISTENCE.

L. T. GXABA
HONOURS PROJECT
1988

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

ABSTRACT

Some consequences of fire on the recruitment of the Leucadendron laureolum and Diastella divaricata were studied. L. laureolum seedling regeneration showed no consistent relation with parent density while D. divaricata showed a positive correlation. This trend of shifting away from areas or places of earlier domination to previously sparsely populated areas may be due to dispersal of L. laureolum seeds by wind.

L. laureolum and D. divaricata seedlings coexist early in their life history and there is a positive correlation between their relative densities. Competition is either at a low rate or is non-existent at this stage or is less important than environmental stress in the life of the species. The weighted lottery process for establishment sites may also be responsible for the coexistence of the seedlings.

Negative correlations observed between adult densities of the two species are regarded as a result of competition as the overstorey L. laureolum suppresses the understorey D. divaricata. It was concluded that fire is the overriding factor determining regeneration patterns. (Trivial conclusion)

Key words: Seedling recruitment, fire, species coexistence.

Introduction.

Much discussion in the theoretical literature has centred on whether communities can be described either as comprising populations at or near stable equilibrium or in a state of non-equilibrium (Chesson & Case, 1975; Grubb, 1977; Cowling, 1987). Competition is identified as playing a crucial role in the structuring of stable communities (Chesson, 1975) while in non-stable communities it is less important in shaping community structure depending on the disturbance regime and species life histories (Cowling, 1987). Since competitive equilibrium requires that the rates of change of all competitors be zero, and since fluctuations in the physical environment, predation and other factors are constantly changing population sizes (Huston, 1979) and the nature of competitive interactions (Wiens, 1977) it seems likely that competitive equilibrium rarely, if ever, obtains in natural conditions. This is of particular relevance for some of the ^{Fynbos} "Gondwanan shrublands" (Cowling, 1987) of the southwestern Cape, South Africa as an understanding of such interactions would be important for management strategies in the region.

In some communities and under some circumstances, disturbances are critical in the maintenance of coexisting species as they affect the relative abundances of the species present (Denslow, 1985). Plant communities may violate the competitive exclusion principle through a "weighted lottery" process for establishment sites (Cowling, 1987). In the lottery model competition is assumed to be for space which is allocated at random to the juveniles of

the two species (Chesson , 1973). Thus every co-existing species is dominant in establishment under some possible combination of environmental conditions (Cowling, 1987). Since these conditions (or patches) neither persist nor are widespread, this results in a series of transient niches (Cowling, 1987). These enhance co-existence. In nutrient-poor soils, weak competitive effects resulting from slow growth rates will further contribute to the maintenance of high species richness (Cowling, 1987).

Fire is the overriding disturbance in the sclerophyllous shrublands of the southwestern Cape (Kruger, 1979) and the major selective agent (Cowling, 1987). Some species of Cape Proteaceae, including Leucadendron lauroolum, are non-sprouting and retain mature seeds in serotinous cones for several years (Bond, 1985), while others such as Diastella divaricata are myrmecochorous (seed dispersed by ants). ^{reb (Bond & Stingsby)} In both species regeneration occurs after fire. Fire, therefore has profound effects on the survival of the two species, and may determine the structure of the community. Season of fire results in different recruitment patterns and these can affect local species richness, especially when the dominant overstorey disappears (Esler, 1987). In addition, recruitment may vary within a fire depending on local site conditions, seed dispersal, etc.

In this study, variation in recruitment of two proteoids namely: serotinous Leucadendron lauroolum and myrmecochorous Diastella divaricata was investigated. The following hypotheses were tested:

1. Variable recruitment maintains species richness and

coexistence is the result of cycle changes which are brought about by the different seasons of burn. ^{This study was done within a burn}

2. The same fire affects individuals in the same community differently.

The first hypothesis was not tested here!

The hypotheses tested were

- 1.) The same fire will result in differential recruitment of a species, specifically
 - a.) Wind-dispersed species are likely to show variable recruitment and little relationship between parent and seedling numbers
 - b.) Ant-dispersed species are more stable in the numbers of a particular fire

Study area.

The study area was located in the south-western portion of the Cape of Good Hope nature Reserve (34°15'S 18°25'E) known as Olifantsbosch. The study site was located in a topographically similar area which consists of level or gently inclined sandstone beds of the Table Mountain Group of the Cape Supergroup. The Table Mountain Group consists mainly of a hard, resistant quartzite sandstone which is white or pale grey in colour when freshly fractured (Taylor, 1984).

The climate of the area possesses the equable Mediterranean type climate characteristic of the western margin of continents in comparable latitudes. Seasonal variation in temperature is small with average summer and winter temperatures of 18.3°C and 13.4°C respectively. Annual rainfall averages 355 mm per year. Wind plays a prominent role in moulding the climate of the area. The summer southeasters blow for longer periods than the winter northwesterly - up to a week or more blowing at 15 - 40 km per hour (Taylor, 1984).

The study site was last burnt in December, 1984 and at the time of sampling the main vegetative ^{type} cover was a Restionaceous Tussock Marsh (Taylor, 1984) with many ericoid shrubs as L. laureolum and D. divaricata were at the seedling stage, with heights of about 15 cm.

Methods.

Field work was conducted during the period April to June 1988. Random numbers tables were used to locate 60 sample plots measuring 10 x 10 m each. In each plot pre-burn parent densities of both species were determined by counting burnt stems. No special count of stems burnt to the ground was taken since it was assumed that post-fire stem counts are equal to pre-burn densities of live shrubs (Bond et al., 1983). The number of live and dead seedlings for both species was recorded for each plot to determine seedling mortality for each species.

Total vegetative cover of each plot was estimated and then classified into monocots and dicots to which percentage cover values were assigned. *Why was this done - effect of soil drainage with monocots (restioids) indicating waterlogged conditions*
Soil depth was determined by randomly digging in four areas within each plot. This was done in order to determine whether there was any relationship between soil depth and the occurrence of the two species in the study site. *+ seedling mortality*
Percentage rock cover was also recorded where it occurred as it would affect seedling establishment through the lack of soil.

NO! These variables were measured to see if there was any relationship between them and Statistical analysis. Parent and seedling densities

For each species the number of dead seedlings per plot was first expressed as a percentage of total seedlings and then correlated with soil depth using regression analysis. This was done in order to determine whether soil depth had any effect in the seedling establishment of the two species.

→ Explain the significance of
this measure

Seedling per parent ratios were worked out and then correlated first with monocot cover and then with soil depth. Regression analyses were also done to determine the relationship between parents and seedlings for each species and between seedlings of both species and between parents of the two species together.

Essentially a correlation analysis
Why not try Spearman's Rank
test as suggested?

There should be a table giving:

	No parents	No seedlings	% dead seedlings	Total parent	Total seedlings
<u>L. laureolum</u>	$\bar{x} \pm$	$\bar{x} \pm$	$\bar{x} \pm$		
<u>D. divaricata</u>					

Results.

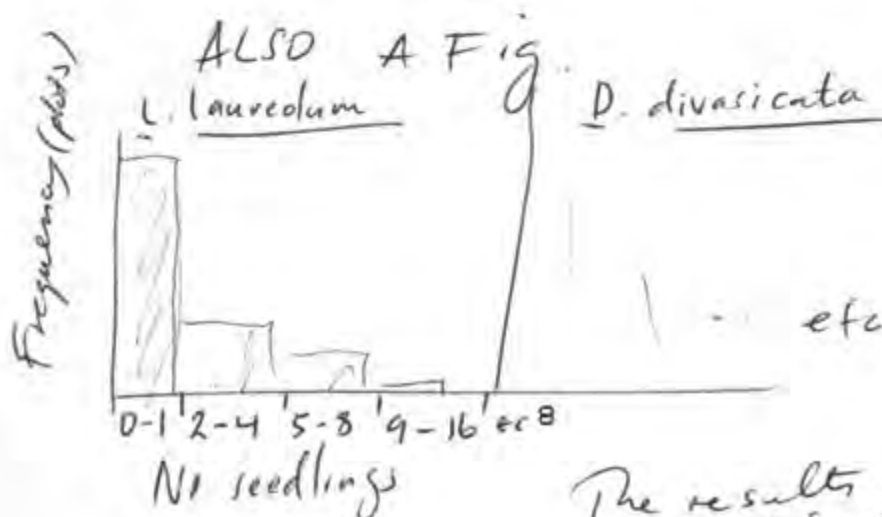
The number of dead L. laureolum seedlings was negatively correlated with soil depth and this was significant at ($p < 0.05$) (Fig 1) while there was no relationship between D. divaricata seedlings and soil depth (Fig 2).

No significant relationship was found between L. laureolum seedlings per plant and monocot cover ($p < 0.05$), while there was a significant correlation ($p < 0.05$) between D. divaricata seedlings per plant and monocot cover (Figs 3 & 4)

respectively. Results showed a negative correlation between seedlings per parent and soil depth for L. laureolum. This relationship was not significant, while a significantly negative ($p < 0.05$) was shown for D. divaricata (Figs 5 & 6) respectively.

For L. laurifolium results showed no relationship between seedling and parent densities (Fig 7) while for D. divaricata the number of seedlings was significantly correlated with parent densities ($p < 0.05$) (Fig 8).

There was a positive correlation between seedling numbers of the two species, while those of the parents were negatively correlated.



The results have been presented in an order which does not reflect their importance and relevance to the hypothesis

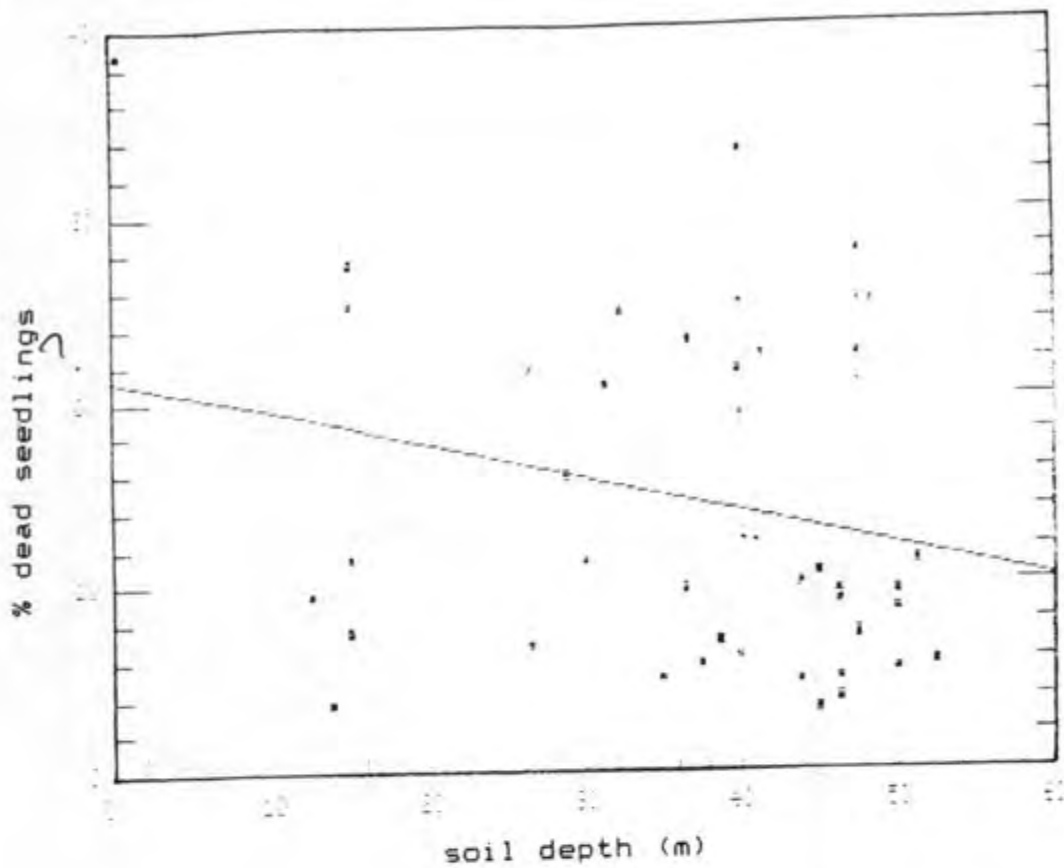


Fig 1. Relationship between soil depth and percentage dead L. laureolum seedlings.

$$r = -0.25 \quad r^2 = 6.54 \% \quad p < 0.05$$

Cannot make out the legend

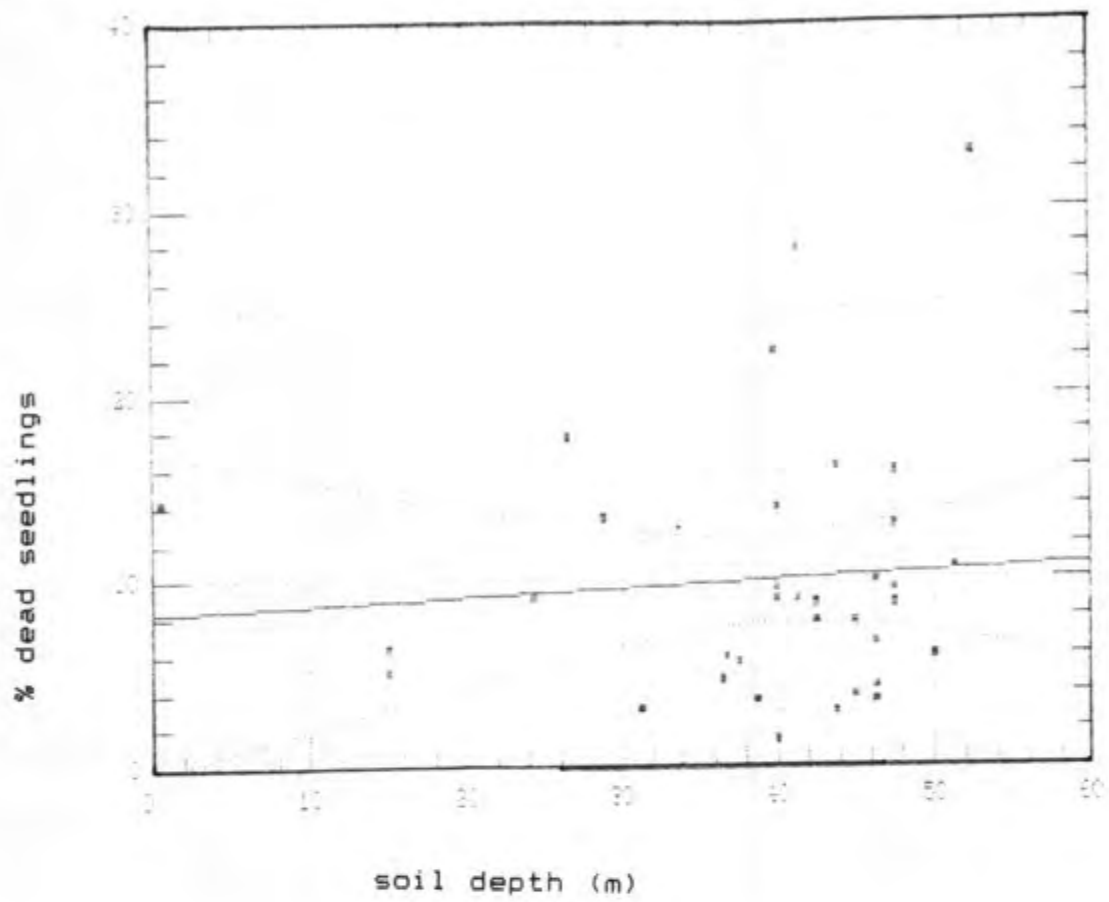


Fig 2. Relationship between soil depth and percentage dead D. divaricata seedlings.

$$r = 0.07$$

$$r^2 = 0.49 \%$$

N S

seedling : parent ratio

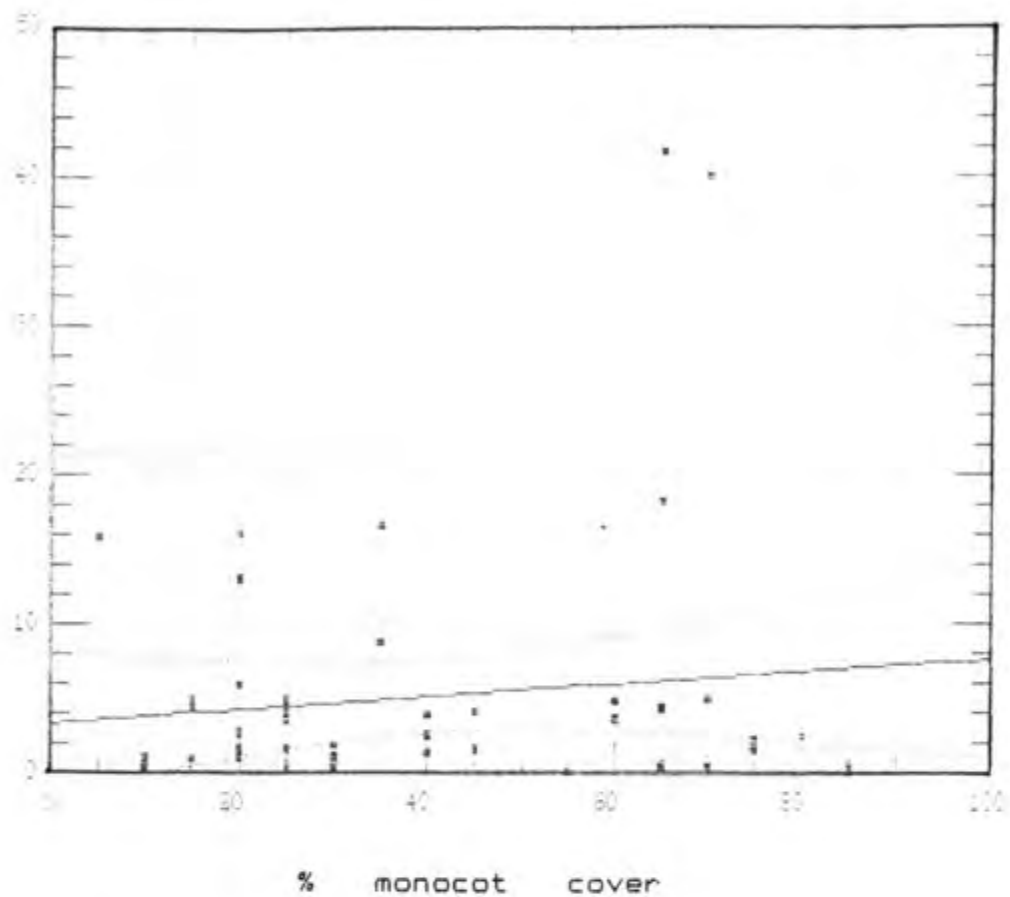


Fig 3. Relationship between monocot cover and seedling per parent ratio of L.laureolum.

$$r = 0.11$$

$$r^2 = 1.42 \%$$

N S

It is not necessary to present all these graphs!

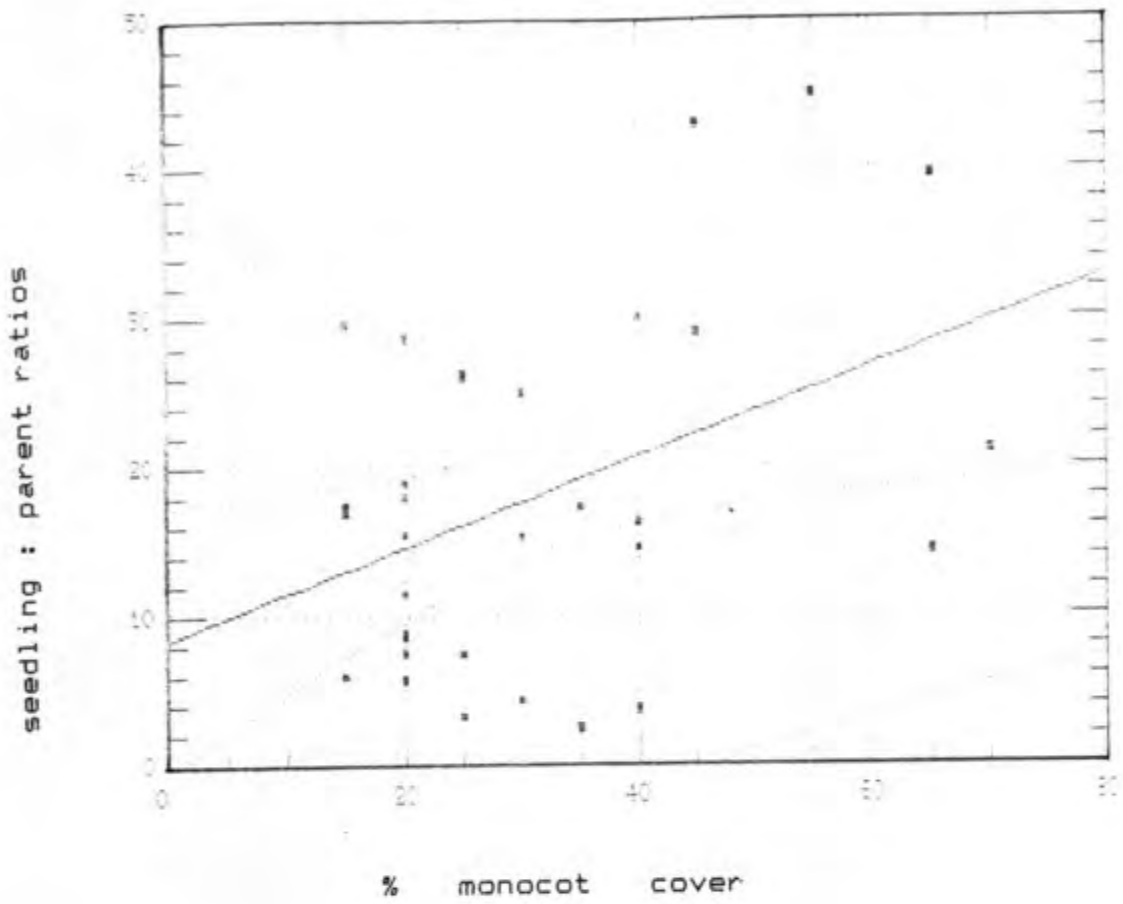


Fig 4. Relationship between monocot cover and seedling per parent ratios of D. divaricata.

$r = 0.40$ $r^2 = 16.66 \%$ $P < 0.05$

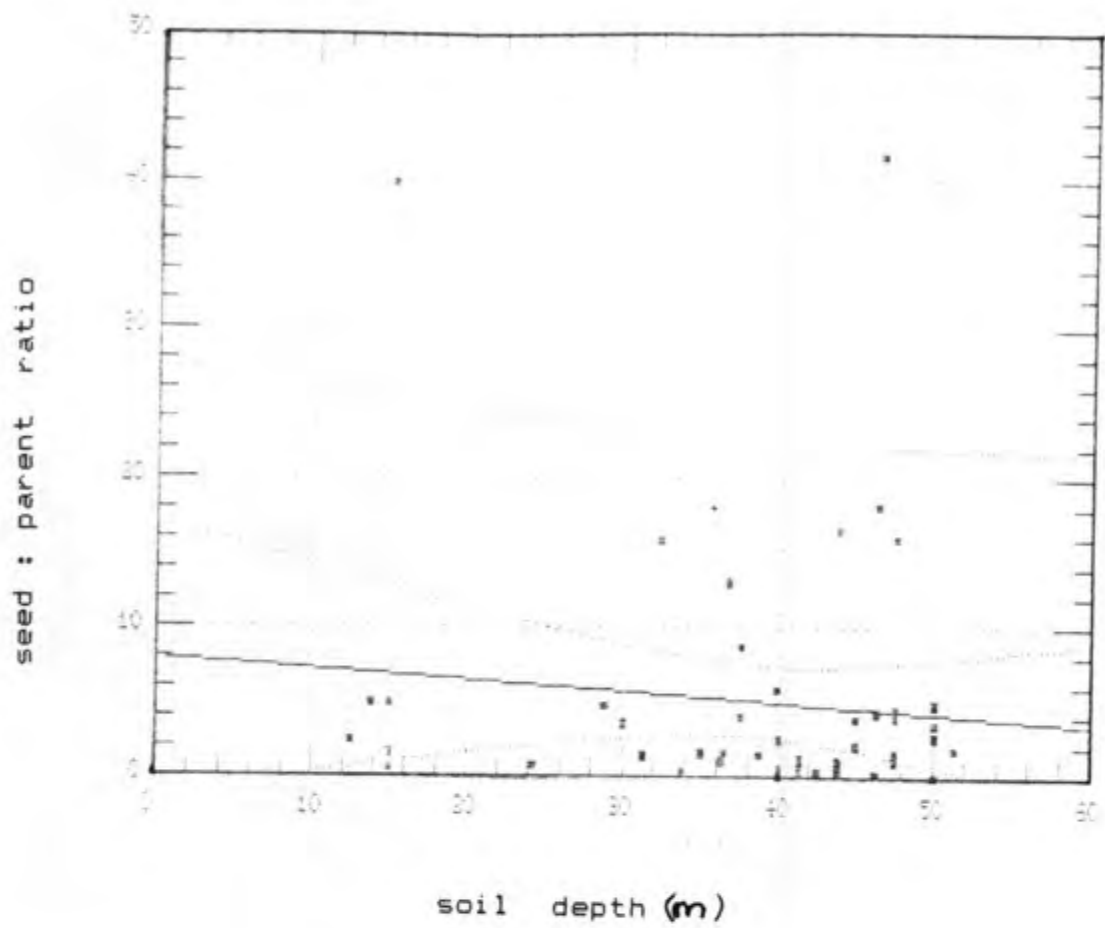


Fig 5. Relationship between soil depth and seedling per parent ratios of L. laureolum.

$r = -0.09$ $r^2 = 0.90 \%$ N S

seed : parent ratio

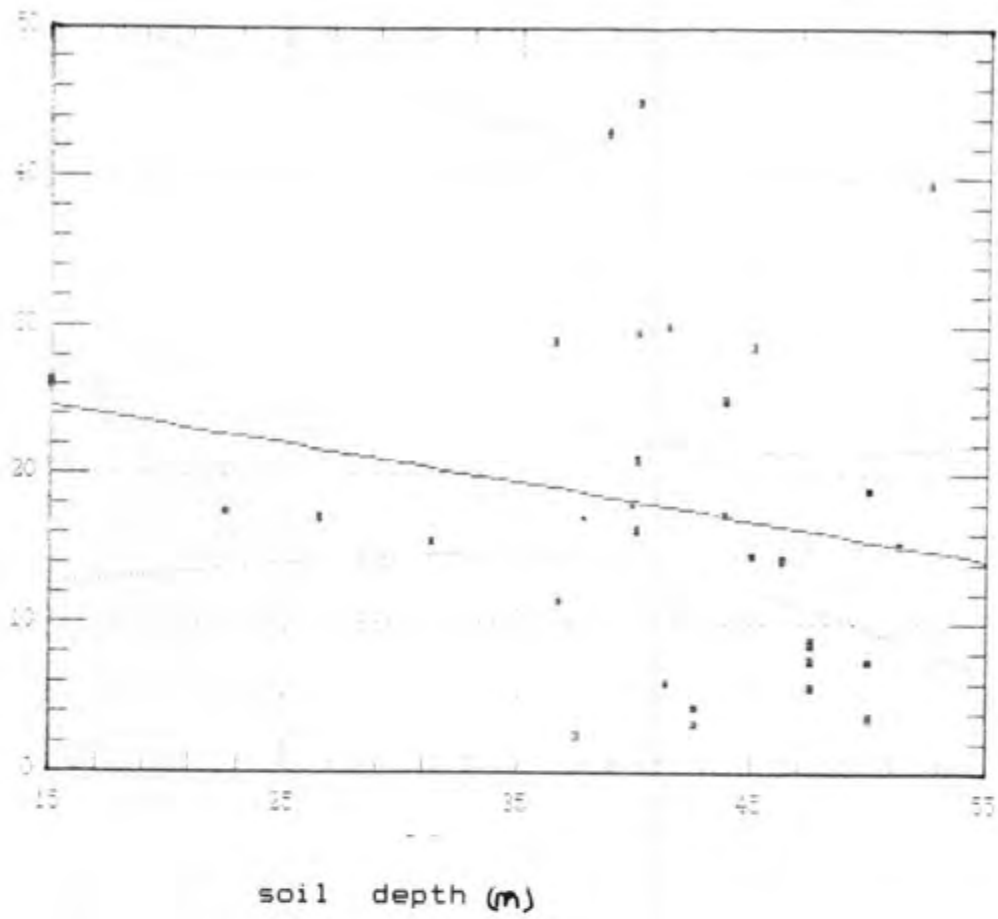


Fig 6. Relationship between soil depth and seedling per parent ratios of D. divaricata.

$$r = -0.21 \quad r^2 = 4.50\% \quad p < 0.05$$

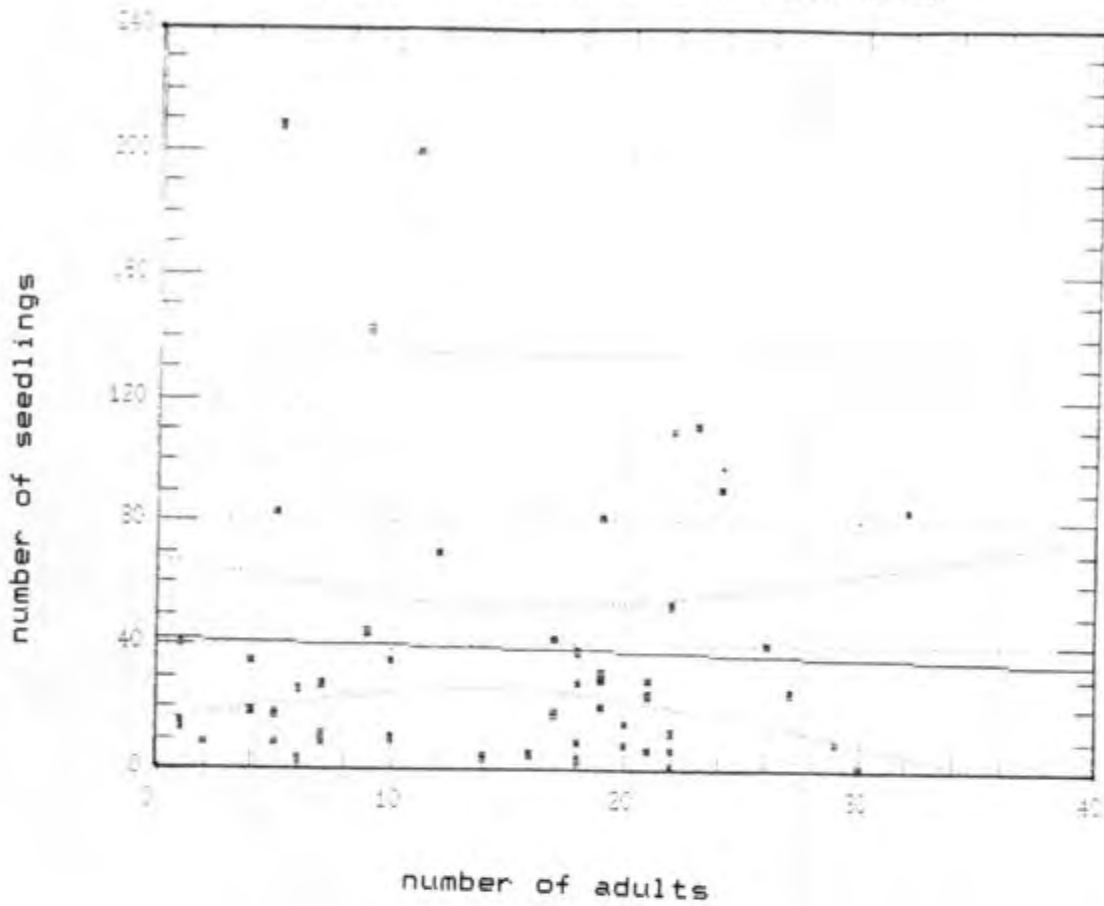


Fig 7. Relationship between parent and seedling densities for L. laureolum

$r = -0.04$

$r^2 = 0.14\%$ NS

This is an important
Fig and should have
followed the Table
and Fig's shown on
p 8

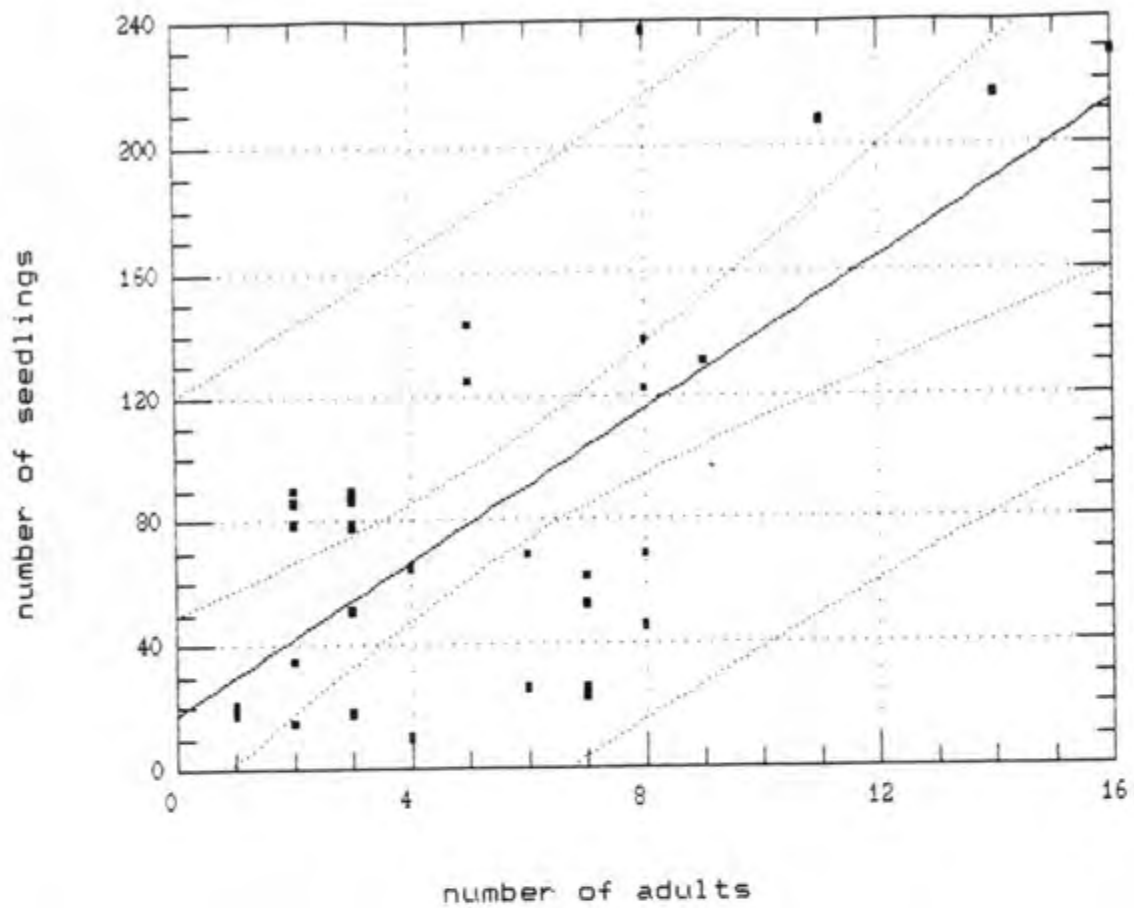


Fig 8. Relationship between parent and seedling densities for D. divaricata.

$$r = 0.68$$

$$r^2 = 47.03\% \quad p < 0.05$$

As for Fig 7

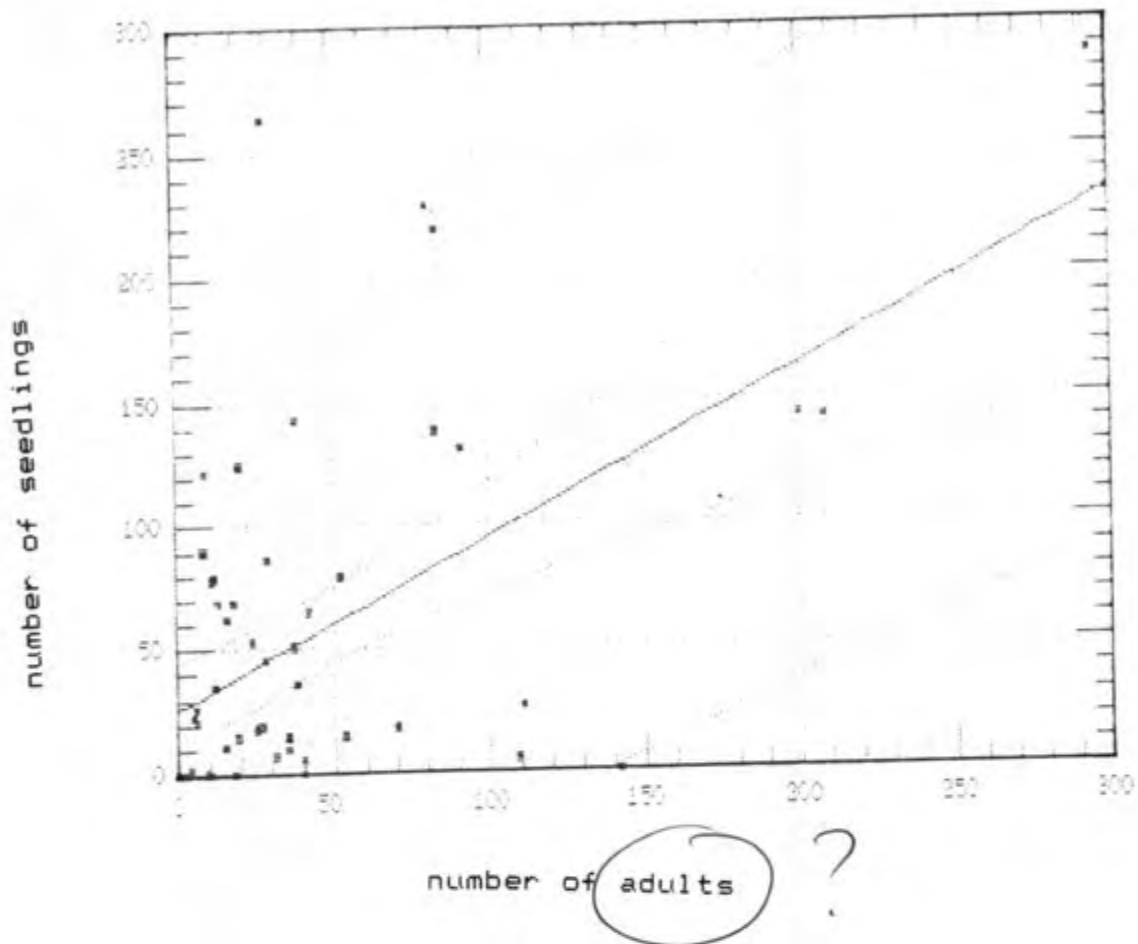


Fig 9. Relationship between L. laureolum and D. divaricata seedlings

$r = 0.55$ $\rightarrow r^2 = 29.86\% \quad p < 0.05$

D. Divaricata adults

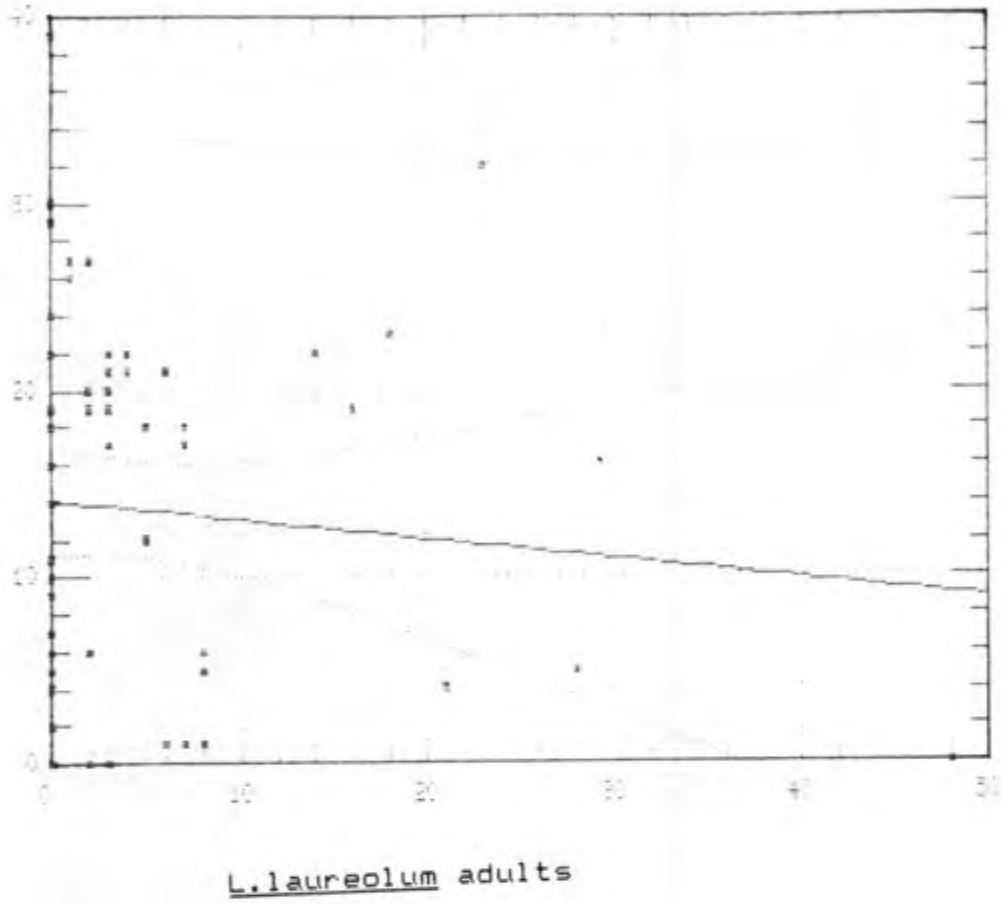


Fig 10. Relationship between L. laureolum and D. divaricata adults.

$$r = -0.09$$

$$r^2 = 0.79\%$$

NS

*Too many zero values
Spurious*

Discussion.

Results obtained from this study show that there is variation in post fire recruitment ^{of} between L. laureolum and D. divaricata. Evidence for this is the lack of a relationship between adults and seedlings in L. laureolum while a positive correlation exists between D. divaricata adults and seedlings. Possible reasons for this variation in recruitment are assumed to be a result of a combination of two factors namely: (a) different regeneration niches (Grubb, 1977), ^{in relation to fire effects} and differences in the effect of fire to the two species.

Because L. laureolum is a serotinous overstorey species, its regeneration niche is different from that of the myrmecochorus D. divaricata. Seeds of the serotinous species are dispersed by wind over longer distances (Bond, 1983) compared to the short distance dispersal of the myrmecochorus species. This dispersal mechanism allows L. laureolum? ^{New paper in S A J Bot which is most NB} ~~D. divaricata~~ to shift around the area after each fire.

The positive correlation shown by the results between seedling numbers of the two species (Fig 9) indicate coexistence of the two species early in their history. Competition is either at a low rate or is non-existent at this stage or is less important than environmental stress in the life of the species. However competition appears to intensify with time as the overstorey species supresses the understorey species. In this study evidence for the effect of competition between the two species is shown by the negative correlation between adult densities. ^{Dubious data} However this competition does not result in exclusion of understorey species

✓ What happened to the data showing this!

because of disturbance-mediated coexistence (Denslow, 1985) which allows competing species to coexist as a result of changes in the environment which reverse the order of competitive superiority among species (Chesson, 1975). In this environment fire was identified as the main form of disturbance facilitating species coexistence.

Rather poorly explained
Major points:

- Variation in recruitment of two species which compete as adults (evidence for this!)
- Myrmecochorous species - short dispersal. Good correlation between no. parents and no. seedlings
- Serotinous species - longer dispersal distances - Poor correlation between no. parents and no. ^{seedlings} species. Shuffling "clouds of species abundance"
- Differential recruitment with a community of D. lauricola minimizes competitive interaction between it and D. divaricata which mediates their long term ¹⁰ coexistence in the community.

Acknowledgements.

I would like to thank R.M. Cowling for his supervision, advice and constant interest in the project.

REFERENCES

- Bond W. 1980. Fire senescent fynbos in the Swartberg, Southern Cape. S.A. Forestry Journal No.114: 68 - 71.
- Bond W.J. 1984. Fire survival of Cape Proteacea - Influence of fire season and seed predators. Vegetatio 56: 65 -74.
- Bond W.J. 1985. Canopy - stored seed reserves (serotiny) in Cape Proteaceae. S.A. Journal of Botany 51: 181 - 186.
- Bond W.J., Vlok J. and Viviers M. 1983. Variation in seedling recruitment of Cape Proteaceae after fire. Journal of Ecology 72: 209 - 221.
- Chesson P.L. Environmental variation and the coexistence of species. Ch.14 In:Diamond D.J. and Case T.J.(Eds) Community Ecology. Harper & Row Publishers, New York.
- Cowling R.M. 1987. Fire and its role in coexistence and speciation in Gondwanan shrublands.South African Journal of Science 83: 106 - 112.
- Denslow J.S. 1985. Disturbance-mediated coexistence of species. In : S.T.A. Pickett & P. S. White (Eds) The ecology of natural disturbance and patch dynamics. Academic Press. London.
- Grubb P.J. 1977. The maintenance of species richness in plant communities: The importance of the regeneration niche.Biol. Rev. 52: 107 - 145.

Huston M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81 - 101.

Kruger F.J. 1979. South African Heathlands. In: Specht R.L. (Ed) *Heathlands and related shrublands. Descriptive studies.* Elsevier, Amsterdam pp 19 - 80.

Manders P.T. & Cunliffe R.N. 1987. Fynbos plant life histories, population dynamics and species interactions in relation to fire: An overview. *S.A. National Scientific Prog. Report* 135: 15-20.

Taylor H.C. 1984. A vegetation survey of the Cape of Good Hope Nature Reserve : II Descriptive account. *Bothalia* 15: 259 - 291.

Walker T.D. & Valentine J.W. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *American Naturalist* 124: 887 - 899.

Wiens J.A. 1977. On competition and variable environments. *American Scientist* 65 : 590 - 597.