ESTABLISHMENT PATTERNS OF THICKET AND FOREST SPECIES IN COASTAL DUNE LANDSCAPES OF THE SOUTHERN CAPE

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Abstract

The small-scale establishment patterns of Kaffrarian Thicket seedlings in fynbos/thicket mosaics on the South African south coast were sampled. Recruitment of mainly bird dispersed thicket species into dune fynbos was shown to be nucleated beneath emergent fynbos shrubs rather than randomly dispersed. At the more species rich St. Francis Bay site, species typical of thicket were observed to establish mainly below *Metalasia muricata* emergents in dune fynbos. Later successional thicket/forest species established almost equally under fynbos emergents and below thicket. Forest species only showed recruitment under forest. Sampling of environmental characteristics, including soil N, organic and water contents and light penetration of canopy within each microsite revealed progressive habitat amelioration. It is proposed that the observed patterns of recruitment in the absence of fire are a result of directed bird dispersal to microenvironments ameliorated by the presence of earlier successional species. However this hypothesis is based purely on inference from spatial patterns of seedling recruitment. The results of an outplanting experiment were inconclusive. Thus further rigorous experimental testing is required to separate the relative effects of dispersal, fire and localised environmental charateristics on the recruitment patterns of Kaffrarian Thicket species.

Introduction

Despite their essentially tropical and subtropical affinity (Cowling 1984), thicket formations constitute a substantial proportion of the Fynbos Biome Flora (Cowling and Holmes 1992). Various aspects of the biology of these impenetrable shrublands differ substantially from those of fynbos. In particular, thickets are dominated by bird dispersed species (Knight 1988), do not have recruitment linked to fire events and once established, are not fire prone (Cowling and Holmes 1992).

While fire, edaphic factors and dispersal agents all contribute to the dynamics of thicket formation within coastal fynbos (Cowling 1984; Cowling and Holmes 1992), the exact mechanisms of succession are unclear. Pierce (1990) has suggested that thicket seedlings establish from bird dispersed seed under emergent fynbos shrubs. This model is similar to that developed by Manders and Richardson (1992) for the establishment of Afromontane forest nuclei under perches provided by fynbos emergents. These authors have shown that recruitment of forest species is associated with nucleation and habitat amelioration, and occurs in the absence of fire.

This study attempts to differentiate the relative importance of the following ~~3~~ three factors in thicket establishment and development: dispersal, facilitation by amelioration and fire. Seedling recruitment and microsite environments are examined at a small scale (ie. in plots equivalent to the canopy of fynbos emergents). This scale is most likely to reveal patterns of recruitment and soil development which presumably occur in early forest succession (Campbell et al. 1988, cf. Campbell et al. 1990).

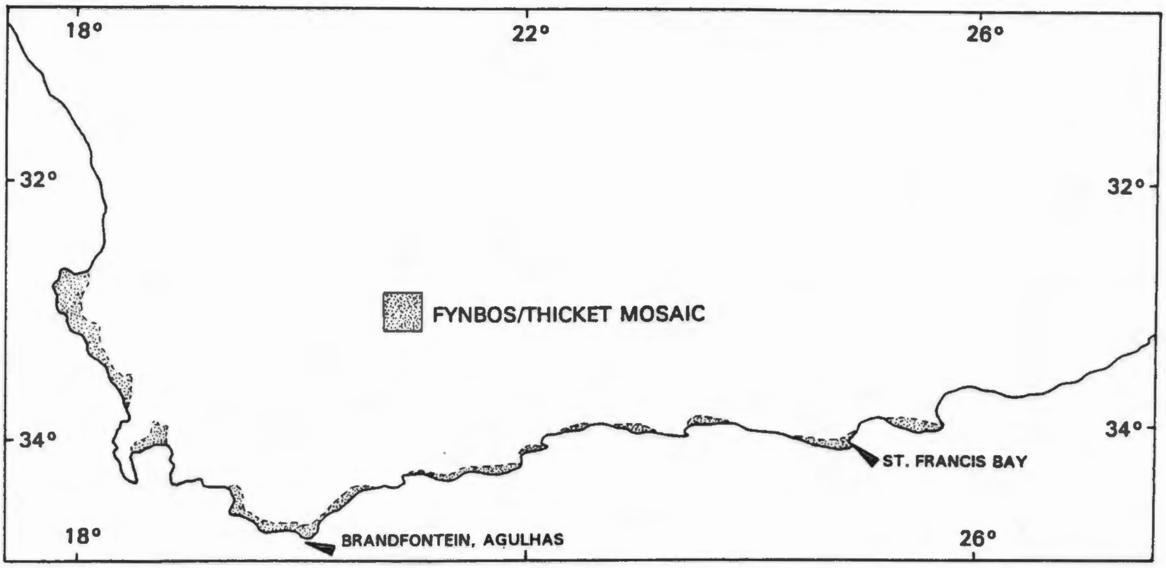

Figure 1. **The distribution and extent of dune fynbos/thicket mosaic in the Cape Floristic Region (After Cowling and Holmes 1992). The areas delimited on the south coast consist of Kaffrarian Thicket, with depauperate outliers extending as far westward as the Cape Peninsula in the south-western Cape. Place names indicate the south coast sites where were collected, Brandfontein west of Agulhas and St. Francis Bay, north of Cape St. Francis.**

Thickets are particularly prevalent in dune fynbos relative to other fynbos communities, possibly due to the relatively high nutrient status here (Cowling and Holmes 1992). The mosaic of Kaffrarian Thicket (*sensu* Cowling 1984) and dune fynbos which occurs along the south coast of South Africa (Fig. 1) provides an ideal formation in which to study succession from fynbos to thicket. There are many sites in which these communities are adjacent and colonisation of the fynbos is likely to occur. Environmental conditions such as soils are generally uniform at a local scale, allowing the assumption that differences in community structure and edaphic factors are a result of biological activity, not differential establishment on originally dissimilar soils. In addition, at a broader scale, thicket and dune fynbos mosaics occur along a range of climatic conditions, allowing the generality of observed pattern to be assessed. Large scale perturbation by humans has resulted in the widespread occurrence of all stages along succession from grassland to forest in these areas (Acocks 1972).

Study sites

Data were collected from two sites on the south coast of South Africa (Fig. 1). The first site is situated in the coastal dunes of the private nature reserve Brandfontein at 34o50'S, 19o59'W, west of Agulhas. The second is at St Francis Bay, just north of Cape St. Francis, at 24°50'W and 34°12'S. All data from St. Francis Bay was collected by Cowling (unpubl.).

The vegetation at both sites consists of a mosaic of Dune Fynbos and Kaffrarian Thicket (*sensu* Cowling 1984). Thicket at St. Francis Bay consists of South-East Dune Thicket as described in detail by Cowling (1984). Structurally, this is a closed shrubland to low forest dominated by evergreen sclerophyllous shrubs and trees. Endemism is low, with the phytochorological spectrum here dominated by Tongaland-Pondoland endemics and linking species. Forested areas have multispecies canopies (Cowling 1984). The thicket vegetation at Brandfontein, Agulhas is depauperate in comparison, but typical of Dune Kaffrarian Thicket. The only forested areas here are entirely dominated by *Sideroxylon inerme*, the white milkwood, which usually reaches heights of 3 to 5 m. The Dune fynbos is dominated by the small leaved shrubs *Agathosma collina, Metalasia muricata* and *Passerina paleacea.*

The soils of both these sites are well drained Fernwood calcareous sands (Macvicar et al. 1977). These dune soils are neutral to alkaline medium sands. Fertility is high, but the availability of nutrients such as phosphorus may be limited by high pH values. Rainfall patterns at Brandfontein are typical of the southern Cape, where a high proportion of the rain falls in winter. Rainfall at St. Francis Bay in the south-eastern Cape is more erratic and less seasonal, although there tend to be a few drier months in midsummer (Cowling 1984).

From this point on, references to fynbos should be taken to mean Dune Fynbos. Thicket refers to closed shrubland, while forest refers to the low forest of Kaffrarian Thicket.

Methods

Microsites sampled

Four microsites along the succession from fynbos to forest were sampled at both study sites. This was done in order to determine Kaffrarian Thicket recruitment patterns and the microenvironmental characteristics which are presumably related to these patterns. These microsites (2 each in fynbos and thicket) were:

(1) Open Dune Fynbos. This consisted of areas within the dune fynbos with little or no cover. Sands here are white, with little organic matter present.

(2) Under the canopy of emergent shrubs in the fynbos (see Fig. 2). The microsite immediately below the canopy (typically 0.7 to 1.5 . high) of some larger fynbos species was sampled. Primarily *Metalasia muricata* and *Agathosma collina* were sampled at Brandfontein, but only *M. muricata* was sampled at St. Francis Bay. There is some accumulation of litter in these microsites.

Figure 2. Dune Fynbos at Brandfontein on the Agulhas coast. Note the presence of emergent *M. muricata*, *A. collina* and isolated *E. racemosa* individuals, as well as the typically low cover between these emergents in the foreground.

(3) Underneath thicket canopy (Fig. 3). Plots below a continuous cover of thicket (approximately 1 - 2 m high) were examined. At Brandfontein dominant thicket species were *Olea exasperata, Euclea racemosa* subsp. *racemosa* and *Pterocelastrus tricuspidatus*. There was further accumulation of litter in these microsites, but soils are still sandy.

Figure 3. Thicket vegetation at Brandfontein on the Agulhas coast. Note the continuous cover and the presence of the dominants *O. exasperata* and *E. racemosa*.

(4) Underneath *S. inerme* canopy (milkwood) at the Brandfontein site (Figs. 4 & 5) and forest at St Francis bay. The microsite below the canopy (usually 4 to 6 m high) was sampled. Soils are more developed here, with a continuous litter layer above darker, more organic rich soils than are found in the other microsites.

Figure 4. *S. inerme* canopy emerging from coastal thicket at Brandfontein on the Agulhas coast.

Figure 5. The interior of *S. inerme* forest at Brandfontein. Note the continuous litter layer and the height of the canopy (approx. 4 m)

Cowling (1984) presents data from St. Francis Bay that indicates that the soils of South Coast Dune Fynbos have approximately 0.04 to 0.19 % total nitrogen, 1,500 to 2,300 ppm calcium and a pH of 6.7 to 7.2. Soils of Kaffrarian thicket had approximately 9 to 15 % total nitrogen, 1,000 to 20,000 ppm calcium and a pH of about 4 to 7.

Patterns of seedling and ramet abundance and size in microsites Spatial patterns of seedling recruitment were determined from randomly placed 1 × 1 m plots situated in each microsite described above. At the Brandfontein site, seedlings (individuals below 15 cm in height) of each species were counted and measured for height in 50 plots for each microsite. The number of ramets (vegetative shoots from below-ground stems) in each plot was also noted. At St. Francis Bay, thicket and forest seedlings were counted in 60 plots within each microsite. Here all individuals below approximately 50 cm in height were considered to be seedlings. Canopy cover and composition was noted for all plots at both sites.

Physical characteristics of microsites

Soil moisture

All soil analyses were performed on soil from the Brandfontein site. Gravimetric water contents were determined from soil collected on three occasions from late summer to late winter (10 April, 28 June and 23 September 1993). Samples were taken from 5 cm below the soil surface. These were brought back to the laboratory in airtight jars, weighed on a 4 figure Mettler balance and oven dried at 80°C to constant weight.

Soil chemistry

Soil nitrogen and organic carbon contents were determined from 3 samples from each microsite. All 3 samples from fynbos emergent microsites collected below *M. metalasia* canopies. All samples were processed by Matrolab in Cape Town.

Light

The amount of light reaching the soil surface in each microsite was compared to the amount outside the canopy at both sites. Light was measured using an electronic meter to determine photosynthetically active radiation (PAR). Measurements were taken in early winter (20 - 21 May 1991) at St. Francis Bay and mid-winter at Brandfontein (25 June 1993).

Germination experiments

In each microsite

In order to determine the effect of microclimatic and physical differences on seed germination, seed of three thicket species was sown in each microsite at Brandfontein. Seed of *Euclea racemosa* and *Sideroxylon inerme* were collected from individuals fruiting at Brandfontein. *Rhus glauca* seed was collected from one fruiting plant in the Bontebok National Park. Seed of *S. inerme* and *Rhus glauca* were sown as collected from the parent plants, while the pulp of the *E. racemosa* fruit was mechanically removed. This was in order to simulate the condition of naturally bird dispersed fruit.

Seed was sown in tubular wire mesh exclosures with a diameter of 15 cm (mesh size: 15 × 19 mm) in late summer/early autumn (10 April 1993). All seed (50 seed of *E. racemosa* and *S. inerme* and 100 seed of *R. glauca* in each exclosure) was scattered on the soil surface. Two replicates of exclosures of the three species were sited in each of the fynbos and thicket microsites. Experimental plantings in thicket and underneath *S. inerme* were replicated three times. Seedlings were counted and measured after two months (25 June) and again after 5 months (23 September).

Effect of avian frugivores on seed germination

The effect of passage through the gut of avian dispersers on seed germination was tested by means of further experiments conducted at the University of Cape Town. Ripe fruit collected from a number of individuals (>4) of *S. inerme*, *O. exasperata* (from Betty's Bay: 18°58'W, 34°02'S) and *E. racemosa* (at Brandfontein) were presented to 3 caged red-wing starlings, *Onychognathus morio*, over a period of three days. Although this species is probably not a natural disperser in thicket vegetation, the fruit were eaten readily. As is typical of some frugivorous birds, many of the depulped seeds, especially *O. exasperata*, were regurgitated (van der Pijl 1982). At the same time as the treatment by birds, fruit of each species was mechanically depulped. Both treatments were air dried and planted simultaneously with whole, untreated fruit two days later. In each treatment, 150 seed of each species were planted in groups of 50 in 22 × 16 cm trays. These contained a 1:2 mixture of sand and potting soil. Seed was covered by a 1 cm layer of soil. The seed trays were watered either daily or on alternate days to prevent the soil from drying out. All treatments were planted in late winter (13 August 1993).

Clipping experiments

Seedlings of *Olea exasperata* (n = 31) with a basal diameter of 2 to 3 mm and a height of

15 cm or less were cut at the level of the soil to simulate the effects of fire. Due to time limitations, other size classes were not clipped. Only seedlings under *S. inerme* canopy were used due to their abundance and ease of access. Seedlings were clipped in mid-winter (25 June 1993) and harvested 3 months later (24 September). The length of the regenerated shoot (if present), the root length and the stem basal diameter were measured. In addition age of the seedlings was estimated from the relatively distinct annual growth rings in sections of the stem base.

Data analyses

The number of seedlings of various classes of species in each 1 × 1 m plot were compared between microsites. Since the data are Poisson distributed, total variation between the microsites was compared by means of the Kruskal-Wallis test. Pair-wise comparisons between sites were performed using the Mann-Whitney U test.

Soil water contents and light penetration through the canopy, both in the form of percentages, were compared using arcsine transformed data. Light penetration in the various microsites was compared with a one-way analysis of variance (ANOVA). Soil water contents were compared for both microsite and change over time using a two-way ANOVA. Variation between groups in all instances was compared using the least squares differences (LSD) multiple range test.

The Lord's range test (Langley 1968) was used to compare total variation in addition to variation between groups where sample size in each group was 3 or less. This applied to the data on soil chemistry and the data derived from experimental sowing.

The time series of seeds germinating after various treatments were compared in a pair-wise fashion using a Kolmogorov-Smirnov two sample test. All statistical analyses, except the Lord's range test were performed using STATGRAPHICS.

Results

Patterns of seedling and ramet distribution and growth

Seedling distribution and abundance

Data from all sites indicate that all seedlings show differential recruitment across the 4 microsites. All significance values given for pair-wise comparisons of seedling densities between microsites are derived from Mann-Whitney U tests.

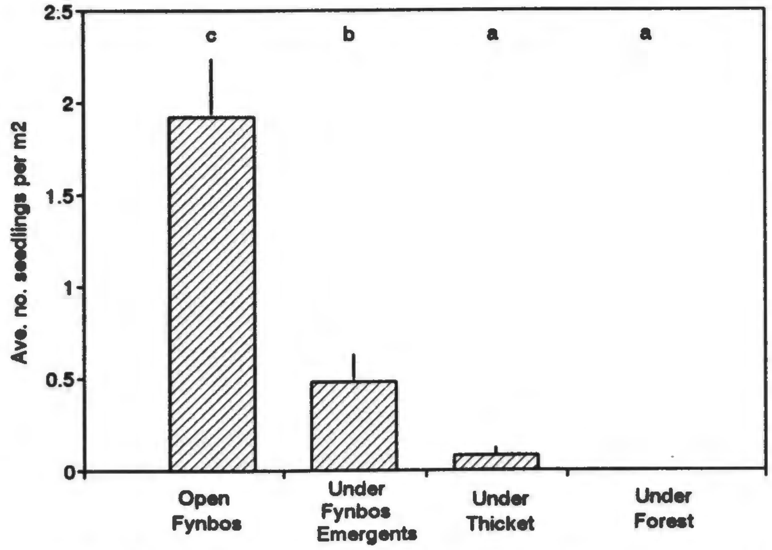

Figure 6. Recruitment of dune fynbos seedlings (ave. no. per m^2) in 4 microsites at Brandfontein, Agulhas. These represent stages in succession from fynbos to forest. Error bars are S.E. Alphabetic characters show significant differences ($p < 0.05$) between microsites. Total variation between sites, as determined from a Kruskal-Wallis test, is significant ($p < 0.001$).

The recruitment of plants species with adult stages present in dune fynbos (Appendix 1) at Brandfontein shows considerable variation between microsites (Fig. 6). It is clear that seedlings of these species are most dense in the open environment between dune fynbos emergents, with successively lower recruitment occurring under emergents and thicket. No seedlings of any fynbos species were found beneath *S. inerme* forest.

The recruitment of species with adults dominant in thicket shows a diametrically opposed pattern (Fig. 7). These seedlings recruit preferentially in the microsites below canopies in all successional stages, especially below thicket. Recruitment in open fynbos is almost non existent, although substantial numbers of seedlings are found below the canopies of fynbos emergents. Compared to the microsite below thicket, recruitment of thicket species beneath *S. inerme* forest is reduced.

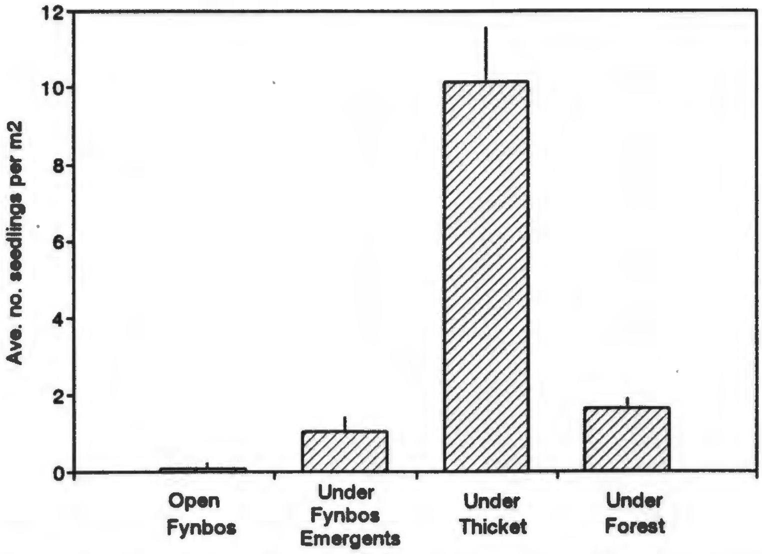

Figure 7. Average numbers of thicket seedlings per m^2 in each of 4 microsites at Brandfontein, Agulhas. Error bars are S.E. Total variation between groups determined by the Kruskal-Wallis test is significant ($p < 0.001$). All groups differ significantly from one another ($p < 0.05$).

This broad pattern of recruitment in thicket species at the Brandfontein site (Appendix 1) is also reflected in the spatial distribution of seedlings of individual thicket species (Fig. 8).

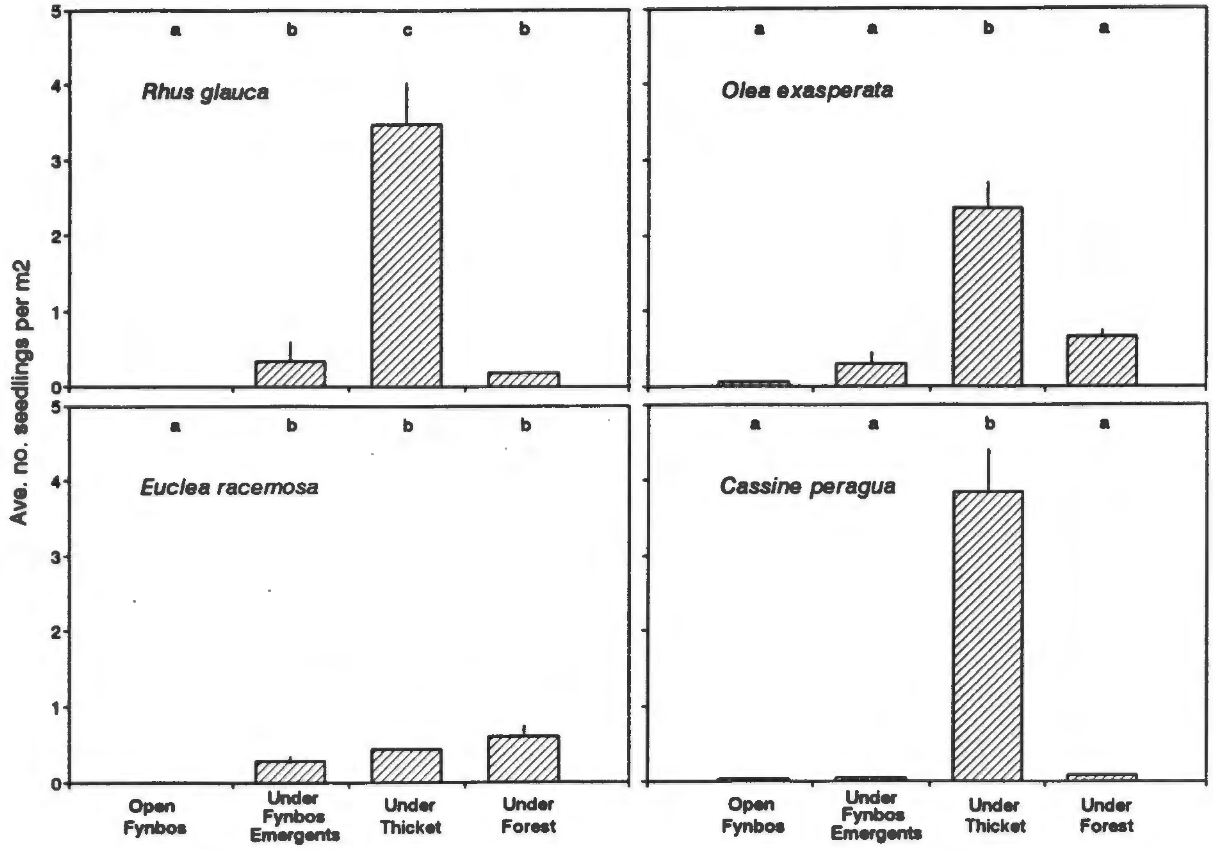

Figure 8. Average number of seedlings per m^2 across 4 microsites for each of 4 dominant thicket species at Brandfontein, Agulhas. Error bars are S.E. Total variation between groups, as analyzed using a Kruskal-Wallis test, is significant for all species ($p < 0.001$ in all 4 spp.).

All species except *E. racemosa* have the highest density of seedlings below the thicket canopy. While *Cassine peragua* shows little recruitment in any other microsite, *R. glauca, E. racemosa* and *O. exasperata* all occur beneath fynbos emergents. In both *R. glauca* and *E. racemosa*, seedling densities are significantly higher below fynbos emergent's canopies than in the areas between emergents ($p < 0.05$ and $p < 0.001$ respectively). Only *E. racemosa* shows higher recruitment in the forest in comparison to the thicket microsites, although this difference is not significant ($p > 0.05$). Various thicket species at Brandfontein thus show differential abilities to establish within the 4 microsites. Generally, however, recruitment under thicket is highest, and there are significant differences between recruitment in the open fynbos and beneath the canopy of fynbos emergents.

Seedling recruitment patterns at St. Francis Bay (Fig. 9.) are presented for each of 3 broad groups of species. These represent seedling recruitment by the adult species of consecutive successional stages (see appendix 2 for species names). The classification was derived from Cowling (pers. comm.).

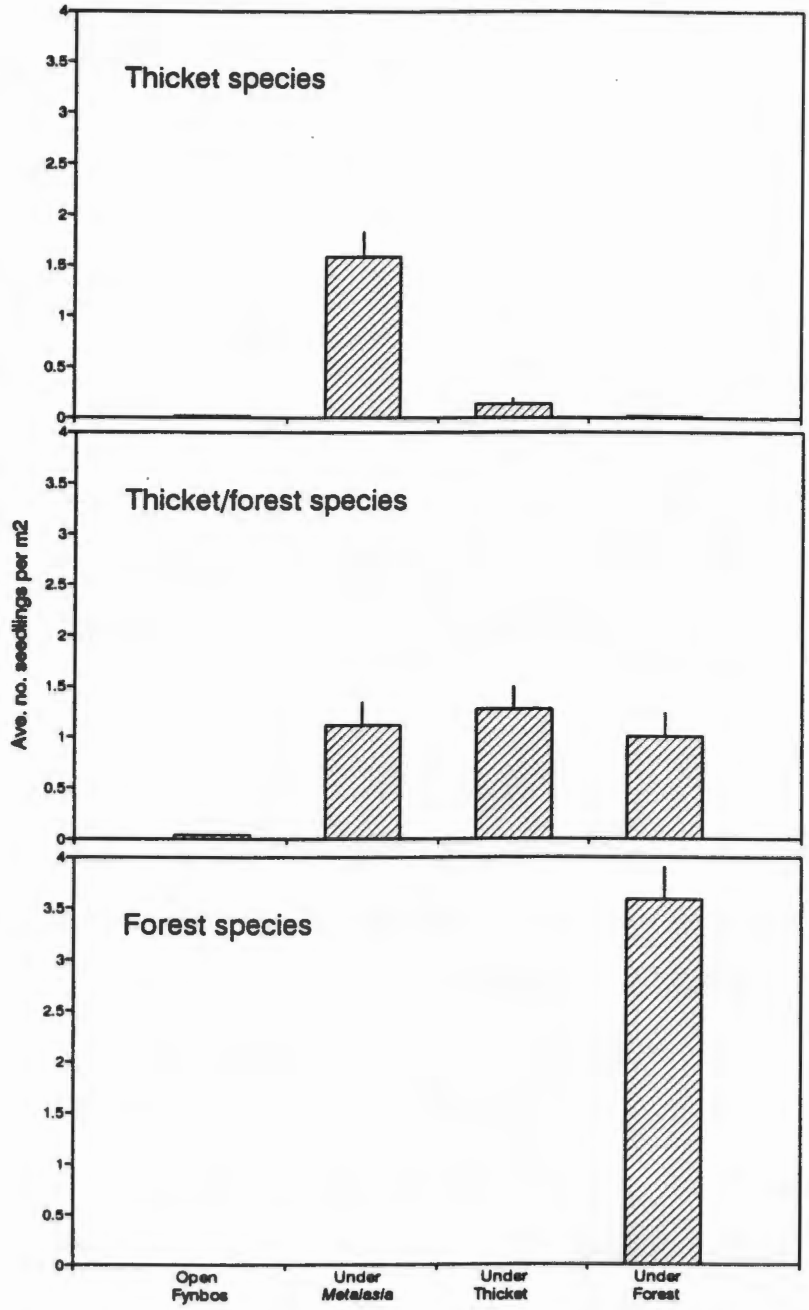

Figure 9. Seedlings densities (ave. no. per m^2) within 4 microsites at St, Francis Bay. Vegetation categories represent groups of species of adult plants from consecutive successional stages. Error bars represent S.E. Kruskal-Wallis tests indicate that all vegetation categories show highly significant variation between sites ($p < 0.001$; $p < 0.001$ and $p < 0.001$ for thicket, thicket/forest and forest respectively).

These data from St. Francis Bay clearly show that as is the case at Brandfontein, all Kaffrarian Thicket species show a recruitment pattern that is non-random. At this site, the more species rich flora allows analysis of variation in patterns of recruitment by later successional vegetation than at Brandfontein. Unlike the situation at Brandfontein, seedlings of thicket species show the highest recruitment below emergent *Metalasia muricata* shrubs in the fynbos ($p < 0.001$ compared to any other microsite) and not below thicket. Although thicket species' recruitment beneath the thicket microsite was higher than recruitment in open fynbos and below forest, these differences are not statistically significant ($p > 0.05$ in each case). Recruitment of species typical of a thicket/forest formation show approximately equal recruitment in all microsites with a covering canopy. Seedling densities in the thicket microsites were slightly higher than those below *M. muricata* canopy and within forest. These differences are not significant however ($p > 0.05$ in each case). Seedling densities are very low in the open fynbos compared to the other microsites ($p < 0.001$). Finally, recruitment in forest species is confined entirely to the forest microsite, with no seedlings observed in any plots within other microsites. A broad pattern of recruitment in the successive stages (ie. thicket vegetation → thicket/forest → forest) is visible. Thicket species recruit preferentially under the fynbos emergent *M. muricata*. Thicket/forest seedlings establish in slightly lower numbers under emergents, but show increased recruitment under the later successional thicket and forest microsites compared to thicket seedlings. Lastly forest species' seedlings are only observed to recruit in the forest environment.

Seedling size distribution

Data from Brandfontein, Agulhas shows significant differences in the mean size of seedlings between different microsites (Fig. 10). *R. glauca, E. racemosa* and *O. exasperata* were considered because of these species' relative abundance in the three sites shown. Numbers of seedlings found in open fynbos were too low to allow a meaningful estimate of mean size.

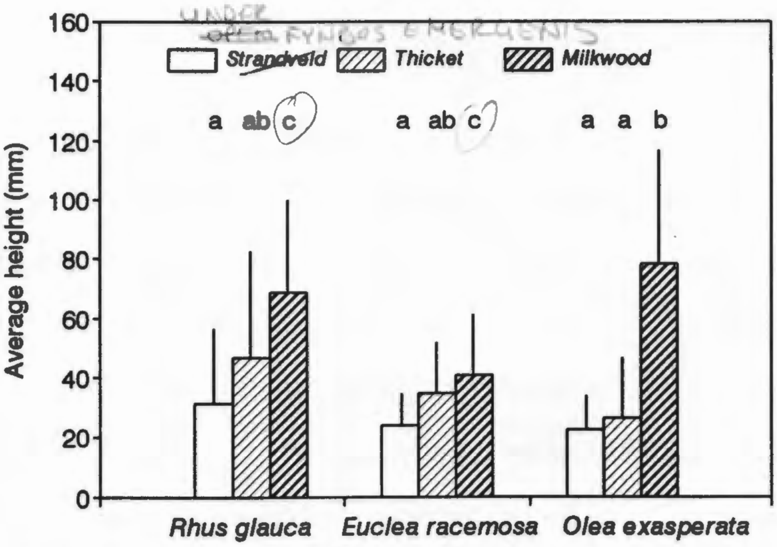

Figure 10. The mean size of three species of seedling in three microsites: ~~open~~ UNDER fynbos EMERGENTS, under thicket canopy and under *S. inerme* forest canopy. Error bars are S.D. Alphabetic characters signify differences between microsites for each species ($p < 0.05$). ANOVA reveals that variation in size across microsites is significant for *R, glauca* and *E. racemosa* ($P < 0.05$) in addition to *O. exasperata* ($P < 0.001$). Alphabetic characters show significant differences between mean size between each microsite from a multiple range test ($p < 0.05$).

Figure 10 clearly shows that in all three species, mean seedling size is lowest under the canopies of fynbos emergents, and highest under *S. inerme* forest canopy. However, no species shows significant differences in mean size between the microsite below fynbos emergent's canopies and under thicket canopy. In addition, neither *R. glauca* or *O. exasperata* seedlings differed in mean size between the thicket and forest microsites.

Ramet distribution and abundance.

If the number of ramets (vegetative shoots) of thicket species coming up in each microsite at Brandfontein are considered (Fig. 11 10) the pattern appears to be similar to that of seedling recruitment at this site (Fig. 7). The major difference is the relatively high density of ramets (mainly from *E. racemosa* and *O. exasperata*) in plots sited in open fynbos vegetation.

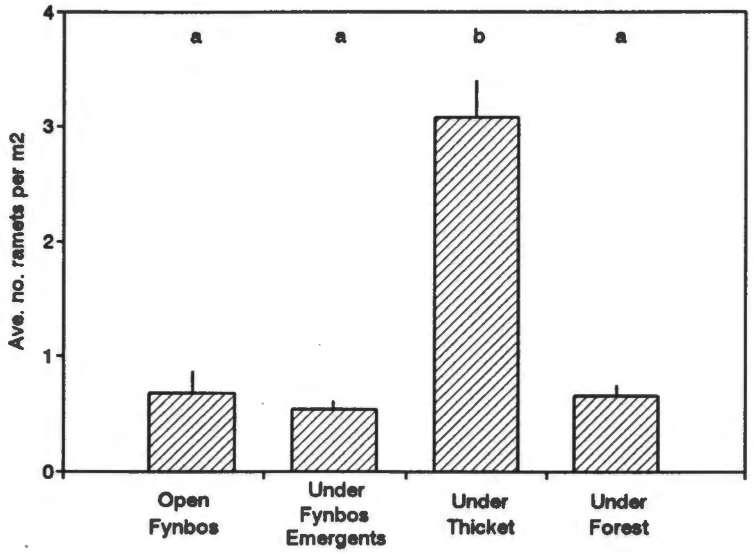

Figure 11. The average number of thicket ramets occurring in each of 4 microsites at Brandfontein. Error bars represent S.E. Alphabetic characters represent significant differences between individual microsites. There was significant variation ($p < 0.001$) across all groups as determined from a Kruskal Wallis test.

In contrast to the patterns of ramet emergence exhibited by thicket species at Brandfontein, *S. inerme* ramets were only found in the environment below this tree's canopy, with an average density of 0.42 individuals per m^2.

Physical characteristics of the microsites

Soil moisture contents

Soil moisture contents within each microsite were sampled at three times during a 6 month period. The results (Fig. 11 12) show a clear and progressive difference between the successive microsites. There is trend of increasing soil moisture contents from open fynbos soils through to the microsite below *S. inerme* canopies.

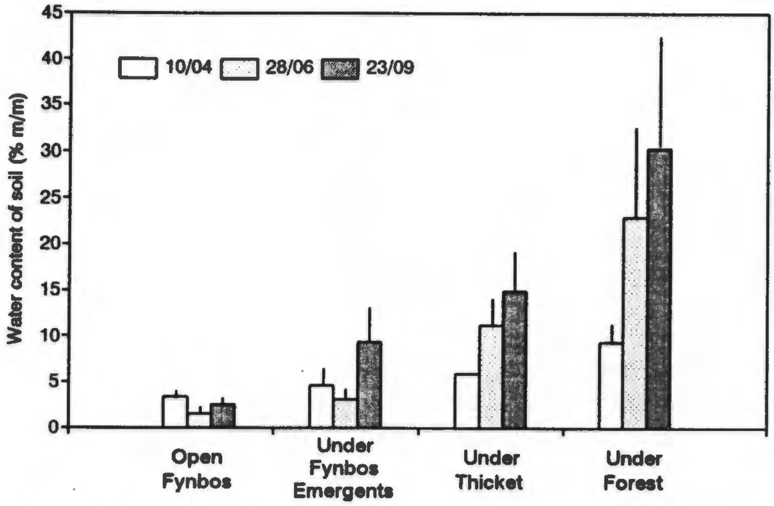

Figure 12. Gravimetric water contents, expressed as a percentage of original soil mass, for each of 4 microsites at 3 different times. Error bars are S.D. A 2-way ANOVA reveals significant variation among the miscrosites ($p < 0.001$) as well as the three sampling occasions ($p < 0.001$). Interactions are also significant ($p < 0.001$). The results of a multiple range test reveal that all groups, both at the level of site as well as over time, are significantly different from one another at the 95 % confidence level.

In addition to the clear differences between the moisture contents of the microsites' soils, there is an increase in moisture content from late summer to late winter. Interactions between site differences and sampling time are also significant, indicating that the differences between the soil water contents increase as the soils get wetter.

Soil chemistry

The soil chemistry data from Brandfontein, Agulhas, are presented in table 1. Although these data are limited, they present a clear picture of progressive soil development under the different microsites representing successive vegetation formations.

Table 1. Soil chemistry data for the 4 successional microsites at Brandfontein, Agulhas. Each cell represents the mean of three values. The result of a Lord's range test for differences among all microsites are shown (NS = not significant, $p > 0.05$; * = $0.001 < p < 0.01$). In addition the range test results derived from pair-wise comparison of individual groups are shown. The alphabetic characters represents significant differences between microsites ($p < 0.05$).

	Open Fynbos	Under *Metalasia*	Under Thicket	Under *S. inerme*	Sig. of site effect
% Nitrogen	0.053	0.087	0.103	0.223	**
Range tests	a	b	b	c	
Organic carbon (%)	0.70	1.40	1.71	3.50	NS
Range tests	a	b	bc	c	

Both total nitrogen content and the percentage of readily oxidisable organic carbon increase through the successional microsites, from open fynbos to *S. inerme* forest. There is no significant difference ($P > 0.05$) between the nitrogen and soil organic contents below *Metalasia* canopy and thicket, and thicket and forest, respectively. There is a significant difference ($p < 0.05$) between the values below the *Metalasia* canopy and *Sideroxylon* canopy however.

Light

The percentage of light (PAR) reaching the soil surface through the canopy in each microsite was determined at both Brandfontein and St. Francis Bay.

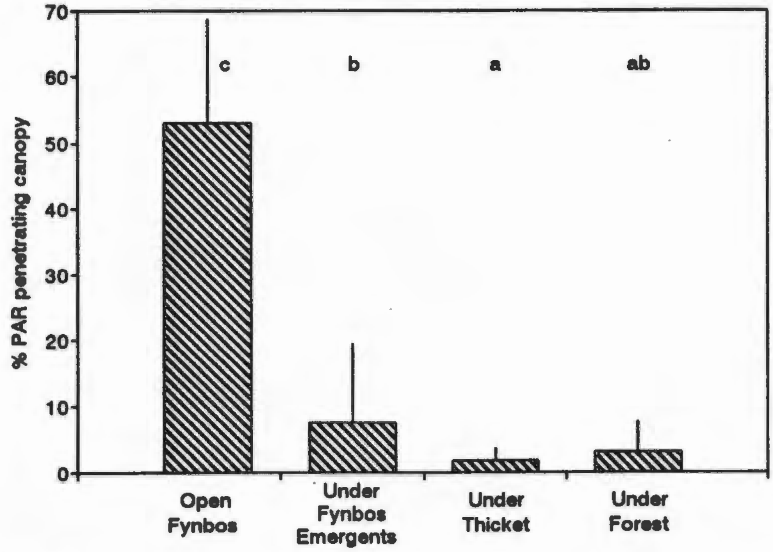

Figure 13. The percentage of PAR penetrating the canopy and reaching the soil surface in each of four microsites sampled at Brandfontein, Agulhas. Error bars are S.D. ANOVA reveals that variation between groups is significant ($p < 0.001$). Alphabetic characters indicate significant differences ($p < 0.05$) between individual groups from a multiple range test.

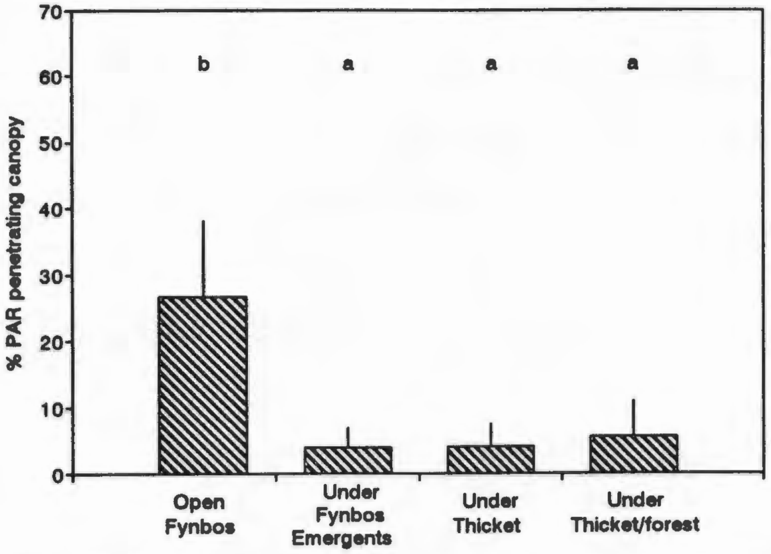

Figure 14. The percentage of PAR penetrating the canopy and reaching the soil surface in each of four microsites sampled at St. Francis Bay, Cape St. Francis. Error bars are S.D. ANOVA reveals that variation between groups is significant ($p < 0.001$). Alphabetic characters indicate significant differences ($p < 0.05$) between individual groups from a multiple range test.

At both these sites there is a large difference between the high percentage of light reaching the soil surface in open fynbos compared to the lower percentage in the other three microsites with their substantial canopies. At the Brandfontein site there is progressive extinction of light by the canopies of open fynbos, fynbos emergents and thicket. The quantity of PAR penetrating the *S. inerme* canopy is higher than that in the thicket microsite. At the St. Francis Bay site, there appears to be little difference between the effect of canopies of fynbos emergents, thicket and forest on quantity of light penetrating the canopy, with the percentage reduction in PAR at all of these microsites being statistically equivalent.

Germination experiments

Experimental sowing in the field.

The average number of seeds germinating per experimental plot (n = 2 in open fynbos and under *Metalasia* canopy, n = 3 in under thicket and forest canopy) are presented in figure 14 (*R. glauca*) and figure 15 (*E. racemosa*).

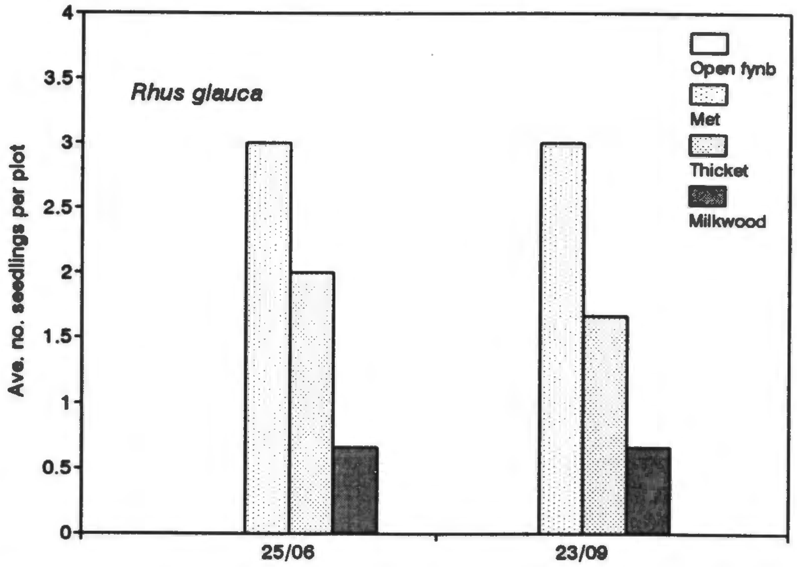

Figure 15. Average number of *R. glauca* seedlings germinating after 2 months (25/06) and 5 months (23/09) in experimental plots (100 seed each) in each microsite. Lord's range tests on individual groups and Mann-Whitney U tests of fynbos vs. thicket/forest plots coalesced revealed no significant differences ($p > 0.05$) between groups.

As a result of inadequate replication, no statistically significant differences in germination between experimental plots of the four microsites. It is worth noting however that no seedlings germinated in the open fynbos microsite either after a period of 2 months or 5 months.

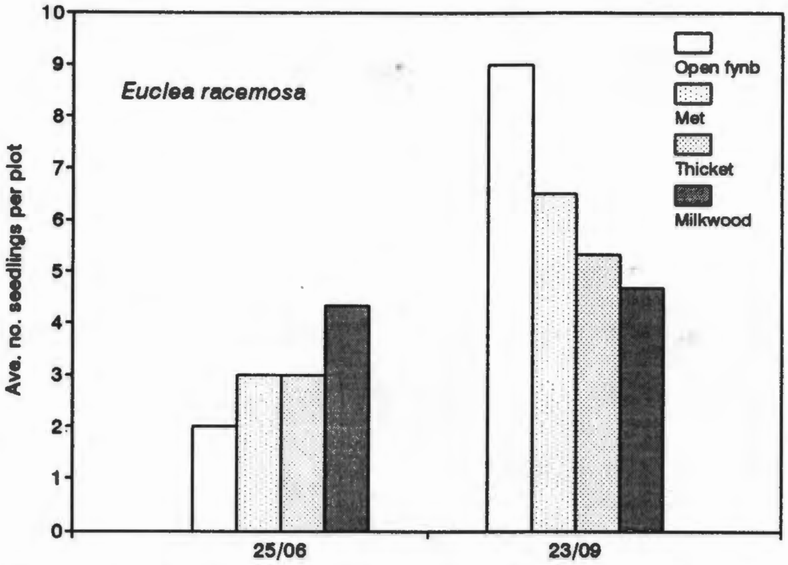

Figure 16. Average number of *E. racemosa* seedlings germinating after 2 months (23/06) and 5 months (23/09) in experimental plots (50 seed each) in each microsite. Lord's range tests on individual groups and Mann-Whitney U tests of fynbos vs. thicket/forest plots coalesced revealed no significant differences ($p > 0.05$) between groups.

E. racemosa seedlings germinated in all microsites, although, as for *R. glauca* , no significant trends could be detected from between sites. What is not evident from this figure, is that seedlings germinating in the moister environment below the *S. inerme* forest canopy suffered substantial predation damage (Fig. 16), especially compared to the seedlings which germinated in the open fynbos microsite.

Figure 17. An example of predation damage (arrowed) typical of seedlings planted below the *S. inerme* forest canopy at Brandfontein, Agulhas.

In general, however, low replication has resulted in inconclusive results in these field germination experiments. They thus reveal very little about the effect of microsite on seedling germination and survival.

The effect of avian ingestion on seed germination.

As is typical in vertebrate dispersed drupes (Loiselle 1990), removal of the fruit's flesh, both by hand and after ingestion by birds (red-wing starlings), has resulted in improved germination compared to whole fruit in both cases where seed germinated (Fig. 17).

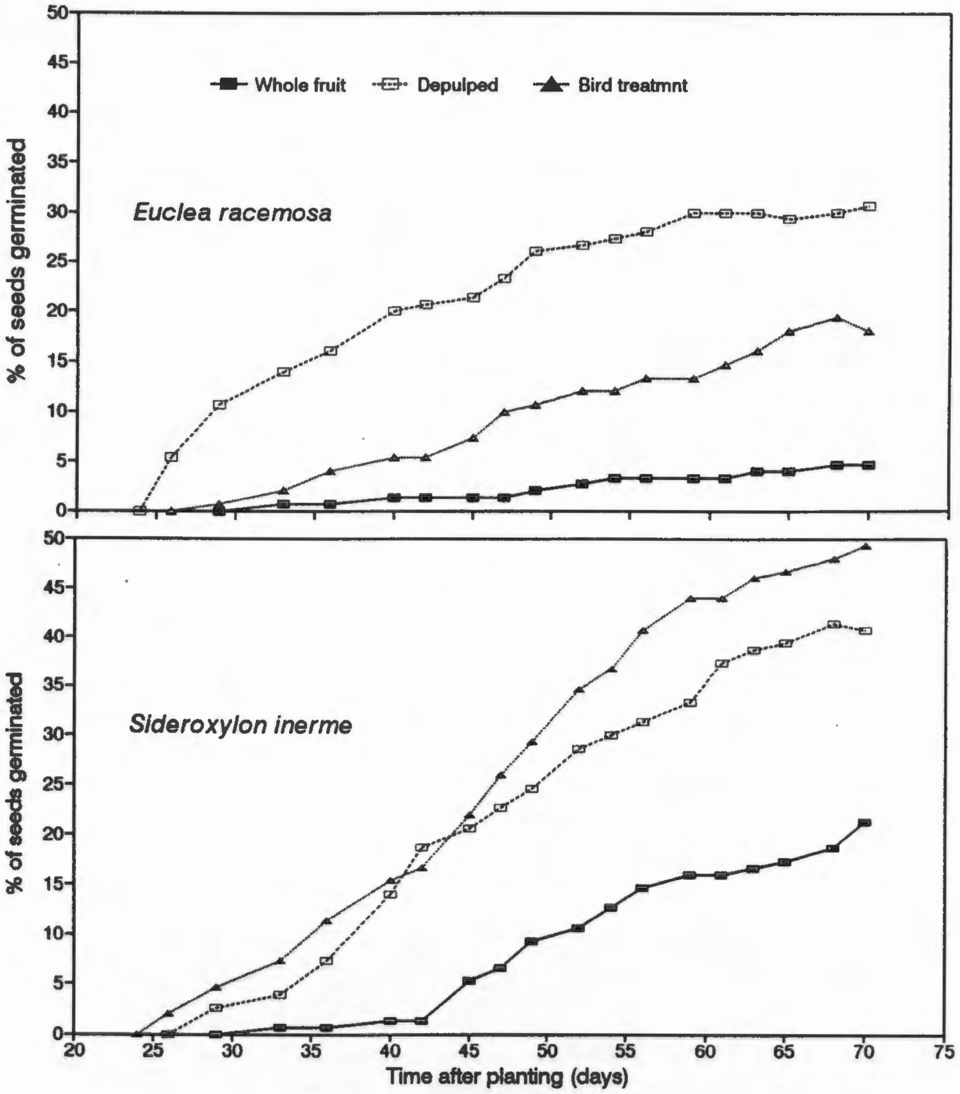

Figure 18. Cumulative percentage of seed germination after no treatment, mechanical removal of pulp and removal of pulp by red-wing starlings. Kolmogorov-Smirnov tests were used to test for differences between different treatments. These test reveal that all *E. racemosa* treatments differ significantly from one another ($p < 0.001$). In *S. inerme*, germination in both pulp removal treatments were significantly different from that of whole fruit ($p < 0.01$). These treatments did not differ from one another ($p > 0.05$).

It is clear from the figure above that removal of fruit pulp resulted in a higher initial growth rates than those of whole fruit in both species. In addition, in *E. racemosa*, mechanical removal of pulp resulted in a higher germination rate than in seed processed by birds. This is probably a result of less thorough removal of pulp than can be achieved by hand (pers. obs.). No seed of *Olea exasperata*, which was subjected to the same treatments, has germinated to date.

Seedling clipping experiment

31 seedlings with a height of approximately 15cm and a basal diameter of 2 to 3 mm were clipped to simulate the effects of fire. This size class corresponded to an estimated age of 1.5 to 3 years. Of these only 2 (ie. 6.5%) failed to resprout, and 1 (3.2%) died. Regressions against root length ($R^2 = 0.77\%$, $p > 0.05$), estimated age ($R^2 = 5.92\%$, $p > 0.05$) and basal diameter ($R^2 = 31.93\%$, $p > 0.05$) failed to explain a significant proportion of the variation in shoot length, probably because of the small variation in size within the sample. However, the results show that most of the seedlings in this size class do have the ability to resprout after removal of their above-ground biomass.

Discussion

The results presented in this paper clearly demonstrate greatly varying patterns of seedling recruitment by thicket species in microsites characteristic of southern Cape dune landscapes. The working hypothesis, that Kaffrarian Thicket succession in Dune Fynbos results from establishment of thicket species under emergent shrubs in fynbos and proceeds through growth and coalescence of these nuclei, resulting in the eventual formation of forest seems to be correct. At both the Agulhas and St. Francis Bay sites, it is apparent that thicket species establish in dune fynbos under emergent shrubs, such as *Metalasia muricata* in the absence of a recent fire. Fynbos species on the other hand, are excluded from these canopied microsites. While thicket succession beyond the formation of a shrubland with *S. inerme* forest at Brandfontein is probably limited by a lack of late successional species, the formation of forest within thicket does occur at the St. Francis Bay site. The actual mechanisms driving the dynamics of thicket establishment at these sites are not clear however.

Cowling (1984) has suggested that dispersal agents, small-scale edaphic factors and fire all play a role in the dynamics of thicket formation. However, the relative importance of each of these factors has not been established. I will thus consider the factors that may play role in causing the patterns observed in this study.

Fire

While many of the characteristics of fynbos vegetation are linked to post-fire dispersal and establishment, this is not the case in thicket. Seedlings of this tropically derived vegetation recruit between fire events. In addition, once established thicket is resistant to burning, and would only be damaged be occasional, very severe fires (Pierce 1990). Seedling sizes within the thicket and forest vegetation were larger than those of the fynbos, suggesting periodic elimination of thicket species in fynbos, but protection of those within thicket vegetation. It is possible that these differences in size could be due to ameliorated environments below the thicket canopy. In general, it seems likely that although regular fire could exclude thicket vegetation from fynbos,it is not the major factor explaining variation in recruitment pattern. Although greater numbers of seedlings were found in the protected thicket environment, establishment within the fynbos did occur, as would be expected between fires. However, this establishment was not random, but nucleated below emergent shrubs in the fynbos, a microenvironment that would not protect seedlings from fire. Another indication of the importance of other factors in thicket development is the variation in species establishment patterns within the fire-protected thicket environment at St. Francis Bay. It is thus likely that other factors play a role in the dynamics of thicket formation leading to the patterns observed here.

Dispersal

The majority of dominant thicket species are bird dispersed, with typically fleshy, large-seeded fruits (Cowling 1984; Knight 1988). Frugivores generally ingest a fruit with both its seed and pulp, defecating the seed intact. As this study has shown, this usually results in an increase in the rate (Loiselle 1990) and the percentage (Fountain and Outred 1991; Izhaki and Safriel 1990) of seeds that germinate afterward, as well as resulting in dispersal some distance from the vicinity of the parent plant (Howe 1986). This may be especially important in the movement of propagules across vegetation boundaries, as has been demonstrated by Manders and Richardson (1992) for the establishment of Afromontane forest species.

Janzen (1988) states that the formation of nuclei of one vegetation type within another is a characteristic of colonization resulting from vertebrate dispersal. It seems likely that this is the means by which thicket species establish in dune fynbos. This dispersal is not random. Perches have been shown to be an important factor resulting in the directed dispersal of bird dispersed seed. Seed is usually defaecated under or within a short distance from a perch (Izhaki et al. 1991; Knight 1988; Manders 1990). Many of the seedlings germinating below fynbos emergents occurred in single age clumps suggestive of recruitment from one faecal deposit (pers. obs.)

In this study, the establishment of greater numbers of seedlings beneath the canopy of emergent shrubs in fynbos suggests that bird dispersal may be an important factor in determining patterns of thicket seedling establishment within the fynbos. The lower numbers of seedlings evident below emergent shrubs compared to the microsite below the thicket canopy could even be a function of the amount of time birds spend in each environment. It has been demonstrated that frugivorous birds generally spend less time on non-food plants than on those species which bear fruit (Izhaki et al. 1991). Seed dispersal to the site below the generally non-fruiting fynbos plants, such as *Metalasia muricata* (Pierce 1990), would thus be considerably lower than below fruiting species of the thicket vegetation. However, there is considerable variation in patterns of seedling establishment within thicket, thicket/forest and forest environment at the St. Francis Bay site. It seems likely that even if various dispersers were preferentially selecting the fruit of particular species (eg. Izhaki et al. 1991), these birds would then remain in the vicinity of these species, at least for the relatively short duration (ca. 30 minutes) which seed spends in the gut of frugivorous birds (Loisselle 1990). Such a factor may explain why forest species at St. Francis Bay establish only under the canopy of their own vegetation type. However, differential dispersal of various thicket species seems unlikely to explain why there are more species establishing under thicket and thicket/forest than under emergent shrubs in the fynbos.

Facilitation by habitat amelioration

Many aspects of this study suggest that facilitation vegetation change by means of habitat amelioration may be important. Clement's (1916) seminal work stressed the importance of habitat amelioration, particularly soil development, by earlier successional plants in facilitating the establishment of later species. More recently, many workers have demonstrated similar processes, whereby the presence of early successional plants results in changes to aspects of their physical environment such as shade (eg. Kellman and Kading

1992; Manders and Richardson 1992), soil development (eg. Yarranton and Morrison 1977) or some combination of such factors (eg. Campbell et al. 1990).

This study clearly demonstrated that habitat amelioration progressed from one successional stage to another, from the environment below fynbos emergents through to climax forest. At Brandfontein soil development (increased nitrogen and organic matter) was already shown to occur beneath fynbos emergents as reported by Manders and Richardson (1992) for mountain fynbos. Water contents were demonstrably higher in microsites representing the later successional stage compared to those representing earlier stages. Light penetration was reduced under the canopies of fynbos emergents and thicket formations compared to more open areas. There was little difference between the light penetrating below fynbos emergents an thicket formations however.

When one compares this evidence of progressive habitat amelioration under different successional stages, with patterns of seedling establishment in these environments, it seems likely that facilitation is occurring. This is especially plausible for the data from the St. Francis bay site, where successive groups of species establish in different microsites within established thicket and forest formations. These patterns are unlikely to be entirely explained by fire and dispersal by birds. This evidence is however entirely inferential, relying in patterns in space to explain changes over time.

Conclusion

While many studies seem to rely on similar inferential techniques (eg. Campbell et al. 1990; Yarranton and Morrison 1977), the only reliable way to determine the relative importance of vertebrate (bird) dispersal, facilitation and fire in the dynamics of thicket vegetation is by means of experiment. Unfortunately the experimental evidence presented earlier is inconclusive. The growth of *Euclea racemosa* in the open fynbos microsite however, indicates that habitat amelioration may not be vital to the establishment of certain thicket species. This would require further testing, with higher replication than has been used here.

The results of this study suggest that succession from dune fynbos to thicket begins by means of directed dispersal by frugivorous birds to relatively ameliorated microsites below emergent fynbos shrubs. This would result in a nucleated pattern of development (eg. Yarranton and Morrison 1977), as is observed in the dune landscapes of the southern Cape. These nuclei would then coalesce by means of both vegetative reproduction by ramets and increased seed rain due to the attraction of greater numbers of bird dispersers. The eventual result would be the establishment and development of climax forest (assuming the presence of suitable propagules), in the more ameliorated thicket environment. It is likely that this process could be disrupted by fire in the initial stages of nucleation. After development of thicket however, the vegetation is likely to be substantially fire resistant. The process described above is largely hypothetical, inferred from the data presented above and previous work on establishment of vertebrate dispersed vegetation. Further experimentation, mainly by means of outplanting experiments on a larger scale than those described here, is required to separate the relative effects of microsite amelioration and directed dispersal in determining patterns of thicket recruitment.

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References

ACOCKS, J.P.H. 1974 Veld Types of South Africa. 2^{nd} Ed. *Mem. Bot. Surv. S. Afr.* 57.

CAMPBELL, B.M., ATTWELL, C.A.M., HATTON,J.C., DE JAGER, P.,GAMBIZA, J., LYNAM, T., MIZUTANI, F. and WYNTER, P. 1988 Secondary dune succession on Inhaca Island, Mozambique. *Vegetatio.* **78**:3-11

CAMPBELL, B.M., LYNAM, T. and HATTON, J.C. 1990 Small-scale patterning in the recruitment of forest species during succession in tropical dry forest, Mozambique. *Vegetatio.* **87**:51-57

CLEMENTS, F.E. 1916 *Plant Succession.* Washington:Carnegie Institute

COWLING, R.M. 1984 A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. *Bothalia.* **15**:175-227

COWLING, R.M. and HOLMES, P.M. 1992 Flora and vegetation. **In:** *The Ecology of Fynbos. Nutrients, Fire and Diversity.* pp 23-61 (Ed. Cowling, R.M.) Cape Town:Oxford University Press.

HOWE, H.F. 1986 Seed dispersal by fruit eating birds and mammals. **In:***Seed Dispersal.* (Ed. Murray, D.R.) pp 123-189 Sydney:Academic Press

IZHAKI, I. and SAFRIEL, U.N. 1990 The effect of some Mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology.* **78**:56-65

IZHAKI, I., WALTON. P.B. and SAFRIEL, U.N. 1991 Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *J. Ecol.* **79**:575-590

JANZEN, D.H. 1988 Management of habitat fragments in a tropical fry forest: Growth. *Ann. Missouri Bot. Gard.* **75**:105-116

KELLMAN, M. and KADING, M. 1992 Facilitation of tree seedling establishment in a sand dune succession. *Journal of Vegetation Science.* **3**:679-688

KNIGHT, R.S. 1988 Aspects of plant dispersal in the southwestern Cape with particular reference to the rôles of birds as dispersal agents. Ph.D. Thesis. University of Cape Town.

LANGLEY, R. 1968 *Practical Statistics.* London:Pan Books Ltd.

LOISELLE, B.A. 1990 Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. *Oecologia.* **82**:494-500

MACVICAR, C.N., DE VILLIERS,J.M., LOXTON, R.F., VERSTER, E., LAMBRECHTS, J.J.N., MERRYWEATHER, F.R., LE ROUX, J., VAN ROOYEN, T.H. and HARMSE, H.J. VON M. 1977 *Soil Classification. A Binomial System for South Africa.* Science Bulletin 390. Department of Agricultural Technical Services.

MANDERS, P.T. and RICHARDSON, D.M. 1992 Colonization of Cape fynbos communities by forest species. *Forest Ecology and Management.* **48**:277-293

PIERCE, S.M. 1990 Pattern and process in South Coast Dune Fynbos: population, community and landscape level studies. Ph. D. Thesis, University of Cape Town.

VAN DER PIJL, L. 1982 *Principles of Dispersal in Higher Plants.* 3rd Ed. New York:Springer Verlag

YARRANTON, G.A. and MORRISON, R.G. 1977 Spatial dynamics of primary succession: nucleation. *The Journal of Ecology.* **62:**417-427

APPENDIX 1

Species recruiting as seedlings and ramets at Brandfontein, Agulhas:

* **denotes a spp. recruiting by means of ramets as well as seedlings.**

** **denotes a species found recruiting by means of ramets**

Fynbos species:

Agathosma collina

Metalasia muricata

Ortholobium fruticans

Passerina paleacea

Phylica ericoides

Thicket species:

Cassine peragua*

Colpoon compressum

Euclea racemosa subsp. *racemosa**

Maytenus procumbens*

Olea exasperata*

Pterocelastrus tricuspidatus*

Rhus glauca*

R. laevigata

R. lucida**

Zygophyllum flexuosum

Forest spp.:

Sideroxylon inerme*

APENDIX 2

Species recruiting as seedlings St. Francis Bay, Cape St. Francis:

Thicket species:

Rhus glauca

Rhus laevigata

Rhus schleterana

Rhus crenata

Colpoon compressum

Species occurring in thicket and forest:

Euclea racemosa

Putterlickia pyracantha

Pterocelastrus tricuspidatus

Rhamnus prinoides

Cassine peragua

Maytenus procumbens

Rhoicissus digitata

Carissa bispinosa

Grewia occidentalis

Cissampelos capense

Cassine aethiopica

Myrsiphyllum asparagoides

Protosparagus aethiopicus

Capparis sepiaria

Secamone alpinii

Cynanchium obtusifolium

Maytenus heterophylla

Scutia myrtina

Sideroxylon inerme

Forest species:

Chionanthus foveolatus

Clauseria anisata

Zanthoxylum capense

Scolopia zeheri

Schotia afra