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Dynamics and Conservation Status of the Swartkransberg Forests

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November 1994

Contents:

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ABSTRACT

The forests of the Swartkransberge, described as a combination of species from the Afromontane and Tongo-Pondoland phytochoria, are the largest remaining patches of lowland forests in the western Cape. Size-class distributions, life history dynamics of the dominant canopy species, gap versus canopy recruitment and effects of anthropogenic disturbance were investigated in order to determine the dynamics and conservation status of the forests.

The short forests, Grootbos, Kleinbos and Steynsbos, were dominated by slow growing sprouting species, which were resilient to anthropogenic disturbance and thus would not require intensive conservation. The tall forests, Platbos and Stinkhoutsbos, were dominated by shade tolerant, predominantly seeding species which did not require gaps for recruitment. They were more sensitive to anthropogenic disturbance, and would therefore require more active conservation.

In the second section of the study, a model of forest dynamics based on forest canopy height was developed.

Regeneration modes and architectural patterns were studied in each forest and related to height. Increased canopy height was found to be strongly related to the reliance on seeding as the dominant mode of regeneration in a forest. Also, that as the height of the forest increased, the branching patterns of the trees became increasingly more monopodial. Thus reproductive mode and their associated architectural patterns changed with canopy height.

This has two important implications for mangers:

a) the model is useful for rapid assessment of forest dynamics and hence easier to determine conservation status.

b) highlighted the importance of sprouting as a regeneration strategy.

INTRODUCTION

Lowland forests cover less than 0.05% of the surface area of the Western Cape, and of these only 10% are adequately protected (Jarman, 1986). The Swartkransberg forests, found in the Stanford/Gansbaai area, are some of the largest remaining lowland forest fragments in the Western Cape (McKenzie et al, 1990). However, due to the increasing in agricultural development in the area, these forests are under increasing pressure.

Based on both floristic and structural studies, the Swartkransberg Forests were described by McKenzie et al (1990) as having distinct affinity to the northern Natal, Tongo-Pondoland phytochoria. They are unique in their species composition, and are the only forests of their kind in South Africa (McKenzie et al, 1990), and thus qualify for protection status. They also form the only remaining habitat for a number of the local fauna e.g. Grysbok, Bushbuck, and numerous birds and bats which rely on the fruits of the trees as a source for food. The forests are found largely on privately owned land (pers. obs.) and despite this enjoy some degree of protection, but have been subjected to both historical and recent disturbance. Already in 1960's, Taylor (1961) had recognised the need to study the dynamics of the forests, in order to determine the effects of disturbance on the forests. McKenzie et al (1990), studied the floristics of the forests, but did not delve deeply into their actual dynamics. The aim of this study is thus to research into the dynamics of the forests, including also the role of anthropogenic disturbance.

Forest dynamics are defined as the complex interaction between life histories of the constituent species, regeneration dynamics and (natural) disturbance regime (Midgley & Gobetz, 1993). A number of methods exist by which forest dynamics can be studied. When size and age of conspecific individuals are correlated, a good fit of the negative exponential function to size class distributions of stems present on a plot, indicates continuous regeneration (Veblen et al, as cited in Midgley et al, 1990). However, due to the difficulties involved in measuring ageing and time constraints, an alternative method was used. The size-class distribution of a species gives an indication of demographic state of the species. A negative exponential curve (an inverse J-shape) indicates continuous regeneration (Midgley et al, 1990). Additionally, characteristics of the species' life history can be inferred from the shape of the size-class distribution (Midgley et al, 1990). Specific leaf area was also used as a indicator of life history strategies, notably shade tolerance. Species that are known to be shade tolerant, have a lower leaf maximum photosynthetic capacity (King, 1991) and consequently a lower RGR (Reich et al, 1991, 1992), which, in turn, is strongly related to SLA. Thus the lower the SLA, the greater the shade tolerance. Gap versus non-gap comparisons were conducted to study the forest recruitment dynamics to gain further insight into regeneration dynamics. Forest area comparisons were made between 1938 and 1989 to determine whether the forests were expanding or disappearing. From this information I deduced the conservation status of the Swartkransberg forests.

Since there are a number of forest patches in the area, and to study the dynamics of each would require a great deal of time and effort, the need for a general model of forest dynamics, which could be applied to all forests, was identified. The study of the Swartkransberg forests revealed two notable trends: regeneration mode and tree architecture patterns changed with forest canopy height. This led to the development of the theory of how canopy height affects regeneration dynamics in forests. A model such as this is useful in rapidly assessing the dominant regeneration strategies in a forest without having to study each of the species. Because regeneration is the key to long term survival, by assessing the regeneration dynamics in this manner, we gain rapid, useful insight into the conservation status of the particular forest.

The study is therefore divided into two sections: Part A. dealing with the dynamics and conservation status of the Swartkransberg Forests, while part B deals with the development of a model of forest dynamics.

A: Conservation status of the Swartkransberg Forests

METHODS

Study site

Location and description:

The five Tongo-Pondoland/Afromontane forests (as described by Mckenzie et al (1990)) are all situated in the Stanford Gansbaai area (Fig. 1).

Short Forests: Grootbos, Kleinbos, Steynsbos, are dominated by *Sideroxylon inerme* and *Euclea racemosa*, with a high representation of *Linociera foveolata* (Table 1). These forests are found on the windward slopes of the Baviaansfontein hills, 300m above sea level, within 7km from the sea. They are exposed to strongly desiccating summer south-easterly winds and the powerful rain-bearing westerly winter winds (McKenzie et al, 1990), hence their wind moulded physiognomy (Taylor, 1961).

Tall forests: Platbos, located on a gentle slope (4°) and Stinkhoutsbos, in a deep valley, are both situated on the eastern (leeward) slopes of the Baviaanspoort Hills, 8.5 km inland. They are thus well sheltered from the winds and coastal conditions by the intervening hills and having deeper, moister soil than the short forest, Platbos has therefore attained a higher degree of development (Taylor, 1961). Taylor describes Platbos as a **Celtis-Olinia-Apodites Tall Forest**, owing to their relative dominance in the forests. The forest sub-dominants include *Canthium mundianum*, *Linociera foveolata* and *Sideroxylon inerme*.

Stinkhoutsbos, on the other hand is dominated by *Ocotea bullata*, *Rapanea melanophloeos*, *Olinia ventosa*, *Apodytes dimidiata*, *Celtis africana* and *Kiggelaria africana* (Table 1).

The forests, other than Platbos, are surrounded by mature Proteoid fynbos. Platbos is largely surrounded by cultivated lands.

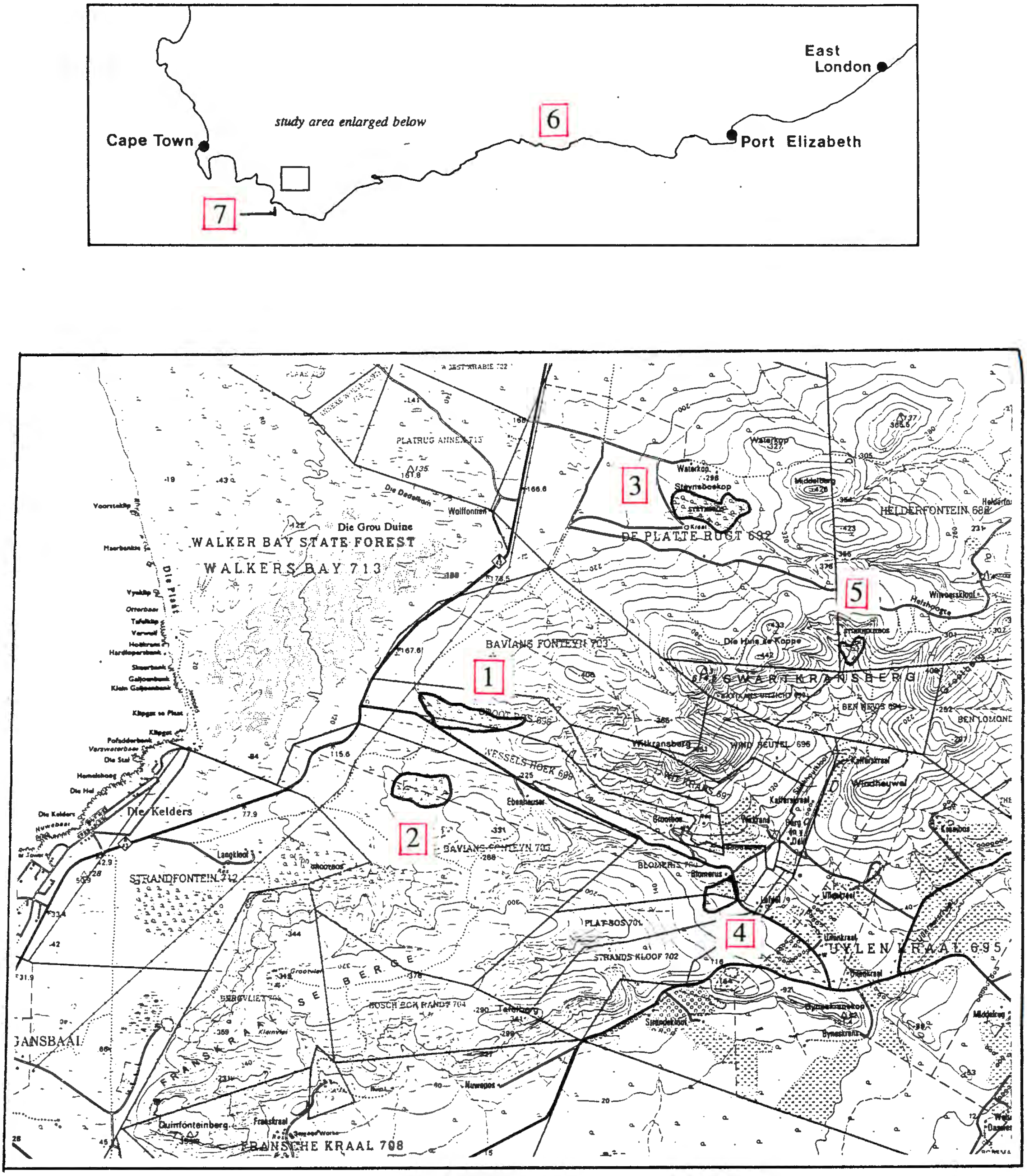


Figure 1. Map showing the location of the study sites.

1: Grootbos; 2: Kleinbos; 3: Steynsbos 4: Platbos; 5: Stinkhoutsbos
6: Groenbos; 7: Danger Point Forest

Table 1 Dominant canopy species of the Swartkransberg Forests

	Forest				
Dominant species	Grootbos	Kleinbos	Steynsbos	Platbos	Stinkhoutsbos
Apodytes dimidiata				*	*
Celtis africana				*	*
Canthium mundianum				*	*
Ilex mitis					*
Kiggelaria africana				p	*
Ocotea bullata					*
Olea europaea subsp. africana			*		p
Olinia ventosa				*	*
Pteracelastrus tricuspidatus	*			p	
Rapanea melanophloeos					*
Euclea racemosa	*	*	*	*	
Linociera foveolata	*	*	*	*	*
Sideroxylon inerme	*	*	*	*	p
Maytenus heterophylla	*	*		p	p

p = presence in the forests, but not as a dominant canopy species

Climate, Topography and Soil:

The climate of the region is considered by Cowling et al (1988) to be relatively uniform. The mean annual rainfall at Gansbaai is 600mm (McKenzie et al, 1990) of which 65-75% occurs in the winter months (between May and October). Average annual temperatures range between 15°C and 16°C (Cowling et al, 1988). Grootbos, Kleinbos and Steynsbos are all located on a gentle East-West slope, 30-40m above sea level. Platbos, found in a gentle North-South valley, is relatively flat in topography. The forests all lie within the strip of coastal limestone where the soils are described as predominantly recent calcareous sands. The soils are organic-rich, dark, alkaline with a high sandy/loam component, which are characteristic of the coastal forest/thicket environments (Cowling et al, 1988).

Sampling Techniques

I. Forest Dynamics

a. Life history strategies

Size class distributions:
Within each forest, four 20m x 20m plots were layed out and in each all individuals of the dominant canopy species was noted. Where small sample numbers occurred, a 50m long 5m transect was sampled. In the case of Stinkhoutsbos and Steynsbos, where using 20m x 20m plots was not feasible because of the extreme density of the undercover and/or the unmanageable terrain, an equivalent area of 5m transects were used.

Size-class information consisted of the following:

i. regeneration individuals: any established individuals, emerging from the ground, greater than 15cm tall but shorter than 50cm. Hereafter they are termed "recruiting individuals" (RI) in the text. Since basal and stem sprouts are still visibly connected to the adults, they were not considered to be individuals.

ii. saplings: individuals taller than 50cm but with a diameter at breast hight (DBH) smaller than 5cm.

iii. poles: individuals with a DBH greater than 5cm and smaller than 10cm.

iv. mature trees: individuals greater than 10cm DBH. In the case of multistemmed individuals, the largest of the stems was noted.

From these data a size-class frequency distribution of each species, in each the forests, were determined.

Specific Leaf Area (SLA):

The area and dry weights (leaves were dried at 65°C for 24 hrs) of 10 sun leaves from the exposed canopy of each species were determined. SLA was determined as leaf area/dry weight ($cm^2.g^{-1}$).

b. Regeneration dynamics

Gap versus Canopy comparisons:

In each of the forests thirty five 2m x 2m plots were randomly sampled for seedlings, in both the gaps and under the forest canopy, to determine the primary sites of recruitment. Seedlings were determined as any self-supporting individual between 10cm and 50cm tall.

c. Disturbance regimes:

A subjective assessment of disturbance for each forest was determined along the same lines as McKenzie et al (1990). The assessment was used as an aid to determining the conservation status of the forest. Disturbances took the form of grazing/browsing, fire, aliens, trampling and woodcutting. The extent of each was rated according to a scale of 0 - 5.

0 = no disturbance
1 = slight disturbance:
2 = moderate disturbance
3 = moderate to severe disturbance
4 = severe disturbance:
5 = very severely disturbed

History of disturbance was also investigated by looking at the aerial photographs from 1938. Further information on disturbance history was obtained from Taylor (1961).

III. *Total area of forests*

The historical changes in the extent of the forests were determined by measuring the areas of the forests in 1938 and 1989 from aerial photographs, using the Arcarea digitiser program. The aerial photographs were supplied by the Cartography Department of the CPA. These measurements were then compared to determine whether the forests have decreased/increased in extent in the last 50 years.

Statistical analysis

Statistical and data analyses, and graphic display were performed using the STATGRAPHICS and QUATTRO PRO software packages. To determine whether there was any difference seedling recruitment patterns between the gaps and under the canopy, T-Tests were used for parametric, homoscedastic data, and Mann Whitney U tests for nonparametric, heteroscedastic data.

RESULTS

I. Short forests:

a. GROOTBOS:

Size class distributions: Most of the species have the typical inverse J-shaped size-class distribution (**Fig. 2**), except *Sideroxylon inerme* and *Maytenus heterophylla. S.inerme* and *M.heterophylla* are both basal sprouters and do not produce RI, hence the positive exponential-like curve of their size-class distribution. This indicates that for the dominant species in the forest, regeneration is well established. All of the dominant canopy species in Grootbos had low SLA (**Fig. 3**) and were thus relatively slow growing.

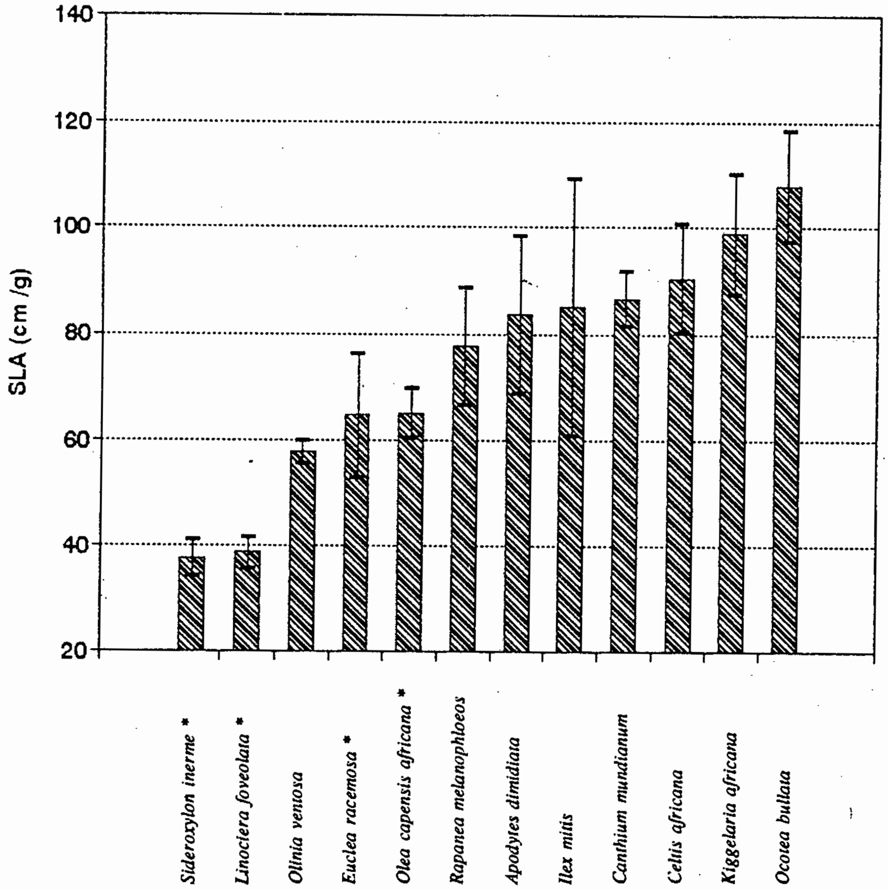


Figure 3. Mean SLA of the dominant canopy species in the Swartkransberg Forests.
* denotes species found primarily in the short forests.

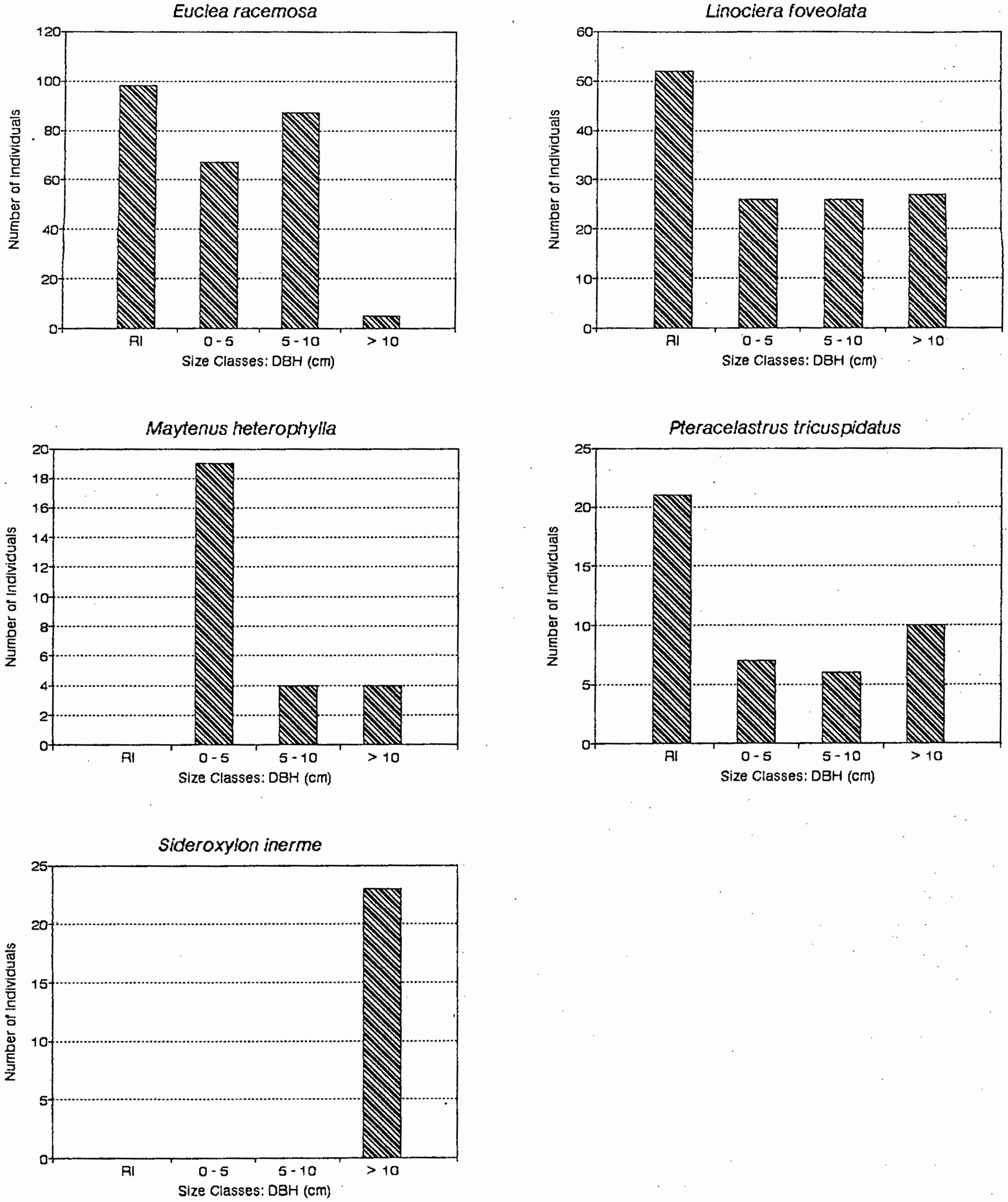


Figure 2. Size class distributions of the species found in Grootbos, near Stanford in the western Cape Province, RSA. RI = Recruitment individual.

Regeneration dynamics: Seedling recruitment was significantly greater under the canopy than in the gaps (Mann Whitney stat = -2.34, p < 0.02) **(Table 2).**

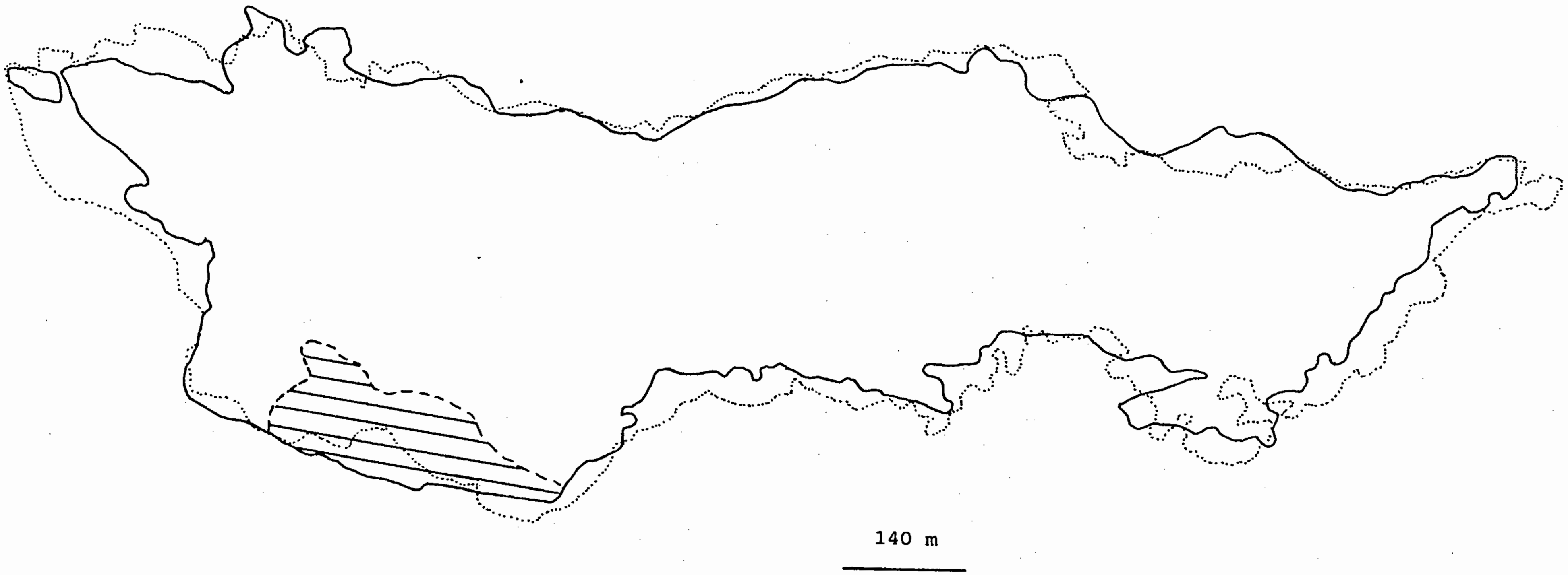
Table 2. Mean number of seedlings per 2m x 2m plot (SE in parentheses) under the canopy versus in the gaps, in the Swartkransberg Forests, near stanford in the western Cape.

	Canopy		Gap		Mann-Whitney U test	
Forest	mean		mean		z stat	Sign. level
Grootbos	9.88	(2.23)	2.86	(1.93)	-2.34	p < 0.02
Kleinbos	9.31	(1.39)	4.57	(0.69)	-2.88	p < 0.002
Steynsbos	17.46	(5.44)	2.5	(1.63)	-2.39	p < 0.02
Platbos	12.2	(1.88)	5	(1.9)	-2.193	p < 0.02
Stinkhoutsbos	7.72	(1.21)	6.33	(1.62)	NS	

Disturbance: The main source of disturbance in Grootbos were from alien invasives (mostly *Acacia saligna*), trampling (by horses and cattle) and woodcutting (both present and historic) **(Table 3)**, especially in the western portions. Grootbos is the most disturbed of the Swartkransberg forests.

Table 3. Disturbance levels for five factors in the Swartkransberg forests.

	Disturbance Factor					
Forest	Grazing	Fire	Aliens	Trampling	Woodcutting	Total
Grootbos	2	2	3	3	4	14
Kleinbos	2	1	1	3	2	9
Steynsbos	1	0	2	1	0	4
Platbos	2	3	2	2	3	12
Stinkhoutsbos	0	2	1	0	4	7
Total:	7	8	9	9	13	46



KEY:
——— forest perimeter: 1989
.... forest perimeter: 1938
▨ alien invasion: 1989

Forest area
1938: 0.4018 km^2
1989: 0.3337 km^2

Figure 5. Comparison of Grootbos forest area: 1989 vs 1938.

Area: The total area of Grootbos had decreased in size from 1938 to 1989 (**Fig.4**). This is graphically depicted in **Figure 7**.

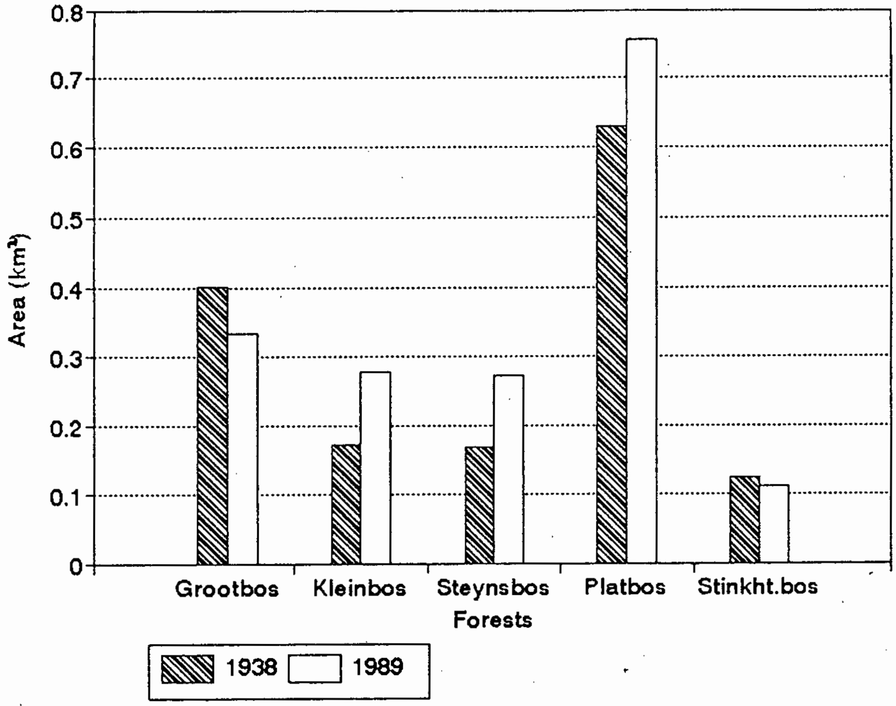


Figure 4. Change in forest area between 1938 and 1989 of the five Swartkransberg Forests near Stanford, western Cape Province, South Africa.

KLEINBOS:

Size class distributions: Most of the dominant canopy species, except *S.inerme*, displayed inverted J-shaped size-class distribution (**Fig.6**). Most of the species in the forest had relative low SLA (**Fig. 3**).

Regeneration dynamics: As with Grootbos, seedlings largely recruited under the canopy (mann whitney U stat = -2.88, $p < 0.005$) (**Table 2**).

Disturbance: Trampling and woodcutting were the two disturbance factors that were seen to have the greatest impact on Kleinbos (**Table 3**). Farmers graze their stock in the surrounding fynbos (pers. obs.), and the cattle wander into the forest, creating wide, highly disturbed paths through the forest. From the aerial photographs taken in 1938, evidence of large scale woodcutting

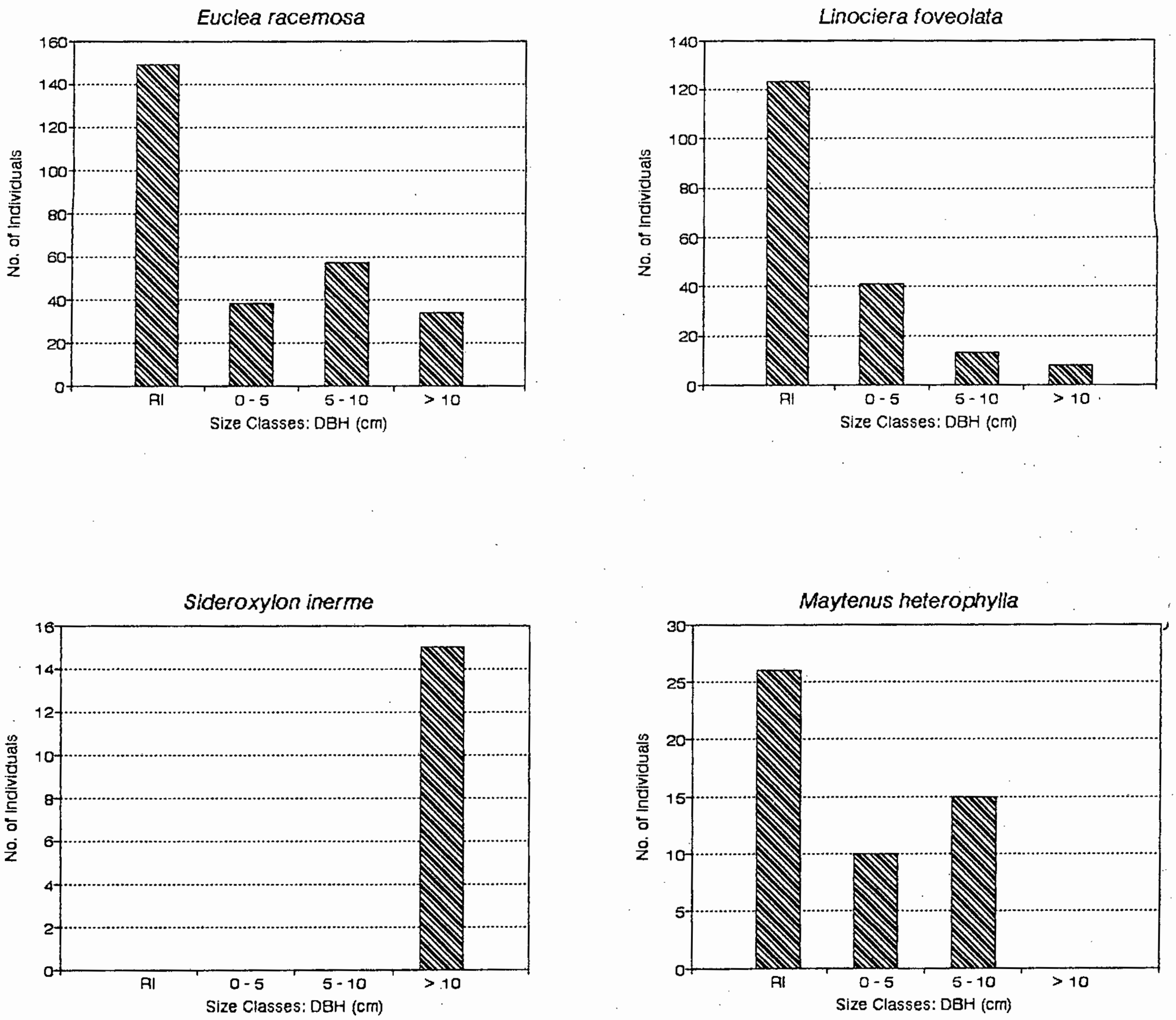
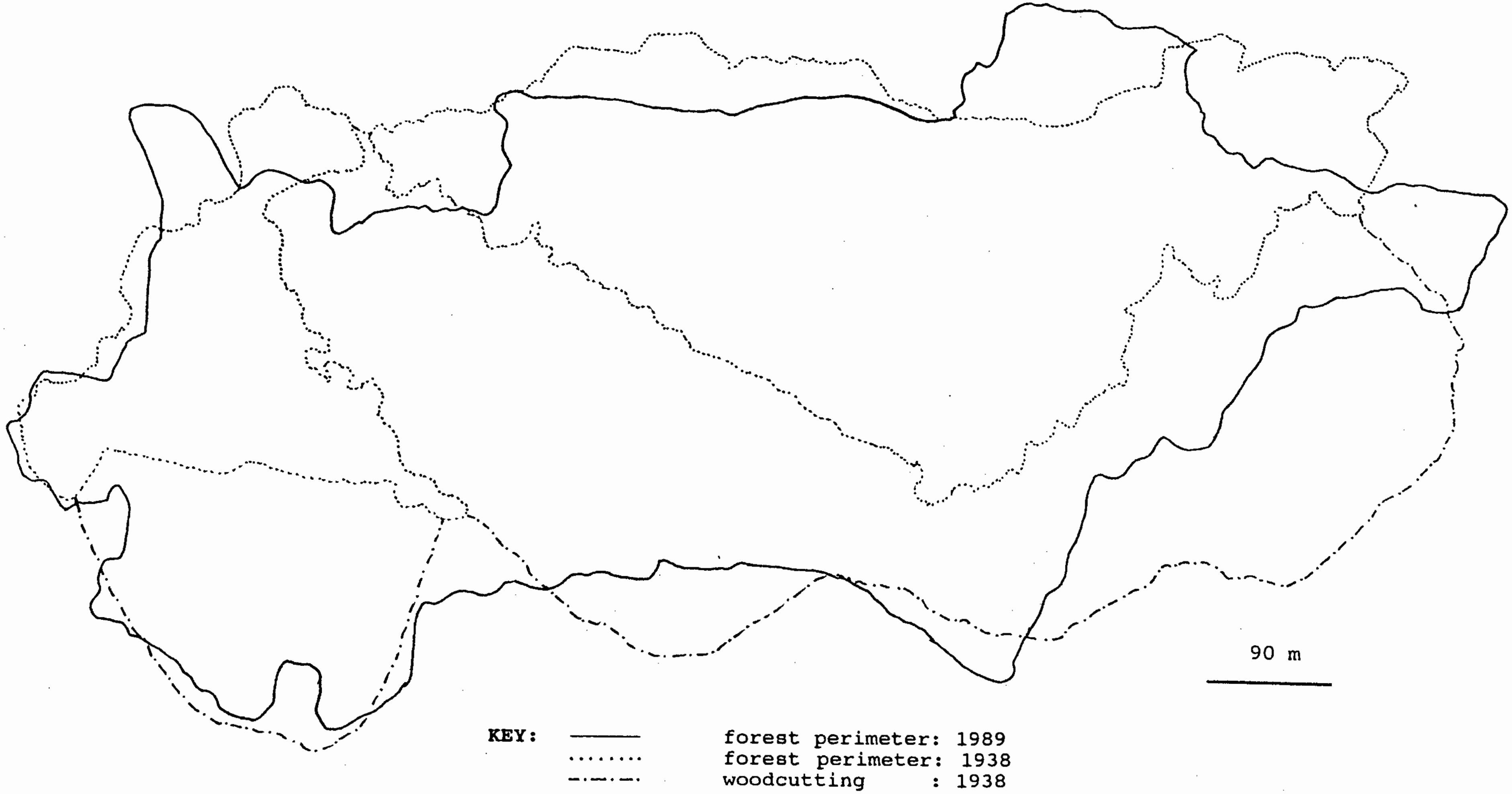


Figure 6. Size class distributions of the species found in Kleinbos, near Stanford in the western Cape Province, RSA. RI = regeneration individual.



Forest area
1938: 0.1725 km^2
1989: 0.2785 km^2

Figure 7. Comparison of Kleinbos forest area: 1989 vs 1938.

is very obvious. Large tracts of the forest had been felled just prior to the photograph being taken, which had regrown by 1989 **(Fig.7)**.

Area: Kleinbos increased significantly in area from 1938 to 1989 **(Figs. 4 & 7)**.

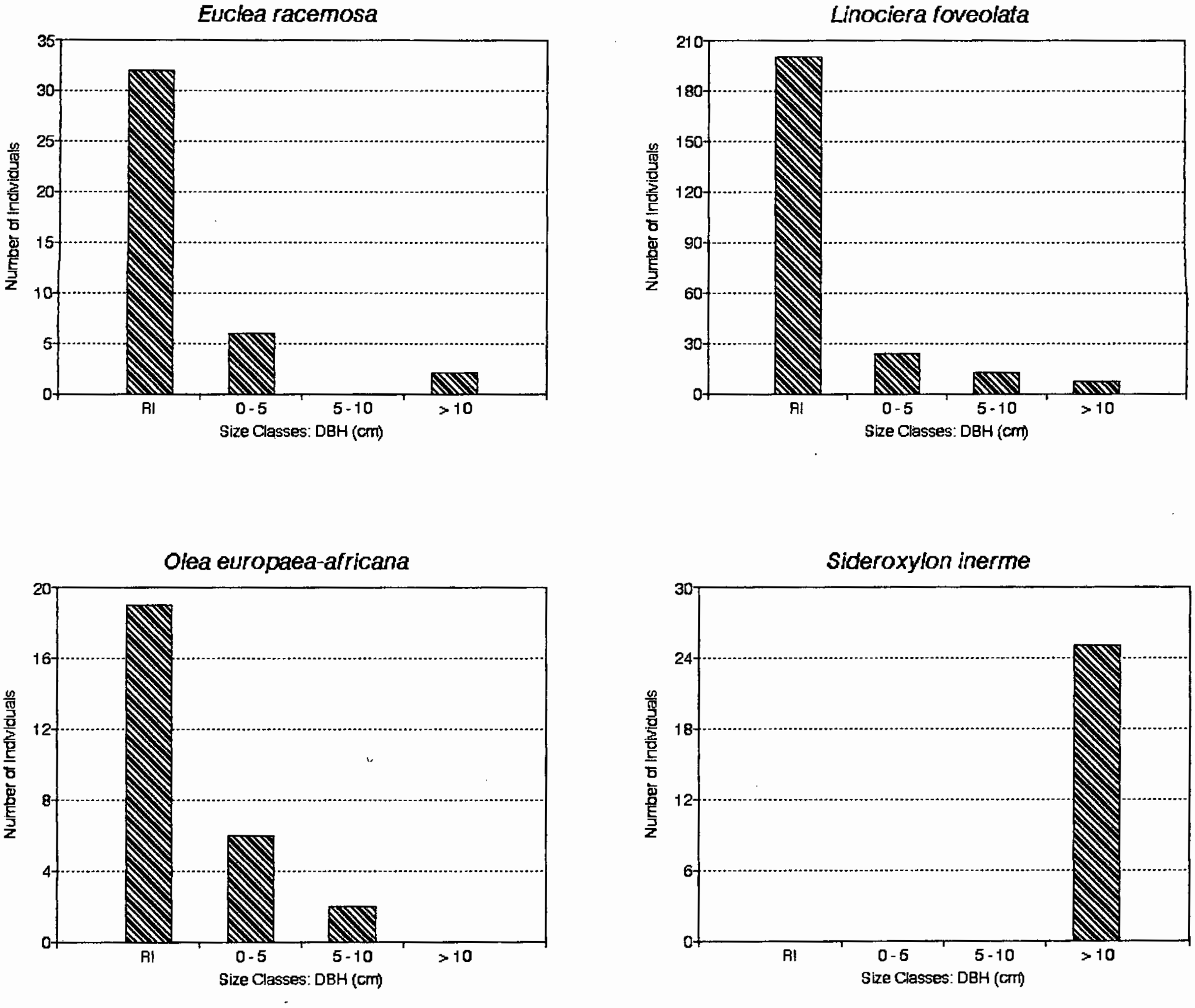
STEYNSBOS:

Size class distributions: *E.racemosa, L.foveolata* and *O.europaea subsp. africana* all displayed distinct inverse J-shaped size-class distributions, while *S.inerme* did not have any individuals in the 0-10cm DBH size-class **(Fig.8)**. Like Grootbos and Kleinbos, the species found in Steynsbos had relatively low SLAs **(Fig. 3)**.

Regeneration dynamics: As with Grootbos and Kleinbos seeders recruit under the canopy **(Table 2)**.

Disturbance: Steynsbos was found to be relatively undisturbed, with aliens invasives contributing the most to overall allogenic disturbance **(Table 2)**.

Area: Steynsbos increased markedly (by 63%) in area from 1938 to 1989 **(Figs. 4 & 9)**.



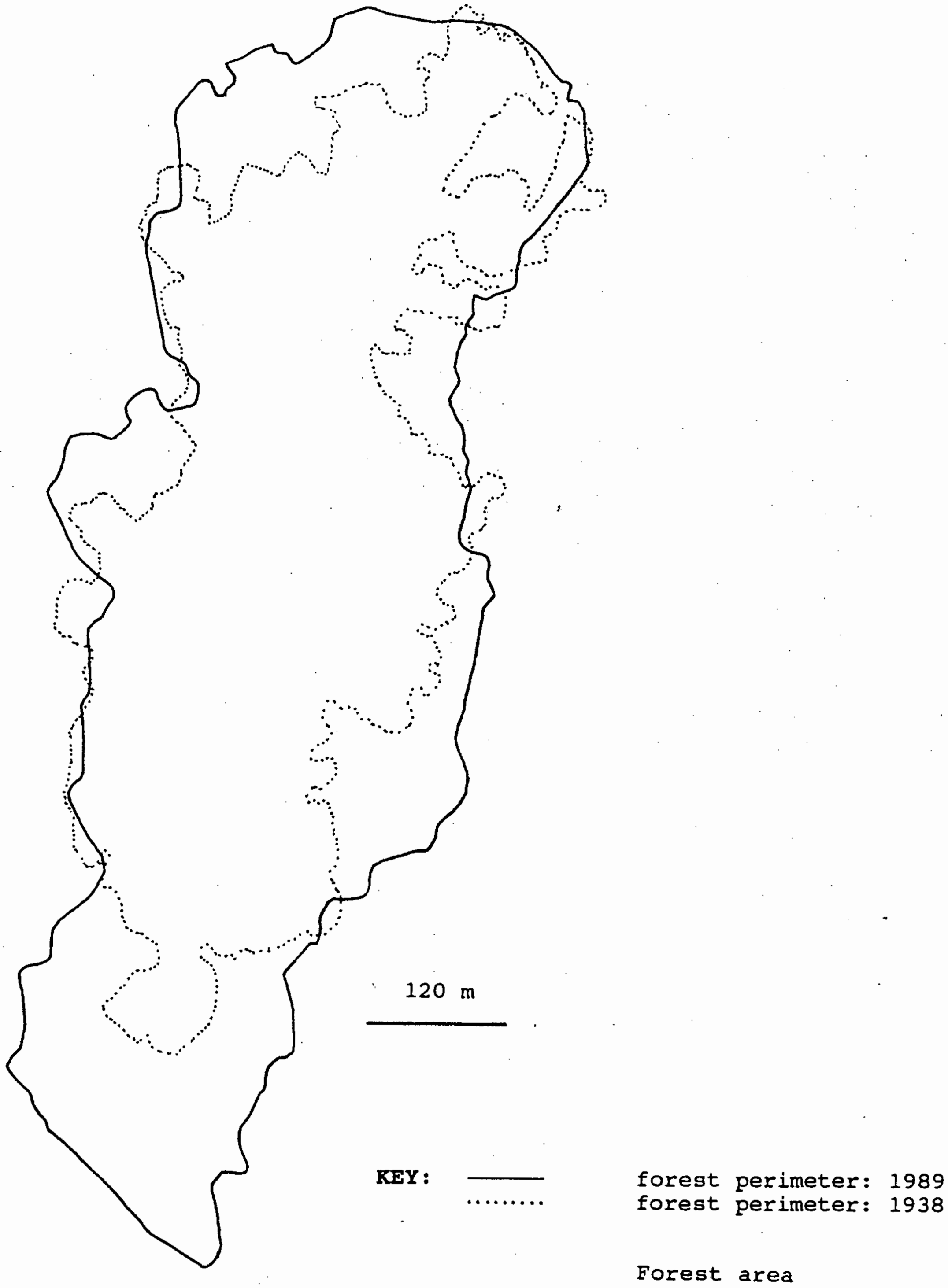
Euclea racemosa

Linociera foveolata

Olea europaea-africana

Sideroxylon inerme

Figure 8. Size class distributions of the species found in Steynsbos, near Stanford in the western Cape Province, RSA. RI = Recruitment individuals.



Forest area
1938: 0.1687 km²
1989: 0.2748 km²

Figure 9. Comparison of Steynsbos forest area: 1989 vs 1938.

II. Tall Forests

PLATBOS:

Size class distributions: The species that relied on the production of RI for survival, *C.africana, L.foveolata, C.mundianum* and E.racemosa, all displayed a negative exponential curve. The basal sprouters, such as *S.inerme*, only had recorded individuals in the largest size-class. *A.dimidiata* had a relatively flat slope and *O.ventosa* had a distinct lack of smaller individuals, with far more individuals in the >10cm DBH category **(Fig.10)**.
The mean SLA of the species in the forest were roughly divided into two categories: those with relatively low SLA *S.inerme, E.racemosa, L.foveolata* and *O.ventosa*; and those with relatively high SLA, *A.dimidiata, C.mundianum* and *C.africana* **(Fig. 3)**, indicating a difference in life history strategies.

Regeneration dynamics: The seedlings of the obligate seeders, *C.africana* and *L.foveolata* were found in greater numbers beneath the canopy (mann Whitney U stat = -2.193, $p < 0.02$) **(Table 2)**, but *S.inerme* and *E.racemosa* were especially in the allogenic disturbance gaps (tree fell gaps, gaps created by trampling) (pers.obs).

Disturbance: Fire, woodcutting and trampling were the main sources of allogenic disturbance in the relatively disturbed Platbos **(Table 3)**. However, judging from the aerial photographs, Platbos was subject to extensive logging in the 1930's.

Area: Platbos increased in area from 1938 to 1989 **(Fig. 4 & 10)**.

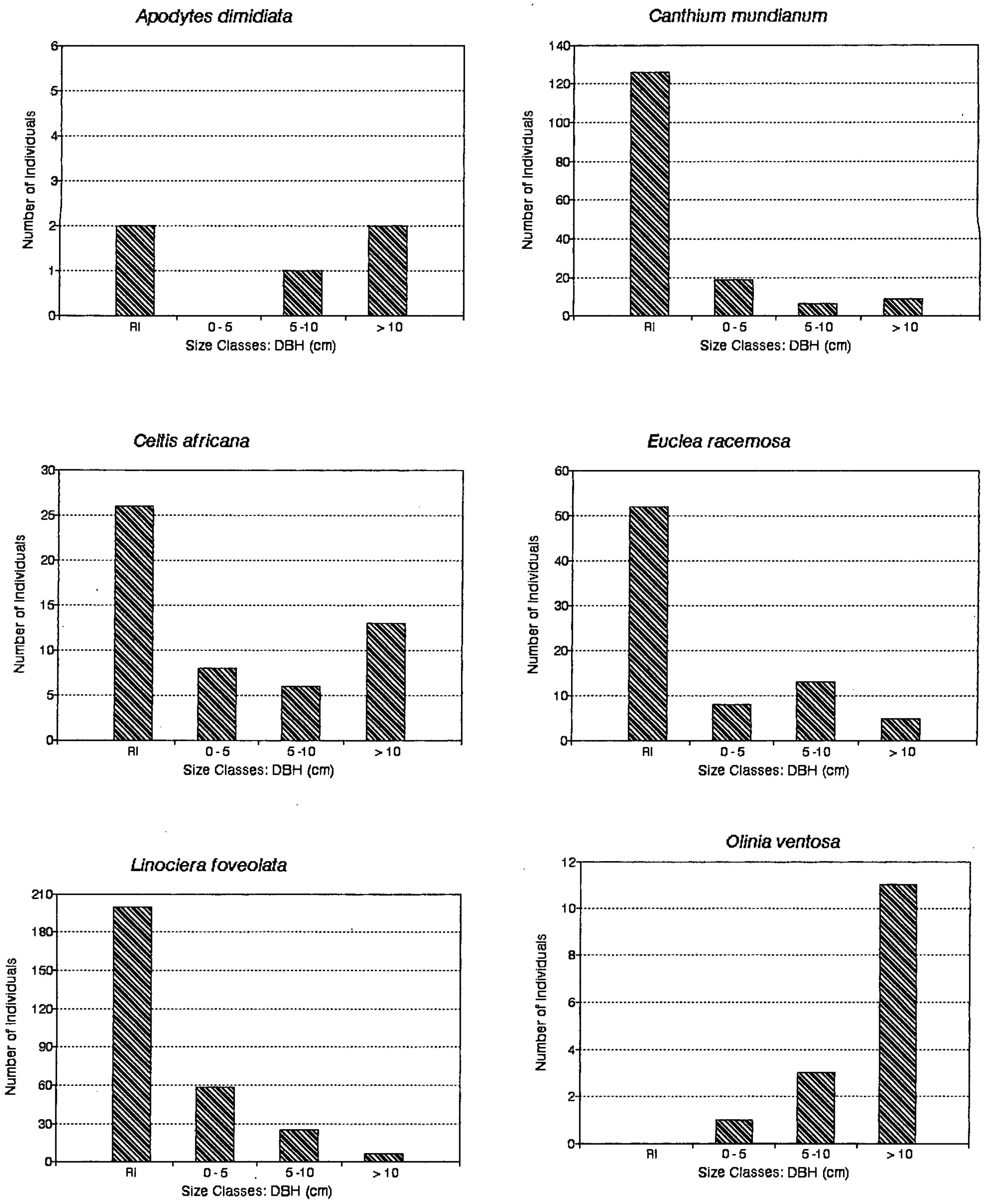
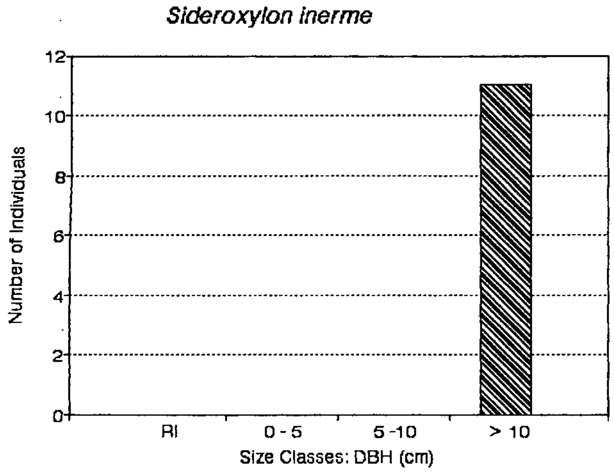


Figure 10. Size class distributions of the species found in Platbos, near Stanford in the western Cape Province, RSA. RI = recruitment individuals.

Figure 10. cont.



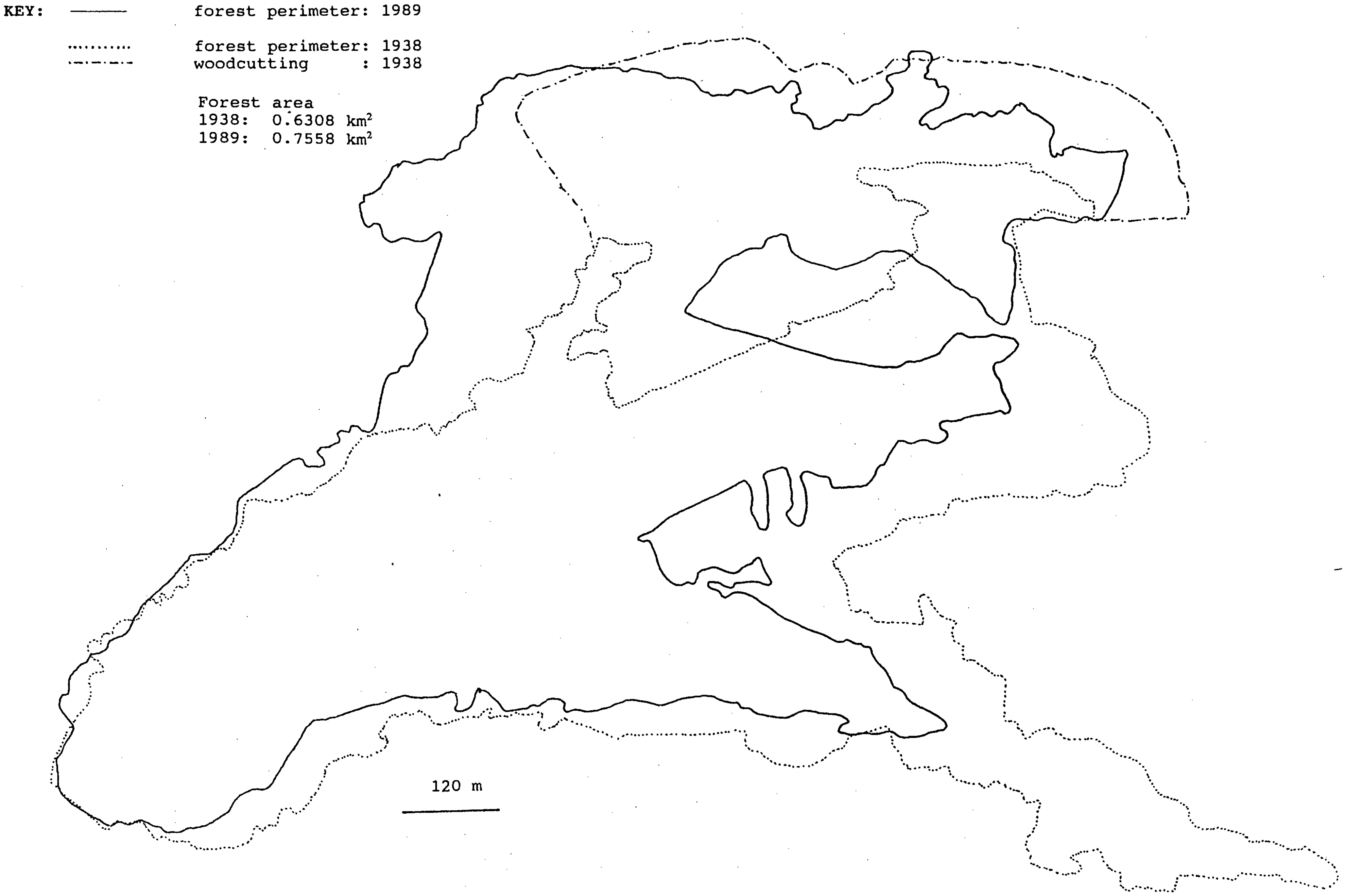


Figure 11. Comparison of Platbos forest area: 1989 vs 1938.

STINKHOUTSBOS:

Size class distributions: Most of the species displayed the characteristic J-shaped curve. Notable exceptions were *O.ventosa* and *I.mitis* which showed an opposite trend. *O.bullata* and *A.dimidiata*,~~which~~ had relatively flat size-class distributions **(Fig. 12).**

Regeneration dynamics: Regeneration was ubiquitous throughout the forest, since no difference was found between seedling recruitment in the gaps and under the canopy (Mann Whitney U stat. = -2.78, $p > 0.1$) **(Table 2).**

Disturbance: Stinkhoutsbos, a moderately disturbed forest, was subjected to logging and occasional fires, but was relatively free from the influence of farming practices (grazing and trampling) and alien invasives **(Table 2).** The forest also showed significant signs of past logging practices indicated by a number of old, rotting *O.bullata* stumps, and old coppice growth in the occasional *Curtisia dentata*.

Area: The area of Stinkhoutsbos decreased slightly from 1938 to 1989, probably due to logging **(Figs 4 & 13).**

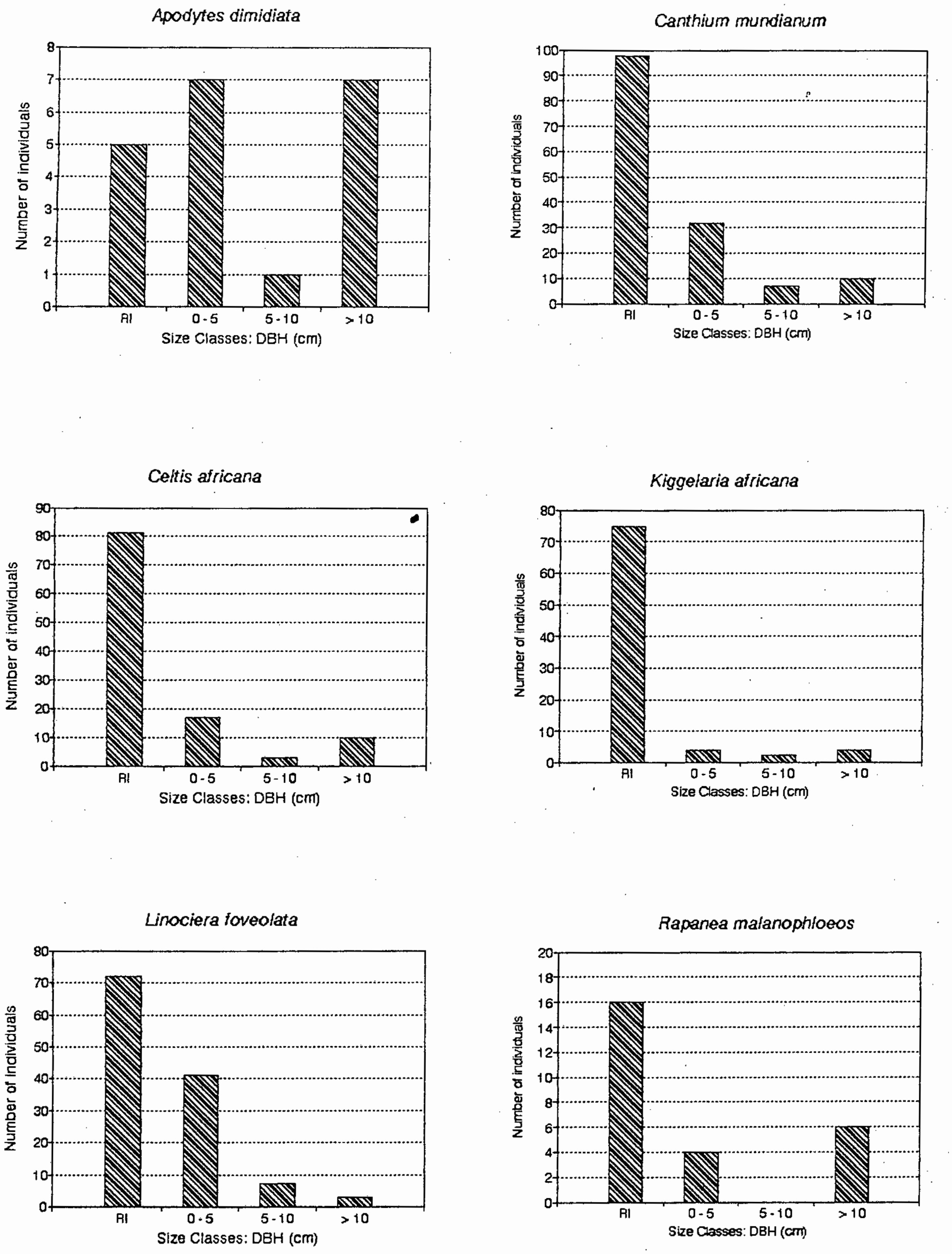
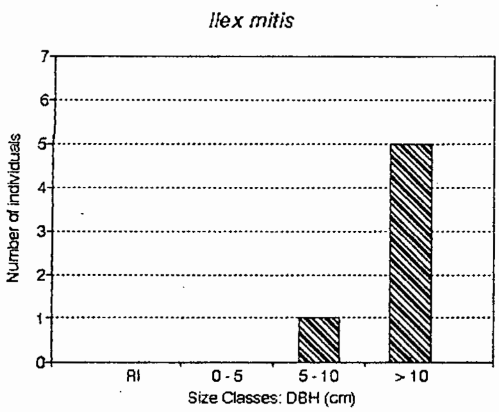
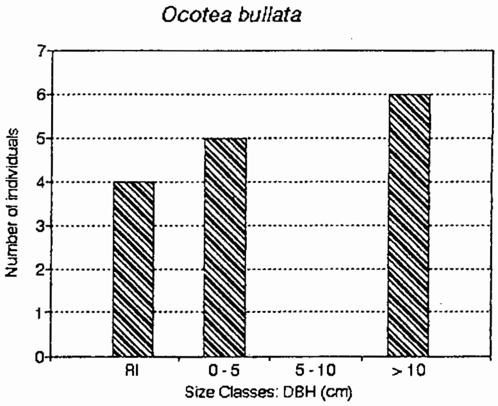
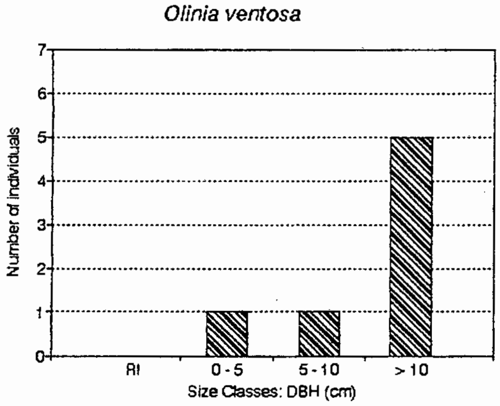


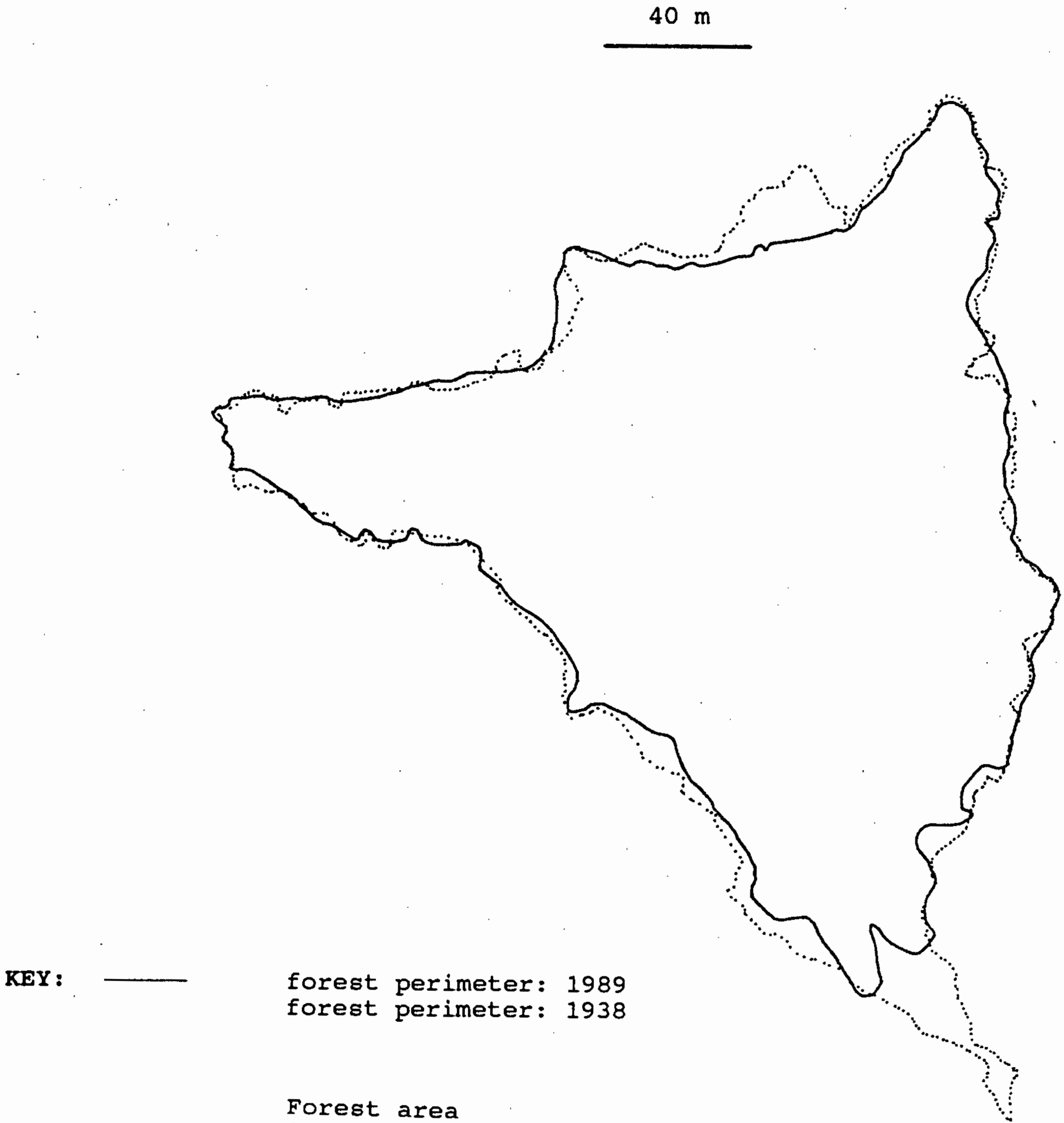
Figure 12. Size class distributions of the species found in Stinkhoutsbos, near Stanford in the western Cape Province, RSA. RI = recruitment individuals.

Figure 12. cont.









Forest area
1938: 0.1225 km²
1989: 0.1104 km²

Figure 13. Comparison of Stinkhoutsbos forest area: 1989 vs 1938.

DISCUSSION

SHORT FORESTS

Both McKenzie et al (1990) and Taylor (1961) noted that the short forests are all remarkably similar in structure and species composition. Therefore, since the dynamics of these forests are similar, I will discuss them as a whole, and later refer to the individual threats posed to each one of the forests.

Forest dynamics:

Life history strategies:

Natural selection tends to maximise the fitness of a plant i.e. it's genetic contribution to future generations (Bloom et al, 1985). Sprouting can be considered a strategy of maintaining a plants fitness. My use of the term regeneration is based upon the assumption that in reproducing, sexually or vegetatively, the dominant canopy trees aim to reach the canopy, insodoing ensuring it's survival. Thus resprouting can be included in this definition of regeneration.

The inverse J-shaped curve displayed by most of the canopy dominants indicates that are reproducing continuously. *S.inerme* and *M.heterophylla*, both being basal sprouters, which regenerate by the production of lateral sprouts (pers. obs.), are also in no danger of local extinction.

The sprouters, *S.inerme, E. racemosa* and *M.heterophylla*, which dominate these forests (Mckenzie et al, 1990), regenerate largely in the disturbance gaps (pers. obs.). They have very low SLA (Fig. 3), indicating a low RGR (Reich et al, 1991, 1992). These forests all occur on the exposed slopes of the Swartkransberg range, and are thus subjected to harsh winds and extreme fluctuations in weather that characterises the coastal belt. The plants may therefore allocate a great deal of their resources to both structural and chemical defences, at the cost of growth (Loehle, 1987, Coley et al, 1985), hence their low SLA. These species, once established, spread laterally since they cannot grow tall, forming a dense, low canopy.

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The seeding species, *L.foveolata, P.tricuspidatus* and *O.capensis* subsp. *africana*, which contribute a small degree to the overall biomass of the forests (McKenzie et al, 1990), generally recruit under the canopy (Table 2) possibly because they are likely to be outcompeted in the gaps by the sprouters. This is not to say that the seeders don't require gaps to gain the canopy, but rather that their recruitment is restricted to sites beneath the canopy, since they are excluded from the disturbance gaps by the sprouters. The seedlings are likely to remain in a suppressed state until a small gap forms, whereupon they capitalise on the increased light availability, and increase their growth rates in order to gain the canopy (Clark and Clark, 1992). These patterns of seedling growth has been termed "waves of release" (J.J.Midgley pers.comm.).

They are characterised by having relatively low SLA (Fig. 3), indicating that they too, are slow growing (Reich et al, 1991, 1992), and could thus be described as shade tolerant (Clark & Clark, 1992). Interestingly, the seeders don't overtop, and thus outcompete, the sprouters (pers. obs.), possibly because their extension growth is kept in check by the harsh weather conditions to which the forests are exposed.

Thus the sprouters dominate the short forests by maintaining their dominance in the gaps, while the seeders form small communities within the canopy.

The role of anthropogenic disturbance:

When comparing the forest areas in 1989 to what they were in 1938, it is obvious that the forests are able to withstand a certain degree of disturbance. Kleinbos was subjected to extensive woodcutting in the early 1930's (Fig.9), but has recovered, and forest now covers most of the area laid bare by the logging. Taylor (1961) reported that Grootbos was also subjected to tree felling in the 1960's, but the vegetation has since recovered. Thus the short forests could be considered fairly resilient to allogenic disturbance. However, since sprouters are favoured by gap formation, excessive disturbance, especially trampling and grazing by domesticated herbivores and fire, could well lead to a decline in the seeding species from these forests. This was especially evident in Grootbos, where a distinct fenceline contrast was noticed: on the one side, cattle and horses roam freely through the forest, while on the other, stock were excluded. On the trampled side, there was a distinct lack of the seeding species, except in the larger size classes, suggesting that they are not maintaining in the highly disturbed sites.

However, when left undisturbed for a lengthy period the forests have the potential to expand into the surrounding fynbos. Steynsbos has been largely undisturbed **(Table 3)** and as a consequence, the forest perimeter expanded considerably **(Fig.4)**, as can be seen comparing the area in 1938 to that of 1989 **(Fig.9)**.

Conservation status:

The majority of the species in these short forests are fairly resilient and can thus maintain themselves when faced with allogenic disturbance such as, browsing, trampling and small scale woodchopping. Browsing and trampling may however, affect the recruitment of the seeders. The fast growing alien invasives, such as *Acacia saligna*, are more likely to pose a threat. These legumes can quickly invade a gap and due to their prolific growth, outcompete the slower growing forest species. They form very dense stands, and are thus impenetrable, even to the shade tolerant forest species. The alien problem does not seem to be too extensive as yet, so it would be controllable.

Thus the short forests probably do not require very intensive conservation, apart from regulating woodchopping, removal of alien invasives and the minimising trampling/browsing in the forests, as these pose the greatest threat to the forests.

TALL FORESTS

Platbos

Forest dynamics:

Life history strategies:
Most of the canopy species display the inverse J-shaped size-class distribution, associated with continuous, well established regeneration (Midgley et al, 1990). Notable exceptions are *A.dimidiata*, *O.ventosa* and *S.inerme* **(Fig. 10)**. The exponential curve of *O.ventosa* indicates a difference in life history strategy, namely that it is capable of growing old and big, and survives by persisting rather than continual regeneration. Additionally, the characteristically low SLA **(Fig. 3)** of *O.ventosa*, suggest that it is slow growing (Reich et al, 1991; 1992), and thus most likely shade tolerant (Clark & Clark, 1992). A low RGR is indicative of high allocation to structural and chemical defences, and hence extended longevity (Loehle, 1987). Similarly, the flat slope and low SLA of *A.dimidiata* suggest that it is shade tolerant and slow growing and can grow to advanced age. *Celtis africana* represents an interesting case. It is an obligate seeding, dominant canopy species in the forest, but is deciduous and had a high SLA **(Fig.3)**. It regenerates largely under the canopy, and is thus shade tolerant to a degree.

Many studies of life history strategies of forest species, have compared and contrasted "gap requiring" and "shade tolerant" species (Clark and Clark, 1992). The two strategies can be divided into "slow growing and shade tolerant species" and the "fast growing, gap requiring species". In Platbos, however, the combination of sprouters and seeders, results in a difference in dynamics: the slow growing sprouters dominate in the gaps while the seeders, which are largely shade tolerant, regenerate under the canopy **(Table 2)**. Thus, the niche that the pioneer or "gap requiring" species would fill has been taken over by the sprouters. Past disturbance events, most likely fire, may have maintained the presence of sprouters in the forests, when the seeders would generally have outcompeted these species.

The role of anthropogenic disturbance:
In the event of a disturbance, the sprouting species, *E.racemosa, C.mundianum* and *S.inerme* are likely to grow into the gaps. The shade tolerant species *A.dimidiata, O.ventosa* and *C.africana*, regenerate under the canopy of the sprouters and grow through the canopies, resulting in eventual overtopping of the sprouters. Therefore species such as *C.africana* and *A.dimidiata* dominate in the tall canopy, while the sprouters establish in the gaps, and disturbance will ensure their continued presence in this forest. Furthermore, sprouter dominance in the gaps could well be maintained by the grazing action of large herbivores such as bushbuck and grysbok (pers.obs.): seedlings are likely to die following grazing, while sprouting species can simply resprout. The canopy gaps created by *C.africana* dropping their leaves could also have played a role in maintaining the presence of sprouters in the forest.

Furthermore, when considering the aerial photographs of the forest in 1938, signs of large scale woodcutting are evident. The forest has since regrown, but the patches are dominated mainly by *S.inerme* and *E.racemosa* with the occasional *K.africana* and **(Fig.11)**. This indicates that in the event of large scale disturbance, the sprouters will come to dominate the forest. However, if left undisturbed for a number of years, the dominant species (*A.dimidiata, O.ventosa* and *C.africana*) may well re-establish in these patches.

Conservation status:

Although the forest has recovered from the large-scale logging of the 1930's, the only species to return to those areas were the more resilient sprouters, *S.inerme* and *E.racemosa*, and to an extent the seeder, *L.foveolata*. Presumably, if left undisturbed, the forest will regain it's previous composition, where it was dominated by *C.africana*, *A.dimidiata* and *O.ventosa*. However, since it is surrounded by cultivated lands and human settlement, a source of continual disturbance, the chances of this occurring are slim. Unless controlled, cattle will still roam through the forest, enlarge gaps and graze the seedlings. People will still enter into the forest to fell trees for fuelwood and for furniture, further exacerbating the problem of disturbance. The sprouting species may well maintain under these conditions, but the seeding species will be adversely affected. The seeders are probably adapted to natural grazing pressures, by producing more than enough seedlings to satisfy the natural herbivores, but the added pressures of cattle may reduce their reproductive output severely.

The low overall count of A.dimidiata and O.ventosa is also of concern. Due to extensive logging in the past, their numbers may have been whittled away, until few remain. Coupled with this is the added pressure on their regeneration, thus these species would require special attention.

The large perimeter to area ratio of Platbos results in the forests being even more vulnerable to disturbance. Proof of this is the gradual erosion of the forest perimeter on the east, north and western sides **(Fig.11)**. Thus this forest would indeed require more than the casual conservation it is afforded presently. An effort must be made to reduce disturbance within the forests, to allow the return to dominance of A.dimidiata, O.ventosa and C.africana. This would require the restriction of access to the forest by domesticated herbivores, the removal of aliens, the cessation of felling of trees, and the minimising of burning around the perimeter.

Thus the forest requires urgent, active conservation management.

Stinkhoutsbos

Forest dynamics:

Life history strategies:

Stinkhoutsbos, the forest with the greatest affinity to the Afromontane Forests, was dominated by *O.bullata*, *O.ventosa* and to an extent *A.dimidiata*. *C.africana*, *R.melanophloeos*, *C.mundianum* and *K.africana* form the group of sub-dominants. The dominant species are characterised as being slow growing (except surprisingly, *O.bullata*) **(Fig.3)** shade tolerant, with low reproductive output in terms of seedling number. The sub-dominants on the other hand, are characterised by slightly increased growth rates and a greater reproductive output **(Fig.3)**.

However, the difference in growth rate is slight. The range of SLA, and RGR, for tropical forest trees, as described by Reich et al (1991), range from 40 $cm^2.g^{-1}$ to 500 $cm^2.g^{-1}$, indicating that the species found in Stinkhoutsbos, which display a range in SLA from 38 $cm^2.g^{-1}$ to 108 $cm^2.g^{-1}$, are all relatively slow growing. Thus, if they were to be classified as "gap requiring" or "shade tolerant" they are all likely to fall into the latter category. Therefore, most of these species do not rely exclusively on gaps for recruitment. Clark and Clark (1992) suggest that the seedlings of late successional species remain in a slow growing, suppressed state, and capitalise on any small increases in light. Indeed, many of the gaps were choked with *Carissa bispinosa* and *Rhoicissus tomentosa*, a weedy climber (pers.obs.), which are known to suppress recruitment in forest gaps (Botha, 1992). However, in treefall gaps without climber choke, the relatively faster growing *C.mundianum* root-sprouts, *K.africana* and *C.africana* seedlings did emerge. Presumably, once these patches mature, *A.dimidiata*, *O.ventosa* and *O.bullata* will recruit beneath the canopy of these trees.

The role of anthropogenic disturbance:

Since Stinkhoutsbos forest dynamics are largely driven by autogenic change, excessive allogenic disturbance, especially anthropogenic disturbance, will result in disruptions of the forest dynamics. Woodcutting, which was by far the most severe disturbance in Stinkhoutsbos **(Table 3)**, has had far-reaching effects on the forest. *O.bullata*, more commonly known as Stinkhout, is a much sought after tree for the furniture trade (McKenzie et al, 1990). Indeed, since the first farmers in the area named the forest after *O.bullata*, one can assume that it must have been plentiful in the forest. However, as a consequence of past logging practices, their numbers have dwindled significantly. Furthermore, since the tree is long-lived and reproduces infrequently, the felling of a single adult results in a large demographic loss. The same could be said for the other long-lived, low reproducing species, *I.mitis* and *O.ventosa*. Thus continued logging, compounded by low reproductive output, could well result in the disappearance of these species from the forest.

Fire too, is likely to pose a threat. In a large gap, towards the centre of the forest, that was burnt 12-14 years ago (aged by the node count of a *Leucadendron* found in the gap), has been colonised by faster growing fynbos thicket species such as *Rhus* and *Leucadendron*. No RI of the species in the forest were found in this gap, indicating that even after 14 years, they have failed to colonise the gap. It is widely accepted that fires in undisturbed, closed canopy evergreen forests, fire is rare (Kauffman, 1991), but owing to the disturbed state of Stinkhoutsbos, the likelihood of fire is increased. Therefore frequent fires could well lead to a gradual eroding of the forest boundaries.

Conservation status:

As with Platbos, the dominant canopy species of Stinkhoutsbos are particularly vulnerable to allogenic disturbance events and eventually, these are likely to lead to their decline. The tall forests, which might be stable i.e. a low turnover of species and individuals, are not as resilient to disturbance as the short forests. Indeed, even though the overall area of the forest has decreased only slightly since 1938 **(Fig.4 & 13)**, indications are that the composition is changing. This was primarily due to woodchopping. The burgeoning flower trade of the area may well represent a danger to the forest. Farmers seek to manipulate the succession by frequent burning, so as to enhance their flower yield (van Wilgen et al, 1992). Since Stinkhoutsbos is also vulnerable to fire, it could well be under further pressure due to the increase in fire frequency. As with Platbos, the high perimeter to area ratio makes this forest particularly vulnerable.

Like Platbos, Stinkhoutsbos also requires intensive conservation. However, here the focus is particularly on reducing woodcutting and minimising fire risk. The one problem that may affects both Platbos and Stinkhoutsbos in the long term is fragmentation (McKenzie et al, 1990). The isolated island-like nature of the forests, could well mean that replenishment of the disappearing Afromontane species, would be unlikely.

CONCLUSION

Thus, in general, short forests dynamics are governed by abiotic factors and largely allogenic disturbances, while tall forest dynamics are dominated by biotic (competitive) interactions and autogenic disturbance. Sprouting species *S.inerme* and *E.racemosa* dominate the short forests. These forests, Grootbos, Kleinbos and Steynsbos are fairly robust and have survived past, extensive disturbance, and so require low-key conservation. Conservation measures include reducing woodcutting and trampling by stock in the forests and the control of alien invasives.

The tall forests, Platbos and Stinkhoutsbos, dominated by long-lived tree species that produce relatively few seedlings and/or sprouts, are particularly vulnerable to anthropogenic disturbance. They both require more intensive conservation management and protection, although, Stinkhoutsbos to a lesser degree than Platbos. There are a number of forest patches such as these, dotted across the landscape (pers. obs.), and if the importance and subsequent protection of these forests is well publicised, other landowners may be encouraged to conserve any forest patches on their farms.

B: A general model of forest dynamics based on canopy height.

Introduction

The model is based upon the relationship between canopy height and regeneration modes. It is a deterministic model that predicts that forest structure, in particular forest height, largely determines regeneration patterns. Since this is a model based on pattern, in the following section I shall explore the possible processes selecting for these patterns.

Firstly, some of the assumptions and definitions need to be specified. I define the concept of regeneration in this theory, based upon the assumption that in reproducing, sexually or vegetatively, the trees aim to reach the canopy. This excludes the understorey species from the theory. However, this is intentional, since it is more often than not the canopy species that are of primary concern in conservation e.g. they are the often the target of logging practices.

Regeneration Mode: Three modes of regeneration were defined:

Seeding: the plants reproduce primarily by producing seeds.

Root Sprouting: The trees reproduce by sending up sprouts from their root stock. This form of sprouting may result in multistemmedness, depending on the distance from the tree that the sprouts emerge from the main stem.

Stem/basal sprouting: Trees reproduce through meristems beneath the bark of the stems/base. Sprouting of this kind results in multistemmedness **(Fig. 14)**.

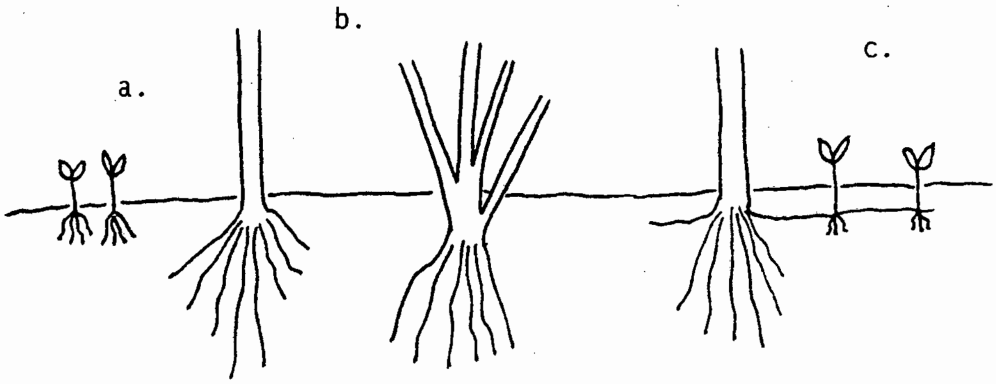

Figure 14. Three modes of regeneration as defined in the model.
a. Seeding b. Base/stem sprouting c. Root sprouting

Theory

In order to fully understand how height affects regeneration characteristics, one first has to explore the determinants of canopy height and the nature of both tree architecture and regeneration strategies.

Forest Structure:
Gross features of stand structure in a mature forest, are largely dependant on climate. However, on shorter time scales, the physical environment (habitat conditions), together with disturbance regime, largely determine forest stand structure (Landsberg, 1986). Habitat conditions include resource availability, local weather conditions (precipitation, air temperature & humidity) and physical stresses (eg. strong winds).

In general, where conditions are favourable eg. a sheltered site; high availability of resources (nutrients and/or water) and minimal allogenic disturbance, productivity is high (Coley at al, 1985; Poorter, 1989) and thus canopy height is tall. On the other hand, where conditions are less than ideal, e.g. sites exposed to harsh weather conditions (strong winds and extreme temperature fluctuation) and high levels of disturbance, the productivity is likely to remain low (Landsberg, 1986; von Andel and Biere, 1989) and the forest canopy short. Low nutrient levels would exacerbate the situation, in that low levels decrease productivity. Furthermore, since short forests are found in areas of comparatively high disturbance (eg. fire and wind), the species within the forests are likely to be adapted to these conditions. For instance, species accustomed to frequent disturbance, tend to produce more wood at the base of the tree (Waring and Schlesinger, 1985). Sprouting is an adaptation to frequent disturbance (Waring and Schlesinger, 1985). Additionally, tall trees could not grow under these conditions since they are very susceptible to windthrow.

Thus canopy height is determined by a one, or a co-action of a combination of the above mentioned factors. In essence, where conditions are favourable and stable, forests can grow to excessive heights; and where habitat conditions are poor, and disturbance high, the canopy is short.

How does canopy height relate to regeneration mode?

Correlations between growth habit and environment have long been known, indicating that tree architecture and their fundamental branching patterns, are advantageous in certain habitats (Kuppers, 1989; Sakai, 1989). Tree architecture patterns are deterministic i.e. they are a product of genetic make-up and optimal growth conditions. Also, most woody species are modular organisms i.e. they grow according to a blueprint of branching patterns (a module), which is periodically/continuously repeated (Kuppers, 1989). This means that the architecture of the tree, depends in part on the growth conditions in the regeneration habitat. Thus in tall forests, where there is less light near the forest floor relative to short forests (Horn, 1971), the adaptive architectural patterns will be directed towards growing tall, usually resulting in monopodial growth form (branching with a main axis due to apical dominance, and reduced/missing lateral branches) (Kuppers, 1989; Sakai, 1989; Homes & Cowling, 1993). Conversely, in a short forest where more light is available at the forest floor, branching patterns are characteristically sympodial (branching without a main axis but many lateral branches, due to sub-apical dominance) (Sakai, 1987, 1989), in order to exploit the available light. Thus small-scale changes at the branch level carry over into the larger scale of the crown. How does reproductive mode relate to this?

Tall forests lack basal sprouting species because the sympodial nature of their architecture would limit the height to which they can grow. Sakai (1987, 1989) predicts that a tree displaying sympodial branching patterns cannot grow as tall as a monopodially branching tree, because of the nature of the branching patterns. When comparing monopodial growth to sympodial growth, a distinct difference in branching angle (X^1, **Fig. 15**) and relative dominance of the apical meristem, is evident. It is a wide branching angle (X^1) intrinsic to sympodial growth that limits the tree height.

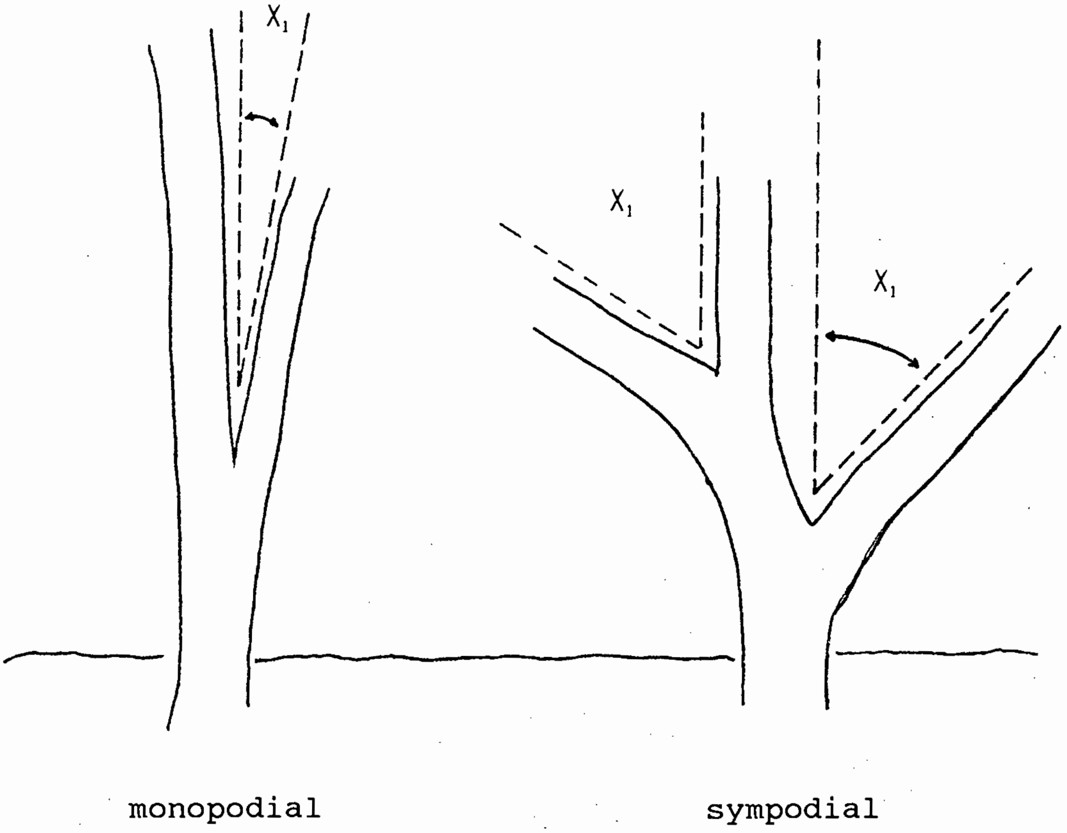

Figure 15. Differences in branching angle between sympodial and monopodial branching patterns.
(after Sakai, 1987, 1989)

Thus a species displaying sympodial growth would thus have limited competitive ability in tall forests in that they are not likely to intercept sufficient light to surpass their whole-plant light compensation point (King, 1991). Furthermore, basal sprouting species cannot attain the height of a seeding species because of the resource costs attributed to supporting secondary limbs. The production of thick bark and dormant lateral and/or epicormic buds characteristic of sprouters will also involve trade-offs in allocation resulting in decreased growth rates (Bloom et al, 1985), and hence a further loss in competitive ability. Vertical growth in root-sprouting individuals will also be hampered by the allocation of resources to the sprouts, unless the connection between adult and sprout is severed.

Regeneration dynamics in short and tall forests.

Tall Forests: Sprouters are further disadvantaged in tall forests by their lack of competitive ability in the regeneration niche. Since the sprouting mode is unsuccessful in the adult trees, the only way in which the sprouters can invade the canopy is through gaps by means of seeds. However, it is well recognised that the seedlings of sprouting species are competitively inferior to the seedlings of obligate seeders (Hunt & Lloyd, 1987; Hansen et al, 1991), therefore excluding the sprouters in the regeneration niche.

Short Forest: The structure of the short forest is determined largely by local abiotic conditions. The seeders do not proliferate in these forests, simply because they cannot compete with the sprouters which are more resilient to disruptive allogenic disturbance. Low canopy is maintained by abiotic conditions, and architectural patterns are thus largely sympodial. The sprouting strategy is probably better suited to these circumstances. Since the conditions are poor, plants must allocate a large proportion of their resources to defences, both structural and chemical. Seeders, which rely on a high relative growth rate to compete in the regeneration niche, would have a high seedling and sapling mortality rate under these circumstances, since there is a allocational trade-off between growth rate and defences (Loehle, 1987). For a plant to grow fast, it must allocate most of it's resources to growth and less to structural and chemical defences, and since the conditions require high resilience, the seedlings will tend to die.

Once the sprouters have established their dominance in a canopy, it is very difficult for seeders to gain a gap in the canopy. If a disturbance should create a gap, the sprouters are likely to dominate since they have an alternative source of resources, unlike the seedlings which rely on seed reserves. Thus increased disturbance favours the sprouts. In the mature short forest, shade tolerant seeders may establish within the forest, but will not dominate the sprouters since they are unable to grow taller than the other species because environmental factors keep the forest short.

Growth rate characteristics

Plant growth rates are strongly related to the availability of resources (Coley et al, 1985; Freijsen & Veen, 1989, Poorter, 1989) and the physical conditions of the habitat (Loehle, 1987). In resource poor habitats, plants display a suite of interdependent characteristics associated with inherently slow growth rates (Coley, et al, 1985). Because resources are not readily replaced, the plants tend to have long-lived leaves and twigs. Slow turnover of plant parts is advantageous because each time a plant part is shed, it carries with it a great deal of it's nutrients (Coley et al, 1985). The plants will also tend to allocate more resources to anti-herbivory protection, such as polyphenols and fibres, which are energetically costly, in order to protect their leaves further (Loehle, 1987). Similarly, in physically stressful environments, plants must allocate more resources to structure components, insodoing decreasing allocation to growth. Conversely, in sheltered habitats since the plants no longer require a great deal of allocation to structural components, growth rates are relatively higher.

Herbivory from large mammals is relatively greater in short forests, since the trees cannot evade the herbivores by growing tall, and so must allocate resource to anti-herbivory defences, further impairing their growth rates.

Predictions

Thus I predict that tall forests will be characterised by the dominance of seeders, with a high SLA and monopodial growth form. On the contrary, short forests will be dominated by sprouters, with low RGR and hence low SLA, and sympodial growth forms.

Methods:

Study sites:

The five Swartkransberg forests, Grootbos, Kleinbos, Steynsbos, Platbos and Stinkhoutsbos, were the primary forests used to test the model. Section A contains the full details of their description. The Danger Point forest, which has a similar species composition to the short forests, is located on the Danger Point peninsula, which is exposed to harsh climatic conditions throughout the year. Groenkop Forest, a true Afromontane Forest, lies on the eastern perimeter of George, at Saasveld College, and was chosen as a taller forest to increase the height range for a more general model **(Fig. 1)**.

Sampling Methods

I. *Seeding index*

From the 2m x 2m plots the regeneration mode of a species was determined (see above). From these data, a seeding index was assigned to each species:

$$SI = \frac{\text{number of seedlings}}{\text{total number of RI}}$$

The SI thus represents the proportion of seedlings found in the forest of each species, and indicates the relative dependence of the species on seeding as opposed to sprouting for regeneration (given those specific conditions) i.e. the SI is an indication of the reliance on seeding for that particular forest.

The SI for the forest was determined as a mean of the species' SI. If no RI were found for a species in the forest, that particular species was omitted from the SI index for the forest, unless information of this sort could be obtained from the literature eg. Midgley et al (1990).

II. Height

Mean height of the forest was determined by measuring the canopy at ten meter intervals, along a compass bearing for 100 meters. Ten such transects were sampled in each forest.

III. *Architecture*

The architecture of tree growth form can be used as an indication of reproductive mode and life history strategy.
Number of stems: Ten individuals per species was sampled in each forest. The number of stems per individual was determined as the number of stems at breast height that have reached the canopy. It is necessary to make this particularly conservative, as the count would otherwise be biased by small shoots which don't contribute to the canopy area of a tree, such as "agony shoots" (Midgley, pers.comm.). To include all the shoots that may branch off the main axis of the stem below the surface of the soil, all shoots emerging from the ground within a radius of 1/10 of the tree height was considered to be a conservative limit.
The height of first branching was measured as the point at which the stem first branches, and at least two of these branches must reach the canopy. A branching index was then calculated as the height of first branching as a proportion of the canopy height. The height index is a measure of the height of first branching relative to the canopy height, thus a crude measure of the nature of the tree architecture i.e. sympodial or monopodial growth form. When each of the above measurements were taken, the height of the canopy was also recorded.

Statistical analysis

Statistical and data analyses, and graphic display were performed using the STATGRAPHICS and QUATTRO PRO software packages. Linear regressions were used to determine wether relationships existed between height and either the seeding index or the architectural patterns.

RESULTS:

There was a significant relationship between mean canopy height (m) and the seeding index (SI) ($r^2 = 0.9066$, b = 0.0.6723, $p < 0.005$) (Fig. 21). Mean number of stems was negatively related to mean canopy height (m) ($r^2 = 0.9582$, $b = -1.664$, $p < 0.02$) (Fig. 22). Mean height of first branching (m) as a proportion of canopy height (i.e. the "branching index") was strongly related to mean canopy height (m) ($r^2 = 0.9558$, $b = 0.4718$, $p < 0.02$) (Fig. 23). This strongly suggest that architectural patterns and regeneration mode is linked to forest canopy height.

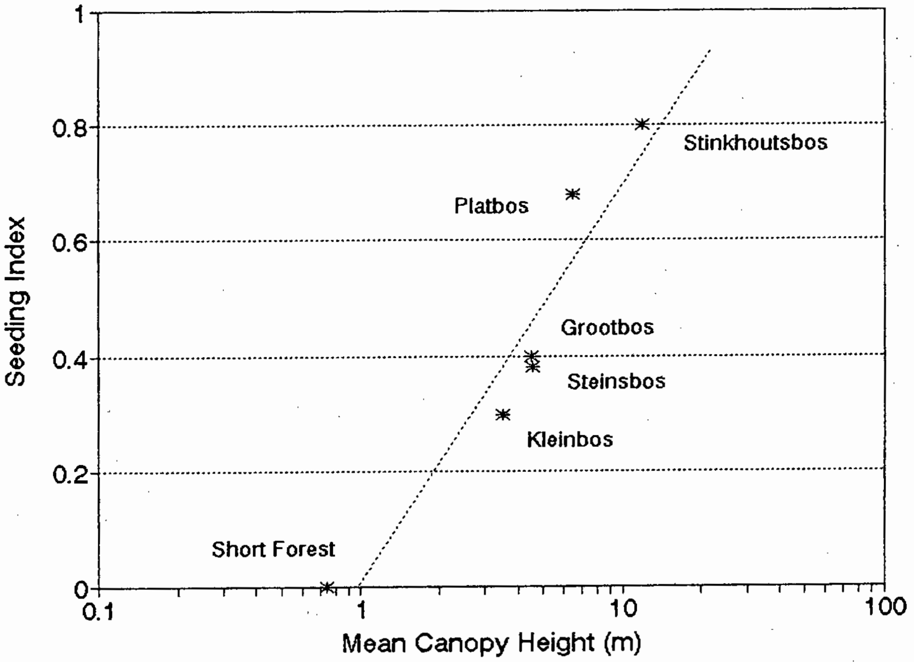

Figure 21. Seeding index in relation to mean canopy height ($r^2 = 0.9066$, b = 0.0.6723, $p < 0.005$).

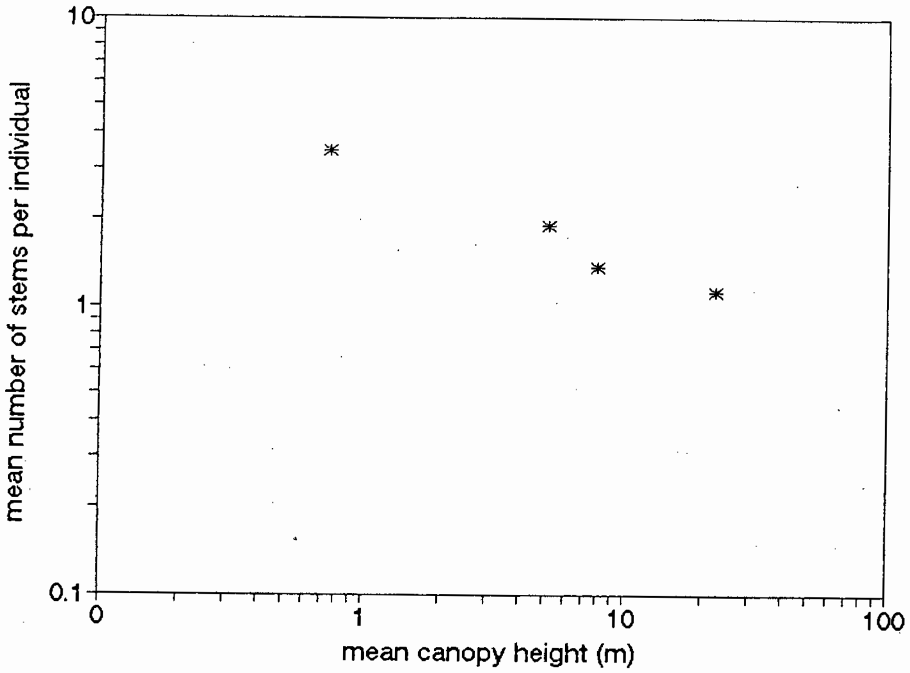

Figure 22. Mean number of stems per individual related to mean canopy height ($r^2 = 0.9582$, $b = -1.664$, $p < 0.02$) (Fig. 22).

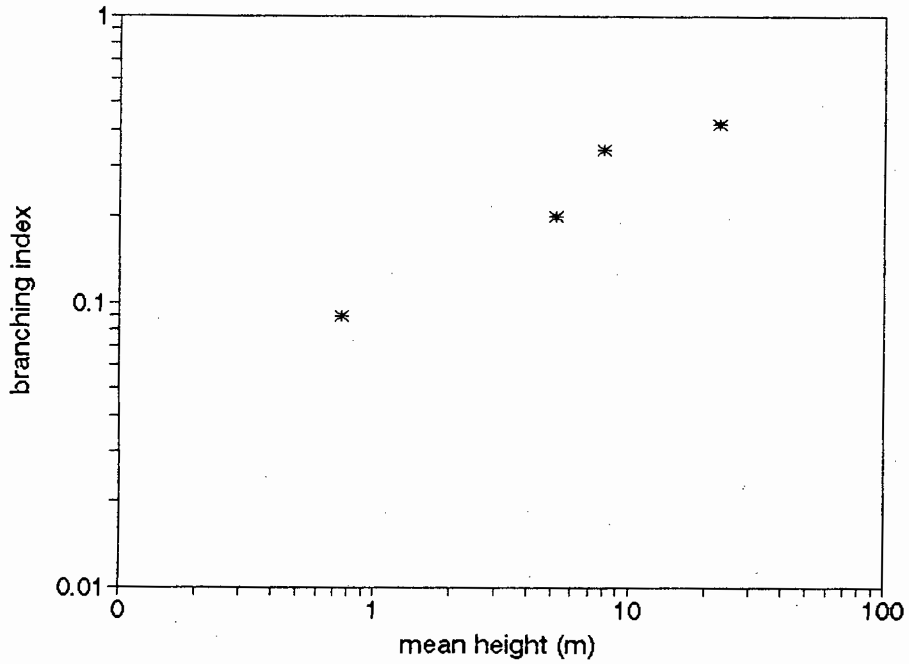

Figure 23. Branching index (mean height of first branching as a proportion of canopy height) related to mean canopy height ($r^2 = 0.9558$, $b = 0.4718$, $p < 0.02$)

From the analysis of SLA in the Swartkransberg forests, the species found in the short forests, *Sideroxylon inerme, Euclea racemosa, Linociera foveolata* and *Olea europaea* subsp. *africana* all have comparatively lower SLA than the species found in the tall forests **(Fig.3)**.

DISCUSSION

Although the results are only based on the study of six forests, a distinct trend is evident. Regeneration mode (Fig.21), and forest architecture (Fig.22 & 23) does change with changes in forest canopy height. It therefore appears that the predictions have therefore fulfilled.

Thus the following patterns can thus be expected:
Short forests, characterised by sympodial growth forms, are dominated by sprouters; and tall forests, typified by monopodial growth forms, by seeders and occasional root sprouters. Furthermore, from this it can be inferred that dynamics of short forests are governed by abiotic factors and largely allogenic disturbances, while tall forest dynamics are dominated by biotic (competitive) interactions and autogenic disturbances.

It is important to bear in mind that this is not a theory of succession, but rather a model based on the comparison of tall to short canopied forests, irrespective of successional dynamics. In many instances I referred to species differences between these forests, but this was simply for ease of explanation. Some species may be able to survive and reproduce in both types of forests, but that they will adapt their reproductive and growth characteristics to suit the local conditions. Thus this model does not necessarily predict species change with changes in canopy height, but changes rather in adaptive form and reproductive mode, regardless of species. Species change from short to tall forest is thus co-incidental. A particular species may dominate in one forest, but could not cope in the other, hence the difference in their distribution. Conversely, a species may have a genome plastic enough to adapt to either conditions, and therefore occur in both tall and short-canopied forests and their reproductive strategy and growth form will conform to the canopy height. There will however, always be exceptions.

CONCLUSIONS

Implications for researchers

A general model such as this will be useful to managers, since initial assessment of forest dynamics, notably the regeneration dynamics, will be easier, especially if dealing with floristics is not required. Additionally, it can also be used as a means to identifies those forests which are most likely to be vulnerable. Furthermore, it highlights the importance of sprouting as a regeneration mode, rather than just an adaptation to enhance survival.

Further study

Since the model was only based on the study of six forests, it requires extensive testing on other forests. Thus further study will include testing the model on a number of forests, but also the comparisons of the growth form and reproductive mode of species common both to short and tall forests, to determine the extent to which their characteristics change. Furthermore, it would be good test for the model if it were applied to different forest phytochoria.

ACKNOWLEDGEMENTS

My thanks to my supervisor Jeremy Midgley, for his sound supervision, useful insights and constructive criticisms.
Donovan Kirkwood and Ronny Stiles for their invaluable help during sampling. My thanks especially to Elwyn and Chris van Schouwen and Mr & Mrs Hug for allowing me access to the forests which were on their properties.
My thanks also to Brian Godfrey for his hospitality at Danger Point.

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