The successional dynamics of *Acacia nilotica* (L.) savanna

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Abstract

Analysis of aerial photographs indicates that woody plant biomass has increased in Hluhluwe Game Reserve, KwaZulu Natal, over a relatively short period. Despite their slow growth rates, Eucleas and other broadleaf species are responsible for the majority of this increase. Nine sites were chosen to examine the recruitment patterns and size-class distributions of *Euclea divinorum* and *E. racemosa*. Analysis of the size-class distribution data suggests that recruitment of Eucleas is slightly higher below adult *A. nilotica* canopies than in adjacent interspaces. The number of seedlings is significantly higher below *Acacia* canopies than in open spaces. Size class data indicate that the largest *Euclea* individuals are found in open spaces and not below *A. nilotica* canopies. Because Eucleas have slower growth rates than *A. nilotica*, the large Eucleas may well have become established before the present *A. nilotica* stand. The data also indicate that *A. karroo* is replacing *A. nilotica* and that broadleaf species other than Eucleas are recruiting in both open and below canopy plots. I suggest *A. nilotica* adults only weakly facilitate the establishment of Eucleas and other broadleaved species, and that increase in woody vegetation is due to changes in the fire regime that allow suppressed broadleaf individuals to escape and become visible. This release may explain the rapid rate of encroachment by inherently slow growing species.

Introduction

'Historical and quantitative assessments indicate that woody plant abundance has increased substantially in the savanna and grassland through out the world during the last 50 - 300 years' (Archer *et al.* 1988).

The increase in woody plant biomass in grassland and open savanna systems, known as bush encroachment, has been widely recognised and documented. Despite this, the rates, patterns and dynamics of the process in savanna systems, are poorly understood (Archer *et al.* 1988).

Plant communities change over time. A central focus of recent plant ecology has been to understand the processes driving the succession (Pickett *et al.* 1987). Clements (1916) developed a view of successional change that even today influences the way many ecologists think. It involves an orderly and predictable progression to a dynamic equilibrium known as the climax, after some initial disturbance. This idea of a predictable sequence of species replacement, known as the **relay floristic** model of succession, has competition as its central process (review by Bond and van Wilgen 1996). When applied to post fire succession, Clementsian theory has proved inadequate because competition is of unknown importance in the post fire environment (Bond and van Wilgen 1996).

Fire ecologists have developed a different set of models and mechanisms to explain post fire succession in woody vegetation. In this case competition is seen to be relatively unimportant and the interplay between disturbance and the timing of key life history events is of more importance (Nobel and Slatyer 1980). In contrast to the 'progression to a self sustaining climax', succession is often cyclical under the same disturbance regime, or results in multiple pathways to alternative communities if the fire regime changes. Therefore, according to Bond and van Wilgen (1996) 'the key to predicting successional change is the timing of key life-history events in relation to disturbance, not position in the competitive hierarchy'. This is essentially the vital attributes model of Nobel and Slatyer (1980).

• Vital attributes

The vital attributes approach, suggests that "temporal changes in plant communities are driven by the relative longevity's of the species at the site and their regeneration requirements in relation to disturbance" (Nobel and Slatyer 1980). This approach can be considered a **non-interactive** view, as the dynamic behaviour of the species depends on their intrinsic properties rather than species interactions. In fire prone communities fire-survival response, reproductive timing, life spans of plants and their propagules and relative growth rates are 'vital attributes', and are of central importance in predicting successional dynamics (Nobel and Slatyer 1980, Bond and van Wilgen 1996). Proponents of competition based models (e.g. Tillman 1990) consider the intrinsic properties of species to be important only in non-equilibrium situations such as post fire environments.

However, in many fire prone communities species interactions can still be important. One of the most obvious is a system in which the species not only react to a fire regime but also alter it (Bond and van Wilgen 1996). A good example of this is the shift from flammable to a non-flammable vegetation, such as savanna/grassland - woodland/forest succession (Smith and Goodman 1987, Archer *et al.* 1988).

One aspect of bush encroachment that has received attention recently is the 'nurse plant' phenomenon (Smith and Goodman 1987, Archer *et al.* 1988, Franco-Pizana *et al.* 1996), wherein one plant facilitates the establishment of another, and in this way promotes successional change.

• Encroachment and facilitation

Environmental conditions under the canopy of woody plants differ from conditions in adjacent interspaces between woody plants (Vetaas 1992). In most cases temperatures are cooler and soil nutrients levels are higher under nurse plant canopies (Archer *et al.* 1988), shade tolerant species should therefore be able to take advantage of these conditions and establish under canopies. However, light can be more limiting than nutrients under shade, thus preventing seeds or seedlings from taking advantage of the high nutrient levels below canopy (Franco-Pizana *et al.* 1996). Nurse plants can **passively** facilitate the establishment of fleshy fruited species below their canopies by acting as perch sites for the birds feeding on the fruits (Smith and Goodman 1987, Franco-Pizana *et al.* 1996). Aggregation of shade tolerant species beneath nurse plant canopies also involves **active** facilitation whereby nurse plant canopies provide higher nutrient levels, and ameliorate soil temperatures in a manner which increases the germination success of the dispersed seeds (Smith and Goodman 1987, Franco-Pizana *et al* .1996). Interestingly, successional mechanisms other than facilitation seem to operate during later stages of shrub establishment and growth (Franco-Pizana *et al.* 1996). Franco-Pizana *et al.* (1996) conclude that the process of conversion of grassland to thorn woodland in Texas is more complex than can be explained by the simple models of succession by facilitation proposed by Archer *et al.* (1988) because growing conditions are not necessarily better under nurse plants than in the open.

Encroachment in savanna communities is often associated with the transition of an open microphyllous woodland (dominated by *Acacia* spp. or *Prosopis* spp. for example) to a broadleaf - deciduous or evergreen community (dominated by *Euclea* spp. or *Celtis* spp. for example) (Smith and Goodman 1986,1987, Archer *et al.* 1988, Franco-Pizana *et al.* 1996). Smith and Goodman (1986), working in a southern African savanna, suggested that temporal and spatial differences in seedling establishment result in this transition. The microphyllous *Acacia* seedlings are restricted to open interspaces, while the evergreen *Euclea* seedlings establish in the shaded environment below the *Acacia* canopies (Smith and Goodman 1986, 1987). The adult microphyllous species therefore act as nurse plants which facilitate the establishment of the evergreen or broadleaf-deciduous species by providing a perch for frugivorous birds. Once established below the nurse plants, the evergreen or broadleaf-deciduous seedlings grow, forming shrub clusters organised around an *Acacia* or *Prosopis* nucleus (Archer *et al.* 1988, Smith and Goodman 1987). As the evergreen Eucleas grow through and above the microphyllous *Acacia* canopy, the *Acacia* is shaded and senescence occurs, leaving *Euclea* dominated shrub clusters (Smith and Goodman 1987). Coalescence of these shrub clusters on mesic sites results in the formation of closed canopy woodlands (Archer *et al.* 1988, Smith and Goodman 1987). Brown and Archer (1995) suggested that understory shrubs, initially facilitated by adult *Prosopis* spp., may inhibit the plant in later stages of cluster development (preventing regeneration or competing for resources). This is evident in the *Euclea / Acacia* succession of Smith and Goodman (1987), where the evergreen Eucleas grow up slowly under the nurse *Acacia* and eventually overtop and kill it. Although the process of facilitation has been described in arid and semi-arid regions throughout the world, it remains to be tested in mesic savanna systems, where conditions for growth are better and growth rates tend to be higher.

Previous studies and field observations in the Hluhluwe Game Reserve suggest that many landscapes especially *A. nilotica* savanna, once characterised by being open savanna, are gradually being converted to thicket and woodland communities (Watson and Macdonald 1983). The species responsible for the woody biomass increase in the Reserve include two evergreen *Euclea* species - *E. divinorum* and *E. racemosa* (Watson and Macdonald 1983, Brooks and Macdonald 1983). The encroachment of Euclea species in the *Acacia nilotica* woodlands (as defined by Whateley and Porter 1983) of the Reserve, is particularly interesting because Smith and Goodman (1987) based their study of facilitation in Mkuzi Game Reserve, which is has very similar savanna systems but in a more arid climate than Hluhluwe (King 1987, Smith and Goodman 1987).

• Aims

What is the driving force behind the bush encroachment in *A. nilotica* woodland ? Is it simply that Eucleas are longer lived and better able to survive fires than *A. nilotica*, or is it the facilitation of shade tolerant Eucleas by dense stands of adult *A. nilotica* ? If Acacias facilitate establishment of Eucleas, one would expect there to be significantly more *Euclea* seedlings under *Acacia* canopies than in adjacent interspaces. The primary aim of this study is to investigate patterns of seedling establishment and regeneration of *E. divinorum* and *E. racemosa*, in relation to *A. nilotica* adults. The study is conducted in *A. nilotica* woodland in Hluhluwe Game Reserve in order test Smith and Goodmans (1987) successional hypothesis, but in a relatively mesic system, to see whether the model is general. The regeneration of broadleaf-deciduous species and *Acacia* species is also investigated. In order to assess the vegetation changes over the last 40 years, aerial photographs from 1954, 1975 and 1992 were examined for sites selected on the basis of having bush encroachment.

Study Site

The study was conducted in the Hluhluwe Game Reserve, (28°00′ - 28°10′ S, 32°00′ - 32°10′ E), situated in the foothills of the escarpment to the west of the coastal plain in central KwaZulu-Natal, South Africa (Figure 1). Hluhluwe Game Reserve makes up the north-eastern quarter of the Hluhluwe-Corridor-Umfolozi Game Reserve complex. The altitude of the Reserve varies from 90 m a.s.l. in the east to ca. 580 m a.s.l. in the north. The mean annual rainfall varies from 910mm on the north-western boundary to 671mm in the south-east (1932-1983). The wet season runs from October to March, although there is frequently mist (above 300m a.s.l.) during the winter months. The mean annual temperature is 18.5 °C. The highest and the lowest mean temperatures occur in January (25.9 °C) and September (11.5 °C) respectively (King 1987).
The physiognomy of the vegetation in the Reserve is described by Whateley and Porter (1983), they recognise two forest, two riverine forest, ten woodland, two thicket and two grassland vegetation communities. The soils and geology are reviewed by King (1987).

Nine sites with mature stands of *Acacia nilotica* were chosen. Although sites could all be classified as *A. nilotica* woodland (Whateley and Porter 1983), they ranged from open savanna with scattered *A. nilotica* adults separated by grassy interspaces, to closed canopy woodland communities with little herbaceous cover and limited open interspaces (Figure 1).

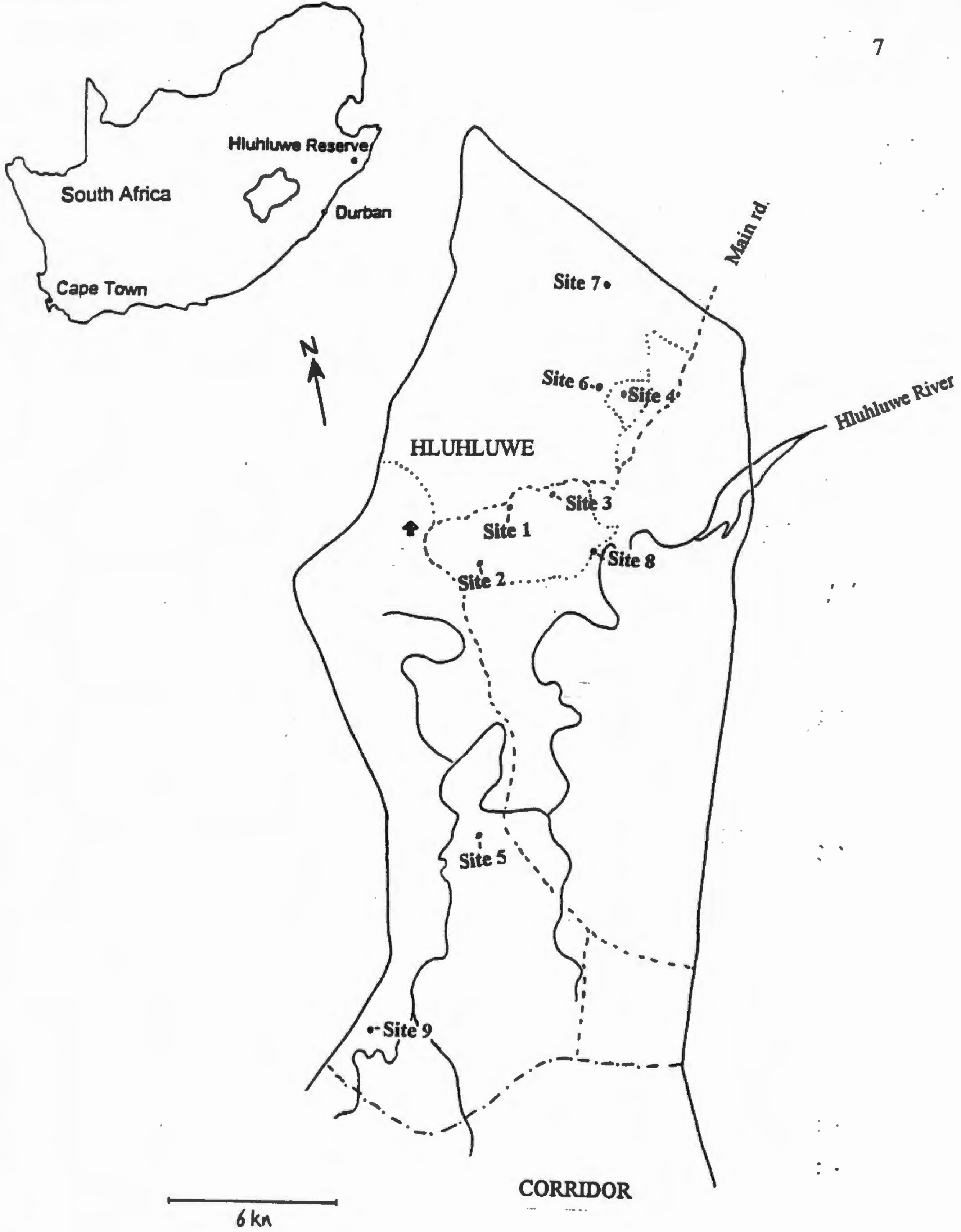


Figure 1. The Hluhluwe Game Reserve, KwaZulu Natal.

- **Site 1** - Small, relatively dense *Acacia nilotica* woodland, with a substantial grass layer and numerous *Euclea divinorum* and *E. racemosa* shrubs.
- **Site 2** - Continuous mixed woodland with *A. nilotica* adults interspersed with *E. divinorum* , *E. racemosa* , *Dombeya rotundifolia* and *Ochna* sp. adults, numerous interspaces with a dense long-grass sward.
- **Site 3** - Large, dense woodland/thicket with *A. nilotica, E. divinorum, E. racemosa, Berchemia* sp. and *Schotia* sp. adults, numerous *Euclea* shrubs present as well as numerous dead *A. nilotica* adults, and a limited herbaceous layer.
- **Site 4** - Small, dense woodland/ forest, large *A. nilotica* individuals sparsely dispersed, numerous forest elements and large *E. racemosa* adults and shrubs and no herbaceous layer.
- **Site 5** - Continuous *A. nilotica* savanna/woodland, adults evenly dispersed and *E.divinorum* shrubs common, substantial grass layer.
- Site 6 - Relatively small thicket/woodland, *A. nilotica* adults sparsely dispersed with large understory of *E. racemosa* shrubs and small trees, some forest elements and substantial herbaceous layer in interspaces.
- **Site 7** - Open *A. nilotica* savanna, with herbaceous layer dominated by *Themeda triandra*, limited shrub growth and no *Euclea* plants at all.
- **Site 8** - Continuous mixed woodland with *A. nilotica* and *Combretum molle*, substantial grass layer, and mixture of *E.divinorum* and *E. racemosa* shrubs and trees.
- **Site 9** - Relatively open *A. nilotica* woodland with *E. divinorum* trees and shrubs, substantial grass layer.

Methods

Field observations.

At each site two linear transects, in randomly chosen directions, were established. Along the first, ten mature *A. nilotica* were selected. Along the second, ten open spaces (5 m in diameter) without any canopy cover were selected (hereafter referred to as interspaces). Initial observations suggested that most mature *A. nilotica* had canopy diameters of between 4 and 6 meters. The diameter of the open plots was therefore set at 5 meters to make the 'open' and 'canopy' plots comparable in area.

The diameter at breast height (DBH), height and canopy radius of each of the selected *Acacia* adults was measured. A census of all arborescent woody plant species was taken in the area below the canopy of each of the ten selected Acacias, and in the ten open interspaces selected, at each site. The species name and height of each woody plant, as well as the 'basal diameter' of the *Euclea* spp., was recorded. *Euclea divinorum* and *E. racemosa* can resprout from below ground portions of the stem after the above ground portions of the plant are removed (e.g. by fire or destructive herbivory) (pers. obs.). The basal diameter was therefore measured between 1 and 4 cm below the ground, and involved making a shallow excavation (ca. 3cm deep) around the stem of the plant. Finally, separate belt transects 2m wide were inventoried for all *Euclea* spp. irrespective of site (canopy or open) at each site in order to determine the overall height size-class distributions.

- **Size-class distributions**

Ideally size-class distributions (SCDs) should provide insight into population age structure and recruitment patterns. Plant height is often used as an indicator of age, but is of limited value in frequently disturbed communities where many species resprout from below ground organs after fires or destructive herbivory. In these communities basal diameter is a more reliable indicator of age because it is less affected by most disturbances. SCDs based on plant height were produced for *Euclea* spp. (in this study *E. divinorum* and *E. racemosa* will be considered equivalent due to their similarities in growth form and regeneration habits). Basal diameter SCDs were also produced for *Euclea* spp. Height SCDs of broadleaf-deciduous species were also produced, the species included *Berchemia zeyheri, Rhus pentheri, Rhus pyroides, Schotia brachypetala* , *Sclerocarya birrea, Dombeya rotundifolia, Cordia caffra, Canthium inerme, Ziziphus mucronata, Strychnos spinosa, Maytenus senegalensis** and *Maytenus heterophylla** (* not deciduous). These broadleaved species were included in the study because, like Eucleas, they all have fleshy, bird dispersed fruits and are relatively shade tolerant. The size-classes used for plant height were: < 0.5 m; 0.5 - 2.00 m; 2.00 - 4.00 m and > 4.00 m. The size-classes for basal diameter were: < 1.5 cm; 1.5 - 5 cm; 5 - 10 cm and > 10 cm.

Descriptive statistics were computed using the program Stat-Graphics. A Mann-Whitney U-test (Zar 1992) was used to compare the frequencies of *Euclea* spp. in the < 0.5m height size class, in open and canopy plots.

• Aerial photography

Aerial photographs from 1954, 1975 and 1992 were examined for sites 1,3,4 and 6 and changes in the physiognomy of the vegetation are described and discussed in terms of facilitation and of the fire history of each site. The black and white orthophotographs for 1954 (1:10 000), 1975 (1:20 000) and 1992 (1:20 000) were obtained from the Trigonometrical Survey, Mowbray. The stereo pairs were examined and the vegetation changes at selected sites were noted. The textural classes used were (i) trees; (ii) shrub; (iii) grass and (iv) bare ground.

Results

- **Survey Results**

Euclea canopy and open plot SCDs

A total of 22 arborescent woody species were encountered in the 90 plots sampled. *Euclea* spp. occurred in 68 % of the below canopy plots and 47 % of the open plots. *E. divinorum* was absent from the three sites in the northern region of the reserve, Sites 4, 6 and 7 (Figure 1). These three sites are at the highest altitude and probably receive the most rainfall of all the sites. *E. racemosa* on the other hand was absent from Sites 5 and 7.

At sites 1, 3, 4, 6 and 9, more than 40 % of the Eucleas found below *Acacia* canopies were less than 50 cm in height (Table 1). At all sites except 7 and 8, more than 85 % of the Euclea individuals in the below canopy plot were less than 2m in height (Table 1). At the majority of sites (6 out of 9) more than 65 % of the Euclea individuals growing in the open interspaces were between 50 and 200 cm in height (Table 1.). The majority of Euclea spp. observed in both open and canopy plots were less than 2m in height, the smallest size class (< 0.5m) was best represented in the canopy plots and the second size class (0.5-2m) was best represented in the open plots. By definition no Eucleas in the larger size-classes (2 - 4m and > 4m) were recorded in the open plots.

The height SCDs for *Euclea* spp., determined from the belt transects, give an indication of the overall *Euclea* population structure because they are independent of the canopy and open plots. These SCDs, hereafter referred to as overall SCDs, (Table 1), are based on larger numbers of observations than the canopy and open plot SCDs, and give an idea of the population structure and recruitment patterns for the whole region. The SCDs for both canopy and open plots at each of the nine sites (Table 1) were added together, producing one SCD which represents all the canopy plots sampled (Figure 2a) and one SCD which represents all the open plots (Figure 2b). The overall SCDs for each site were also added together, to make comparison between the canopy, open and overall SCDs possible. These figures (2a, b & c) serve to illustrate the establishment and recruitment patterns of *Euclea* spp.

Table 1. Percentage of *Euclea* spp. in each **height** size class found in canopy and open plots, and in the overall survey, at each study site.

	Sites								
	1	2	3	4	5	6	7*	8	9
Canopy plot SCD, *Euclea* spp.	*n*=10	*n*=14	*n*=157	*n*=5	*n*=35	*n*=70	-	*n*=26	*n*=26
	%	%	%	%	%	%		%	%
< 0.5m	50	7	61	60	14	59	-	23	42
0.5 to 2m	40	86	33	40	71	36	-	27	50
2 to 4m	0	0	5	0	14	6	-	23	4
>4m	10	7	1	0	0	0	-	27	4
Open plot SCD, *Euclea* spp.	*n*=6	n=2	*n*=22	*n*=4	*n*=25	*n*=3	-	*n*=18	*n*=6
< 0.5m	17	0	23	25	8	33	-	17	0
0.5 to 2m	83	100	73	50	72	67	-	72	50
2 to 4m	0	0	5	25	20	0	-	11	33
> 4m	0	0	0	0	0	0	-	0	17
Overall SCD, *Euclea* spp.	*n*=46	*n*=62	*n*=103	*n*=45	*n*=50	*n*=50	-	*n*=66	*n*=90
< 0.5m	15	18	7	13	14	38	-	2	23
0.5 to 2m	72	61	36	24	44	22	-	68	50
2 to 4m	7	11	14	24	22	26	-	15	24
> 4m	7	10	44	38	20	14	-	15	2

(* no Eucleas observed at Site 7)

The smallest size class (< 0.5m) is the best represented in the canopy SCD (Figure 2a), whereas, in the open and overall SCDs the second size-class (0.5 - 2m) is best represented (Figure 2 b & c). There are relatively few large Eucleas (size-class 3 & 4) below *A. nilotica* canopies, the open plots on the other hand, by definition contain no large Eucleas or Acacias (Figure 2 a & b). The open and overall SCDs are similar,

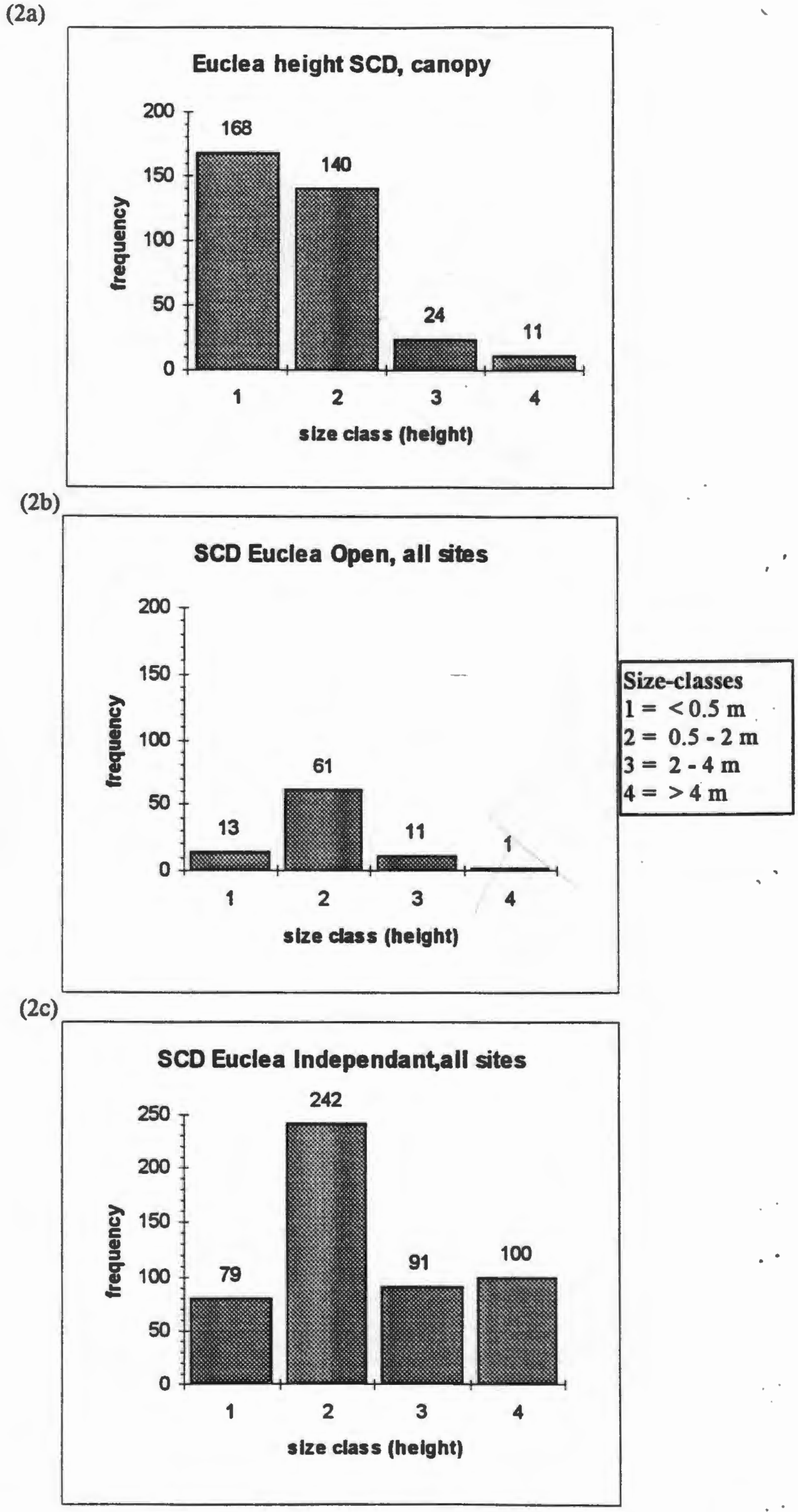


Figure 2. *Euclea* spp. height size-class distributions for canopy plots (a), open plots (b), and overall (c), based on all sites.

except in the larger size-classes (Figure 2 b & c). The overall SCDs are important because they give an indication of the population structure of *Euclea* spp. at each site, regardless of canopy and open sites (Table 2, Figure 2 c). All the *Euclea* height size-classes are well represented. There are more Eucleas in the size-class four (> 4m) than in size class one (< 0.5m), indicating that the *A. nilotica* woodlands sampled contain many large mature Eucleas, and not only Gullivers and seedlings (Figure 2 c).

The Mann-Whitney U-test (Zar 1992) indicates that the frequency of Euclea seedlings (< 0.5m) is significantly higher in the canopy plots than in the open (Table 2). The canopy and open plots are not significantly different for the larger size-classes (Table 2).

Table 2. Results of Mann-Whitney U-test on the numbers of Eucleas in the various height size-classes between canopy and open plots.

Size-class	P value	conditions
< 0.5m	P = 0.0075	1-tailed, $\alpha = 0.05$
0.5 - 2m	P = 0.0925	1-tailed, $\alpha = 0.05$
2m - 4m	P = 0.24	1-tailed, $\alpha = 0.05$
> 4m	P = 0.098	1-tailed, $\alpha = 0.05$

Basal diameter SCDs

The canopy and open plot basal diameter SCDs for *Euclea* spp. (Table 3, Figure 3a & 3b) differ notably in the small size classes (0-1.5cm and 1.5- 5cm). The canopy plots have a 90 % more small Eucleas than the open plots (Figure 3a & 3b). The *Euclea* recruitment patterns are therefore similar for the height and basal diameter SCDs. However, the largest basal diameter size-class (> 10cm) in the open plots is better represented than the largest height size-class (> 4m) in open plots (Figure 2b & 3b). Short *Euclea* shrubs with large basal diameters, which are found in most of the open plots, account for this difference. Superficially these plants resemble seedlings, but they are actually well established plants that have resprouted from underground organs after destructive disturbance events such as fire. In this case basal diameter is a better measure of plant age than height. The basal diameter SCDs therefore give a better indication of *Euclea* recruitment and seedling distribution than the height SCDs.

Table 3. Percentage of *Euclea* spp. in each **basal diameter** size class, found in canopy and open plots.

	Sites								
	1	2	3	4	5	6	7*	8	9
Canopy plot SCD, *Euclea spp.*	*n=10*	*n=14*	*n=157*	*n=5*	*n=35*	*n=70*	-	*n=26*	*n=26*
	%	%	%	%	%	%		%	%
< 1.5 cm	10	29	57	20	11	74	-	27	54
1.5 - 5 cm	60	43	27	80	40	23	-	15	27
5 - 10 cm	30	14	9	0	34	1	-	20	12
> 10 cm	0	7	7	0	14	0	-	38	8
Open plot SCD, *Euclea* spp.	*n=6*	*n=2*	*n=22*	*n=4*	*n=25*	*n=3*	-	*n=18*	*n=6*
< 1.5 cm	33	0	9	0	4	100	-	22	0
1.5 - 5 cm	33	50	59	75	36	0	-	33	60
5 - 10 cm	0	0	18	0	24	0	-	33	20
> 10 cm	33	50	4	25	36	0	-	11	20

(* no *Eucleas* at Site 7)

Other broadleaf spp. SCDs

A total of 14 broadleaf-deciduous or evergreen species, other than *E. divinorum* and *E. racemosa*, were observed at the study site. The height SCDs of the canopy and open plots are relatively similar (Table 4). The smaller size-classes, which are most informative in terms of recruitment, are well represented in both open and canopy plots. The 0.5 - 2m size class is the best represented size-class, in contrast the > 4m size class is almost empty for both plots (Table 4).

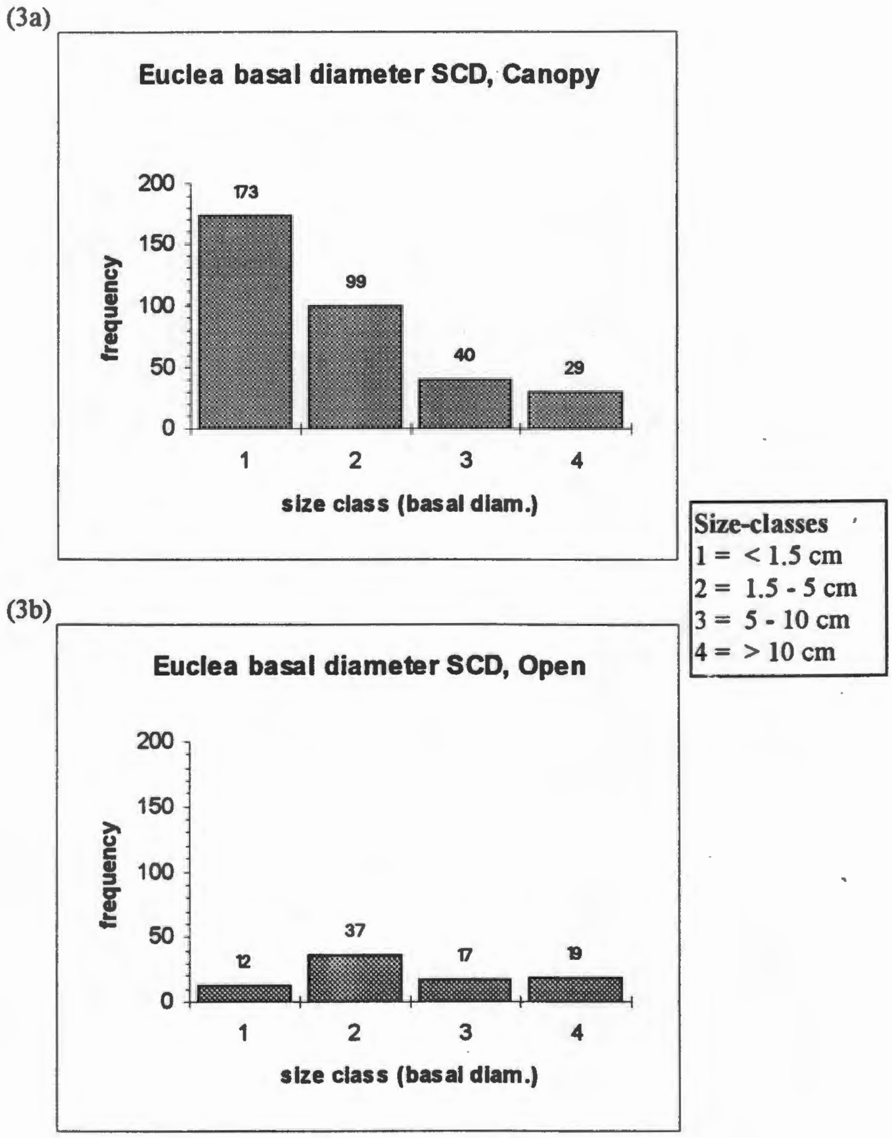


Figure 3. *Euclea* spp. **basal diameter** size-class distributions for canopy plots (a), and open plots (b), based on all sites.

Table 4. Percentage of broadleaf-deciduous species in each **height** size class found in canopy and open plots, at each study site.

	Site								
	1	2	3	4	5	6	7	8	9
Canopy plot SCD Broadleaf deciduous spp.	*n=15*	*n=57*	*n=65*	*n=63*	*n=30*	*n=66*	*n=19*	*n=36*	*n=46*
	%	%	%	%	%	%	%	%	%
< 0.5m	33	21	49	33	33	24	32	36	39
0.5 to 2m	60	79	46	49	53	61	58	36	54
2 to 4m	7	0	5	14	13	15	5	25	4
> 4m	0	0	0	3	0	0	5	3	2
Open plot SCD, Broadleaf deciduous spp.	*n=18*	*n=28*	*n=34*	*n=35*	*n=46*	*n=37*	*n=8*	*n=32*	*n=37*
< 0.5m	50	29	44	17	9	32	13	38	30
0.5 to 2m	50	64	53	69	85	57	88	56	70
2 to 4m	0	7	3	14	4	11	0	6	0
> 4m	0	0	0	0	2	0	0	0	0

Acacia recruitment

The census of woody plant species in *A. nilotica* woodland showed that 78 % of the *Acacia* juveniles observed, in both canopy and open plots, were *A. karroo* seedlings and saplings (Table 5). In contrast, only 7 % of the *Acacia* juveniles observed were *A. nilotica* individuals (Table 5). The three other *Acacia* species, *A caffra, A robusta,* and *A. burkei* accounted for less than 14 % of the *Acacia* recruits (Table 5).

Table 5. Percentage makeup of *Acacia spp.* (excluding adult *A. nilotica*) observed at each site, in both canopy and open plots.

	Sites								
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	tot.
Species	*n=83*	*n=45*	*n=36*	*n=33*	*n=33*	*n=12*	*n=60*	*n=4*	*n=16*	
	%	%	%	%	%	%	%	%	%	
A. karroo	96	91	89	100	27	100	67	0	44	79
A. nilotica	1	4	11	0	36	0	2	100	0	7
A. caffra	2	4	0	0	0	0	32	0	0	7
A. burkei	0	0	0	0	3	0	0	0	0	0
A. geradii	0	0	0	0	21	0	0	0	0	2
A. robusta	0	0	0	0	12	0	0	0	56	4
	100	100	100	100	100	100	100	100	100	100

- **Aerial photography - Description of the changes in the physiognomy of vegetation between 1954, 1975 and 1992.**

Site 1- Zincakeni lookout (Fig. 6a, 7a & 8a)

bearings 28° 5′ 19″ S ; 32° 4′ 50″ E
altitude 220m

The vegetation of this site has changed from a grassland (in 1954) to a closed canopy *Acacia nilotica* woodland (present). The change seems to have occurred gradually as the site was open shrub/grassland in 1975 and a woodland/thicket in 1992. The forest patches adjacent to the site have expanded slightly since 1954. The road to the lookout point was constructed between 1975 and 1992. The majority of the increase in woody vegetation at the site has occurred adjacent to the main road, and in the area between the new lookout road and main road. The roads, which act as effective fire breaks, prevent the spread of fires into the region of the site. The grassland to the south of the lookout has a few scattered shrubs but no large trees.

Site 3 Zincakeni dam (Fig. 6a, 7a & 8a)

bearings 28° 5′ 34″ S ; 32° 5′ 23″ E
altitude 180m

The physiognomic change at site 3 has not been a shift in growth form, but rather an increase in density of the woodland, from an open woodland with trees separated by large interspaces, to a closed canopy woodland with few open interspaces. The main road to the Gate forms the northern border, and the Hluhluwe river the southern border of the block which includes Site 3. Both these borders are very effective fire breaks, the block would have to be burnt specifically if the fire regime is to be maintained, as natural (lightning fire) fires would burn the area very infrequently.

Site 4 upper Magengeni (Fig. 6b, 7b & 8b)

bearings 28° 3′ 56″ S ; 32° 7′ 13″ E
altitude 220m

In 1954 and 1975 the site consisted of a small forest patch surrounded by open savanna with scattered large trees. The 1992 photo shows significant expansion of the forest patch, the border of which seems to be a woodland with large trees separated by open grass patches.

Site 6 lower Magengeni (Fig. 6b, 7b & 8b)

bearings 28° 3′ 56″ S ; 32° 7′ 11″ E
altitude 200m

Between 1954 and 1975 the vegetation of site 6 changed from open grassland to dense thicket/woodland. Over the next 20 years the extent of the thicket increased and trees

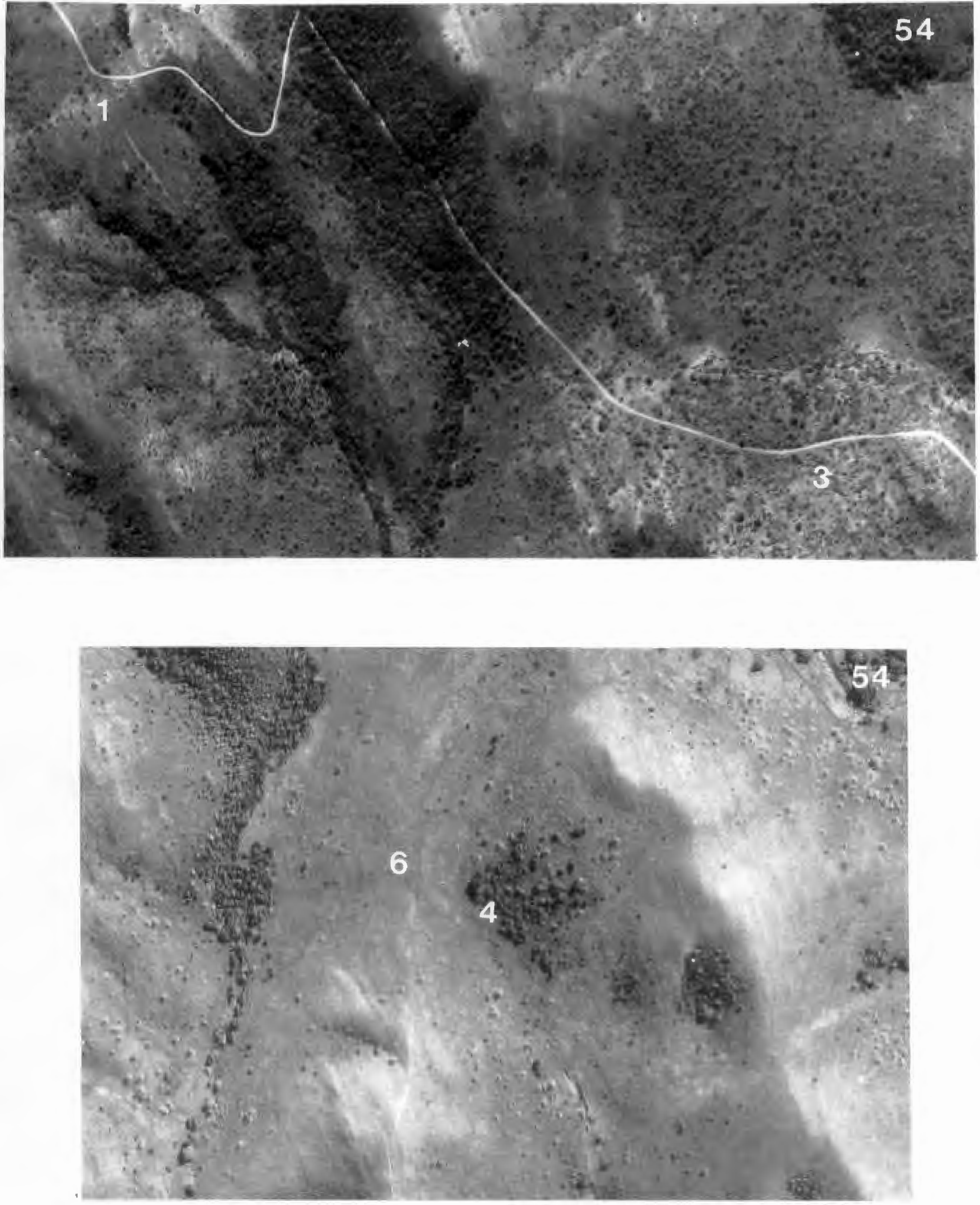


Figure 6(a). Site 1 and Site 3 in 1954 (scale 1:10 000). **6(b)**. Site 4 and Site 6 in 1954 (scale 1: 10 000).

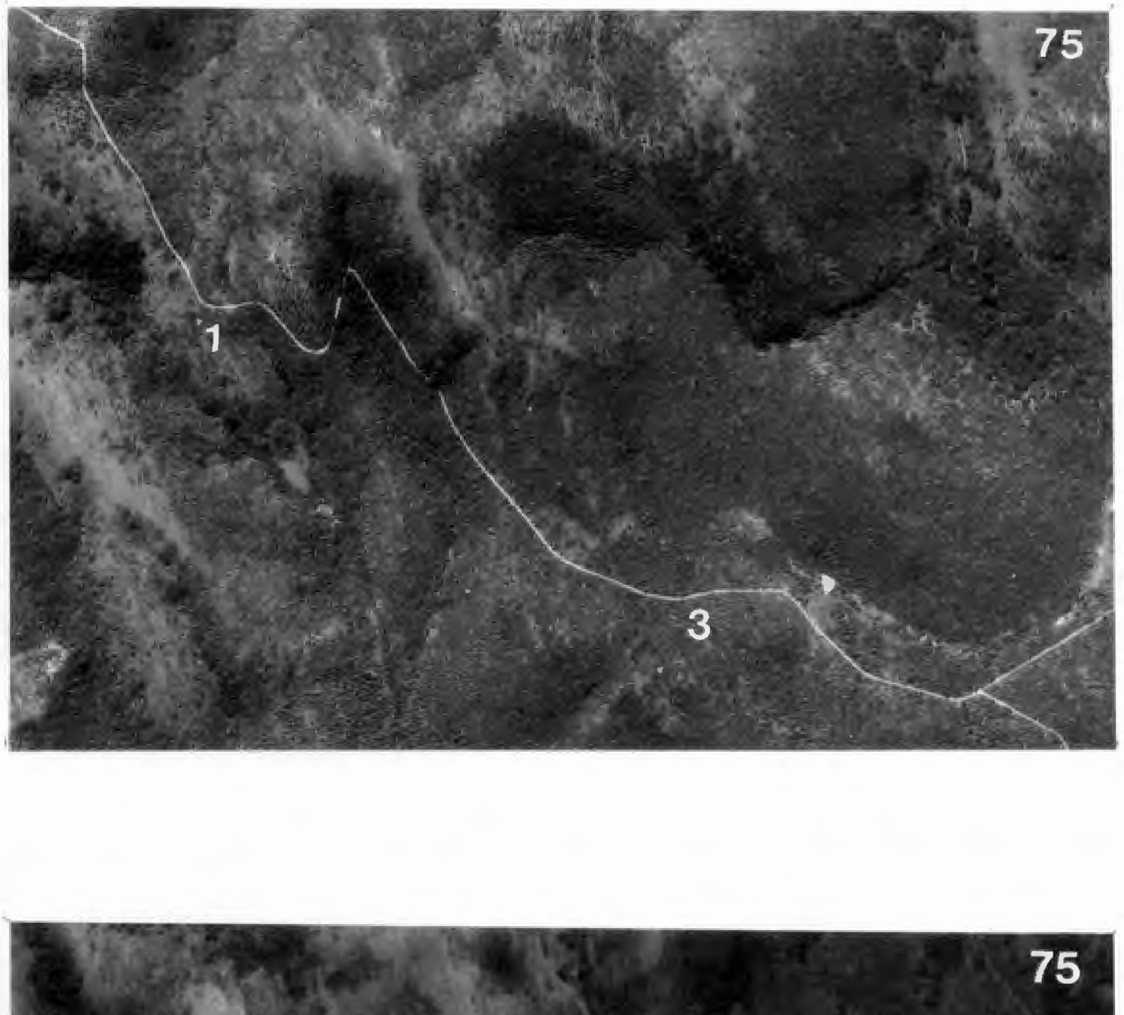
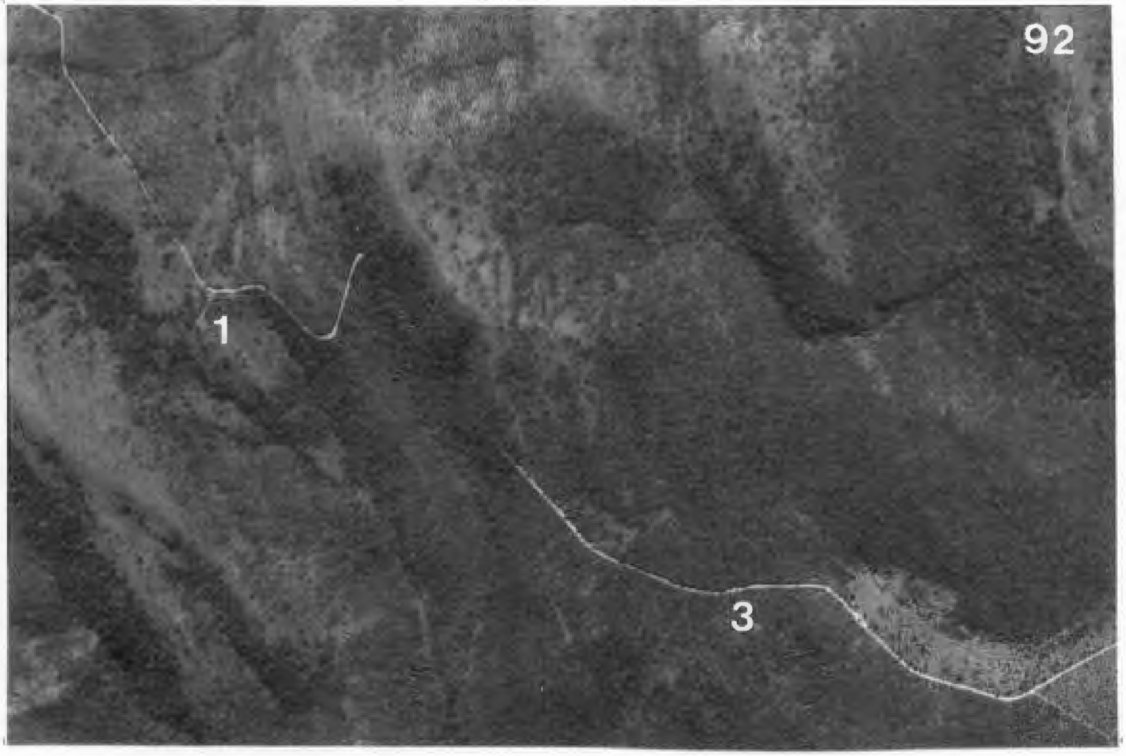


Figure 7(a). Site 1 and Site 3 in 1975 (scale 1:20 000). **7(b).** Site 4 and Site 6 in 1975 (scale 1: 20 000).



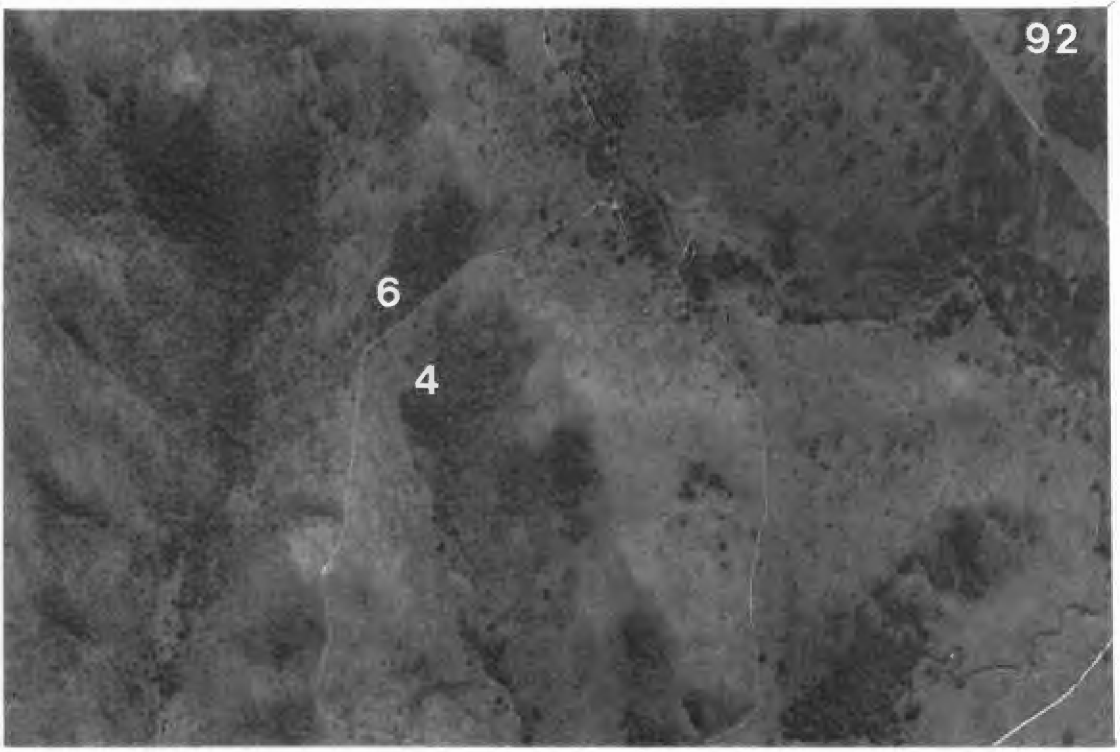


Figure 8(a). Site 1 and Site 3 in 1992 (scale 1:20 000). **8(b).** Site 4 and Site 6 in 1992 (scale 1: 20 000).

and shrubs increased in size. In the 1954 photographs the road, which was probably used infrequently, was narrow, and it is unlikely that it acted as an effective fire break. Between 1954 and 1975 the track has been a relatively wide graded strip, which has acted as a fire break. The road is a short distance from the northern boundary fence of the Reserve, and the intervening block (including Site 6) has not been burnt because of the danger of the fire spreading into neighbouring farm land (D. Balfour pers. com.). Interestingly, the thicket has only formed to the north of the road, in the fire protected block.

Discussion

Seedling facilitation

The results of the Mann-Whitney U-test indicate that there are significantly more *Euclea* seedlings (i.e. < 0.5m size class) below *A. nilotica* canopies than in adjacent open spaces. The height and basal diameter SCDs based on all the sites (Figure 2a,b,c, 3a &b) support this finding. Although the remaining size-classes were not significantly different between canopy and open plots (Table 2), *Euclea* recruitment is higher in the canopy plots than in the open plots (Figures 2 & 3). *Euclea* seedling establishment may therefore be a function of the environmental conditions below tree canopies, or of targeted dispersal of seed to below canopy sites (Franco-Pizana *et al.* 1996, Smith and Goodman 1987). However, the occurrence of *Euclea* seedlings in open interspaces indicates that shaded below-canopy environments are not essential for *Euclea* establishment.

The small size-classes (< 0.5m, 0.5-2m) are better represented than the large size-classes (2-4m, > 4m) in the canopy plots (Figure 2 a); this suggests that either there is high seedling mortality below canopies, or that *Euclea* seedling growth is being suppressed by the *Acacia* canopy in some way. This is similar to findings of Franco-Pizana *et al.* (1996) who showed that *Celtis pallida* seedling emergence was greater below *Prosopis* spp. canopies but that the subsequent growth rate of the seedlings was lower than in open sites. Smith and Goodman (1987) suggest that the dominance of *Euclea* seedlings in under-canopy sites is an early stage in the succession from open *A. nilotica* savanna to a *Euclea* dominated woodland. There is very little sign of Eucleas growing through *A. nilotica* canopies, in fact the low growth rate of *Euclea* spp. make this improbable.

Euclea growth rates

The growth rate of *E. divinorum* is extremely low in comparison to *A. nilotica*. Work by King (1987) indicates that juvenile *E. divinorum* individuals show a 20 % increase in stem diameter per annum, whereas *A. nilotica* juveniles increase by as much as 200 % per annum (Table 6). Smith and Goodmans (1987) successional hypothesis is therefore inadequate as there is insufficient time for *Euclea* seedlings, facilitated by adult *A. nilotica*, to grow to maturity and overtop the parent *Acacia* trees in one generation. The growth rates of mature *A. nilotica* and *Euclea* spp. are relatively similar, plants with a stem diameter of 10cm show an increase of 10 % per annum (Table 6).

Table 6. Growth rates of E. divinorum and A. nilotica expressed as % stem diameter increase per annum (King 1987).

Species	% stem diameter increase per annum		
Acacia nilotica	200	10	10
Euclea divinorum	30	20	10
stem diameter	1cm	5cm	10cm

(adapted from King 1987)

The overall SCD (Figure 2c) shows that there are numerous large Eucleas (> 4m in height) in the *A. nilotica* woodlands. In fact, the fourth size-class is better represented than size-class one (< 0.5m). These large Eucleas are sited away from adult Acacias and are probably a great deal older than the current cohort of *A. nilotica* (D. Balfour pers. com., King 1987).

Euclea Gullivers

The short Eucleas with large basal diameters, that are commonly found in the open plots (Table 4), could be considered 'Gullivers', defined by Bond and van Wilgen (1996) as stunted multi-stemmed shrubs which often dominate communities as adults but struggle to emerge from the herbaceous layer as juveniles. The herb layer interferes with the Gullivers recruitment by suppressing seedlings; slowing growth of established individuals; and by providing fuel for frequent fires which kill or stunt the survivors, thus preventing them from escaping the danger zones (Bond and van Wilgen 1996). Gullivers may persist for years until a break in the fire regime or the herb layer is reduced (drought, over grazing), and they are released from the danger zone.
Shrubland and open savanna can be rapidly transformed into woodland in this way (Bond and van Wilgen 1996).

Although there are more *Euclea* Gullivers in open plots than in below canopy plots, the low growth rate of Eucleas means that Gullivers may in fact be older than the current cohort of *A. nilotica* adults, estimated to be between 40 and 50 years old (D. Balfour pers. com.). The conditions under which the Gullivers became established are therefore unclear. Despite being uninformative in terms of current *Euclea* recruitment patterns and facilitation, Gullivers are an important element in the encroachment process in Hluhluwe because of their potential to 'escape' and grow into large trees.

Because of their short height *Euclea* Gullivers resemble seedlings and can prevent any useful recruitment data from being obtained merely from height SCDs. For example, Smith and Goodman (1987) assumed that all Eucleas less than one meter in height were seedlings, and did not measure basal diameter (Goodman pers. com.). In this case however, the SCDs for basal diameter and height are similar, indicating that height and basal diameter are well correlated.

Other broadleaf-deciduous and evergreen species

The lack of any major differences between open and canopy plot SCDs for other broadleaf-deciduous of evergreen species, indicates that Acacias are not facilitating all shade tolerant, bird-dispersed plants.

Acacia recruitment

The prevalence of *A. karroo* juveniles and lack of *A. nilotica* juveniles in *A. nilotica* woodland is an interesting finding (Table 4). In the Reserve, adult *A. karroo* are found only in hill top thickets and do not occur in *A. nilotica* woodlands (Whateley and Porter 1983). The source of the seed dispersal is therefore not obvious. The low recruitment level of *A. nilotica* is unusual because although some senescent adults were observed, the majority of the *A. nilotica* individuals showed evidence of seed production (i.e. persistent pods). African *Acacia* species are all microphyllous and, in general, their seedlings establish best in open patches, in direct sunlight (Coates Palgrave 1977, Smith and Goodman 1986). However, *A. karroo* seedlings are capable of establishing and surviving in a dense grass sward, are tolerant of low irradiance and of interference (O'Connor 1995). *A. nilotica* seedlings, on the other hand, require truly open spaces and fail to establish in shaded environments (Smith and Goodman 1986). The high rainfall and warm climate of the region is well suited to herbaceous growth, and the tall, dense grass sward which grows in the interspaces at all of the sites may allow the establishment of *A. karroo* but at the same time prevent the establishment of *A. nilotica* seedlings.

Importance of fire

Fire in Hluhluwe

King (1987), who reviewed the fire history of the Reserve, suggested that, although the reserve was proclaimed in 1897, it was only in the 1930's that true management began. Iron age communities, which occupied the region from around 1000 years before present, and modern rural inhabitants of the region traditionally burnt large tracts of land to better the grazing for their live stock. In addition to this the Iron age furnaces which have been found in the reserve (less than one Kilometre from Site 8), required large amounts of fuel wood and may have had a significant impact on the vegetation (Hall 1980). It is reasonable to assume that until the 1930's, when burning was stopped to protect the tsetse fly traps, large portions of the reserve burnt annually or biannually, with the peak in the dry winter months (King 1987). From around 1954 to 1968 burning in the reserve was restricted to peripheral fire breaks. After 1968 sections of the Reserve were burnt (King 1987). According to King (1987), the areas most frequently burnt correspond well to those least affected by bush encroachment.

Most management burning until 1985 has taken place three days after the first spring rains, and each block is burnt approx. every three years. This burning policy is inadequate for two main reasons: 1) burning after spring rains is more damaging to grasses than dry-season burns (Walker & Noy-Meir 1982); and 2) the burns are usually cool because the vegetation is moist and/or the burns are performed on cool windless days (D. Balfour pers. com.).

Tree-grass interactions

In savanna systems there is a tendency for woody vegetation to outcompete grasses when the disturbance regime (e.g. fire or destructive herbivory) is interrupted (Trollope 1984). If fire is excluded from a grassland or savanna, seedlings of woody plants are able to establish and grow out of the danger zone. Herbs tend to suppress woody plant invasion indirectly. After a seasons growth in a grassland or savanna the accumulated herbaceous biomass provides the fuel load for intense fires. In mesic systems more herbaceous material accumulates and the fires are thus more intense. Many young woody plants and many mature trees are killed by these fires. Grasses on the other hand have their growth point at or near ground level where temperatures do not get so high , they are therefore able to survive these intense fires and recover more rapidly than woody vegetation in the post fire environment.

Changes in the reserve

The physiognomic vegetation changes in the Reserve over the last forty years have been remarkable. The shift from grassland to thicket at site four, which has occurred in less than twenty years, and the steady expansion of woodland clusters into interspaces at site three indicate that bush encroachment is a dynamic process that can proceed at different rates, and in different communities (Figures 6-8).

A great deal of the encroachment has occurred in areas in which the fire regime has been altered (e.g. fire interval increased, intensity decreased) by roads and controlled management fires (see Figures 6-8). Roads are very effective fire breaks, and in Reserves such as Hluhluwe with an extensive tourist and management road network natural or unplanned fires affect a limited area. Managers may consider this beneficial to the Reserve because it allows them to control the effects of fire. The long-term usefulness of management burns in maintaining the open savanna and grassland vegetation and preventing encroachment by woody plants, is questionable (Watson and Macdonald 1983).

The patterns of woody plant increase, evident from the aerial photographs, suggest that changes in fire regime since the 1940's are partly responsible. Changes in the fire regime include; a reduction in fire frequency, which allows non-flammable vegetation to become established from dispersed seed and emerge in the fire free period. Although *Euclea* is flammable, the closed canopy thicket it forms, supports less flammable grasses / herbs and consequently less fuel (K. Maize pers. com.) The suppression of fires also allows Gullivers, which often dominate the open interspaces, to escape from the 'danger zone' and grow into large shrubs or trees, further increasing the canopy cover that indirectly excludes fire.

The change to predominantly cool spring burns, favoured by Reserve managers because of their ease of control, may have reduced the number of trees and shrubs actually killed by burns. Consequently, *Euclea* seedlings and Gullivers, which would normally be killed by fires, survive and continue to grow, adding to the woody biomass increase. Prior to the 1940's the Reserve was probably subject to frequent and widespread burns, both natural and anthropogenic (Brooks and Macdonald 1983). This period of frequent and intense disturbance, favoured herbaceous vegetation and prevented encroachment by limiting the survival of woody plant seedlings and preventing Gullivers from escaping the 'danger zone'. The recent suppression of disturbance in the Reserve may have allowed woody plants to emerge from the herbaceous vegetation and encroach into grassland and savanna communities.

Bush encroachment in the Reserve could be reduced by a selective and intensive burning regime. Regions in which severe encroachment has occurred, or is occurring could be identified with the use of aerial photographs. The appropriate blocks could then be burnt in winter to encourage more intense fires which encourage grasses and stunt shrubs and trees. These intense fires would be difficult to contain, but are essential in combating encroachment.

Conclusions

If *Euclea* spp. establish in open sites as well in under-canopy environments, and the growth rate of *Euclea* spp. is one tenth that of *A. nilotica*, as my results and those of King (1987) suggest, the importance of facilitation in *Euclea* seedling establishment must be questioned. The alternative approach, referred to earlier as the vital attributes approach, may be more useful in explaining the forces driving the successional process observed. Eucleas are slower growing and longer-lived than *A. nilotica*, they are highly persistent and can survive destructive disturbances by resprouting (K. Maize pers. comm.). The break in the disturbance regime in the 1940's may have allowed the current cohort of *A. nilotica* to become established. It is likely that *Euclea* spp. were already present in these areas, but were not as visible because the previous disturbance regime kept the majority of them as Gullivers. The break in disturbance regime may have allowed these Gullivers to grow into larger shrubs and trees. There is little evidence of replacement of *A. nilotica* by Eucleas. The encroachment of broadleaf species in the Reserve over the last 50 years may therefore be due to the growth of suppressed *Euclea* individuals rather than an increase in *Euclea* recruitment and growth below adult *A. nilotica* canopies.

Smith and Goodman (1987) suggest that historically elephants maintained *A. nilotica* savanna either by ensuring a high turn over of adult Acacias and reducing the establishment sites for Eucleas, or by reducing tree cover and increasing grass production which increases fire frequency. Since the elimination of elephants from Mkuzi Game Reserve in the 1930's the fire frequency has been reduced and many *A. nilotica* woodlands have been replaced by *Euclea* thickets (Smith and Goodman 1987). I suggest that because elephants were already absent from HluhluweGame Reserve in the early 1900's, it was the alteration of the fire regime by Reserve management that caused the increase in woody plant biomass.

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