Processes affecting the community structure of Dukuduku forest

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PROCESSES AFFECTING THE COMMUNITY STRUCTURE OF DUKUDUKU FOREST

ABSTRACT

Some shade-intolerant tree species in Dukuduku forest have very few seedling recruits, despite the fact that they are relatively common canopy species. Several theories exist for their lack of seedlings. Three of these theories are tested here. The first theory tested is whether an increase in herbivore levels is the cause of recruitment bottlenecks for certain canopy species. The second theory tested is whether shade-intolerant seedlings are reliant on tree falls or canopy gaps for their recruitment. The last theory tested is whether the herbaceous understory suppresses the recruitment of shade-intolerant plants.

Preliminary results indicate that herbivory is not an important factor in limiting the abundance of shade-intolerant. Nor did the creation of canopy gaps initiate the recruitment of shade-intolerant species. Thus, the influence of tree felling or the presence of large herbivores such as elephants is not important in the forest dynamics of Dukuduku forest. It appears that the elimination of the dense understory herb, *Isoglossa*, is most important in creating the conditions necessary for the recruitment of shade-intolerant species. Removal of *Isoglossa* caused greater recruitments of *Celtis africana* and *Albizia adianthifolia* than in any other forest treatments ($p = 0.006$ and $p = 0.01$ respectively). Although *Isoglossa* dies on mass every 5 to 10 years, it probably regenerates fast enough to overshade most woody plants. However, fire is capable of eliminating *Isoglossa* from large areas for up to 10 years. Thus, in conclusion, the diversity of Dukuduku forest probably maintained by fires which periodically kill *Isoglossa*, enabling the shade-intolerant plants to recruit.

INTRODUCTION

Certain canopy tree species found in Dukuduku forest, seem to be undergoing recruitment bottlenecks, that is, they have very low seedling/parent ratios (Midgley *et al.*, 1995a). Seedling/parent ratios could be related to the grain of a forest (i.e. the size and frequency of disturbances within the forest.). For instance, in coarse grained forests, disturbances are often large and infrequent, and seedlings of those plants dependent on disturbance for their regeneration may be scarce. This study was initiated in order to decipher what disturbances are necessary for the recruitment of seedlings showing recruitment bottlenecks.

FOREST GRAIN

Forest grain has been the topic of many recent papers concerning forest dynamics and forest processes (Spies and Franklin, 1989; Midgley *et al.*, 1990; van Wyk and Everard, 1994; van Wyk and Everard, 1995). The grain of a forest refers to the level of disturbance needed to drive forest processes and maintain its present species diversity. For instance, forests of the Southern Cape plateau (South Africa) are thought to be fine grained (Midgley *et al.*, 1990). Such forests are usually dominated by shade-tolerant species which only require small disturbances such as branch or tree falls to reach the canopy (Van Wyk *et al.*, 1996).

At the other extreme are coarse grained forests such as those described by Veblen *et al.*,(1981) and Veblen and Ashton (1978). These forests contain a high proportion of shade-intolerant species such as *Nothofagus* which are unable to regenerate under the shade of the forest canopy. Instead, these plants are reliant on large scale disturbances such as volcanism (Veblen and Ashton, 1978) or flood deposition (Veblen *et al.*, 1981) to clear away the vegetation which prevents their regeneration. These catastrophic disturbances typically affect areas greater than 25 ha. (Veblen, 1989). Naturally a continuum exists between the two extremes of fine and coarse grain.

THE IMPORTANCE OF FOREST GRAIN

Van Wyk and Everard (1994) envisaged that forest grain could become an important tool in the management of South African forests. South Africa is characterised by rapidly changing socio-political circumstances which have a strong bearing on how we view our natural resources. Traditionally, forest material has been used for firewood, building material, traditional medicines and for a variety of tools and weapons. Forests were also heavily exploited by settlers in the late nineteenth century, until a strict hands off policy was implemented for most South African forests (McCracken 1986). Forests have also become increasingly fragmented with local inhabitants applying mounting pressure to forest flora and fauna. Fragmentation effectively reduces forests to islands. These islands are consequently unable to hold the full compliment of flora and fauna. (MacArthur and Wilson, 1963 and MacArthur and Wilson, 1967). Fragmentation and changing socio-political factors result in forests being especially prone to changes in the disturbance regimes responsible for the regeneration of specific groups of forest trees (Van Wyk and Everard, 1995).

DUKUDUKU FOREST

The forest lies on the coarse side of the grain continuum and was classified as such by van Wyk *et al.*, (1996). Two different techniques were used by van Wyk *et al.*, (1996) to ascertain the grain of this forest. Ordination distances were used to compare the woody component of the sub-canopy with the plants of the canopy. In Dukuduku, ordination distances were large, implying that the canopy was different in composition to the sub-canopy. This was coupled with size class distribution curves of several of the more common tree species found in the forest. Canopy trees found in fine grained forests usually have a high seedling to parent ratio. However, in Dukuduku, several species had few seedlings in comparison to the number of canopy individuals. One such tree is *Celtis africana,* (Midgley *et al.*, 1995a) which was predicted to be relatively shade-tolerant (Midgley *et al.*, 1995b). Small individuals are generally absent from the sub-canopy and are thought to require large scale disturbances to

ensure that recruitment takes place (Everard, *et al.*, 1995). In the absence of large scale disturbance, plants like *C. africana* may undergo a recruitment bottleneck and eventually be replaced by plants which are able to survive under the canopy and have a continuous recruitment (Everard *et al.*, 1995).

Dukuduku has been hypothesised as a forest driven by large scale disturbances, however the nature of the disturbance has not been identified although numerous theories were proposed by Midgley *et al.* (1995a). Human activities could be the cause of historic sources of disturbance. These may be in the form of excessive tree harvesting or higher fire frequencies which may open the forest canopy, facilitating the periodic regeneration of shade-intolerant species (Midgley *et al.*, 1995a). Natural fires, cyclones and droughts may also be the cause of large scale mortalities although there is no information regarding the importance of these events in coastal forest dynamics (Midgley *et al.*, 1995a).

Importance of herbivory

The present lack of shade-tolerant species could also be related to increased levels of herbivory. In forest patches such as Dukuduku, the first of the forest fauna to disappear are animals with large territories and also those which are frequently in conflict with man. Large carnivores fall into both of these categories. With few large carnivores, it was predicted by Midgley et al. (1995b) that the numbers of small herbivores (red duiker and bushbuck) may be higher than they were in previous years. Evidence suggests that herbivores may prefer shade-intolerant plants over shade-tolerant plants as a source of food (Coley *et al.*, 1985; Coley, 1988 and Reich *et al.*, 1991). Shade-intolerant plants often have high rates of photosynthesis and short leaf retention times (Coley, 1988 and Reich *et al.*, 1991). Coley *et al.* (1985) stated that plants with a high leaf turnover do not usually invest in herbivore defence mechanisms, they generally invest their nutrients in the production of new leaves, casting off older leaves as they lose their efficiency as photosynthetic organs. Investing expensive chemical deterrents in ephemeral leaves would be a costly exercise for these plants. Thus fast growing plants are often more poorly defended than slow growing plants.

Importance of canopy gaps

In the past, megaherbivores such as elephants were presumably more plentiful. These creatures are renowned for their destructive capabilities and may possibly have created large forest openings in which shade-intolerant species could regenerate (Midgley *et al.* 1995a). In the absence of megaherbivores, it may be necessary to create artificial gaps to meet the regeneration requirements of shade-intolerant plants.

Importance of shading by the understory

The last theory involves the effect of understory vegetation (Midgley *et al.*, 1995a) on the recruitment of seedlings. Previous papers regarding forest dynamics have largely ignored the effects of understory on the regeneration of canopy species. One notable exception is the paper of Veblen *et al.* (1981). Veblen *et al.* (1981) worked on *Nothofagus* forests in the Andes. At high elevations, Veblen *et al.* (1981) found that shade-tolerant trees were unable to exist and that forests consisted of pure *Nothofagus* stands. These *Nothofagus* forests are largely influenced by massive disturbances such as volcanism and mass movements. The forest is also characterised by a dense understory of shade tolerant bamboos, belonging to the genus *Chusquea.* The bamboos and the high canopy cover of *Nothofagus*, suppress the regeneration of *Nothofagus* seedlings. However, large tree falls create gaps where conditions are unfavourable for the bamboo. The harsh conditions in the gaps reduce the size and number of bamboo, this subsequently allows the regeneration of shade-intolerant *Nothofagus* seedlings.

The herbaceous layer of Dukuduku forest is dominated by the shrub *Isoglossa woodii,* which forms a dense stand, sometimes reaching 2.5m in height. The life history of this herb is particularly interesting because the plants have a synchronised reproductive phase (van Wyk and Everard, 1995). This results in mass flowering and seed set, after which, all the plants die and are replaced by seedlings (Ward, 1980 and van Wyk and Everard, 1995). *I. woodii* is able to grow in all but the deepest shade and only the most hardy of shade-tolerant individuals are able to survive in the dark areas uninhabited by *I. woodii.* However, *I. woodii* also thrives in the broad sunlight of forest gaps and forest margins where it suppresses the recruitment of shade-intolerant species (Ward, 1980; pers obs.).

OBJECTIVES

The main objectives of this project are to isolate the factors which influence the regeneration of seedlings associated with Dukuduku, an apparently "coarse grained" forest. By isolating these factors, it may be possible to identify the nature of the disturbances which have over the years helped to create this forest. By isolating the disturbance regime, we would know whether these disturbances are still acting on the forest or if they have ceased to exist due to changing socio-political circumstances, fauna composition or management practices. This would have a strong bearing on forest management. For example, managers may let disturbance occur naturally or it may be necessary to manipulate forest processes in order to maintain the present diversity of plants. The factors examined were the aspects of herbivory, the role of the *I.woodii* understory and canopy gaps on seedling recruitment.

METHODS

STUDY SITE

Dukuduku forest (28°25'S, 32°17'E) is situated on the northern banks of the Umfolozi River flood plain (Van Wyk *et al.*, 1996). The importance of Dukuduku lies in the fact that it is South Africa's largest and best preserved coastal lowland forest. It occupies an area of 3 500 ha., which is 40% of South Africa's surviving coastal lowland forest.

The forest is surrounded by sugarcane plantations (see figure 1.) to the south and exotic timber plantations to the north (Van Wyk *et al.*, 1996). The area reaches a maximum of 60m above sea level with high lying areas corresponding to minor south-trending dune ridges situated on a low plateau. The plateau is surrounded by three flood plains: St Lucia in the East, Umfolozi in the south and Futululu in the south-west. Soils are deep and derived predominantly from recent wind-deposited sands (Van Wyk *et al.*, 1996). Soils are generally nutrient poor due to their susceptibility to leaching. The mean annual rainfall is 1243mm., 60% of which occurs during the summer months (Van Wyk *et al.*, 1996). North-east and south-west winds predominate with the rain bearing winds being from the south-east.

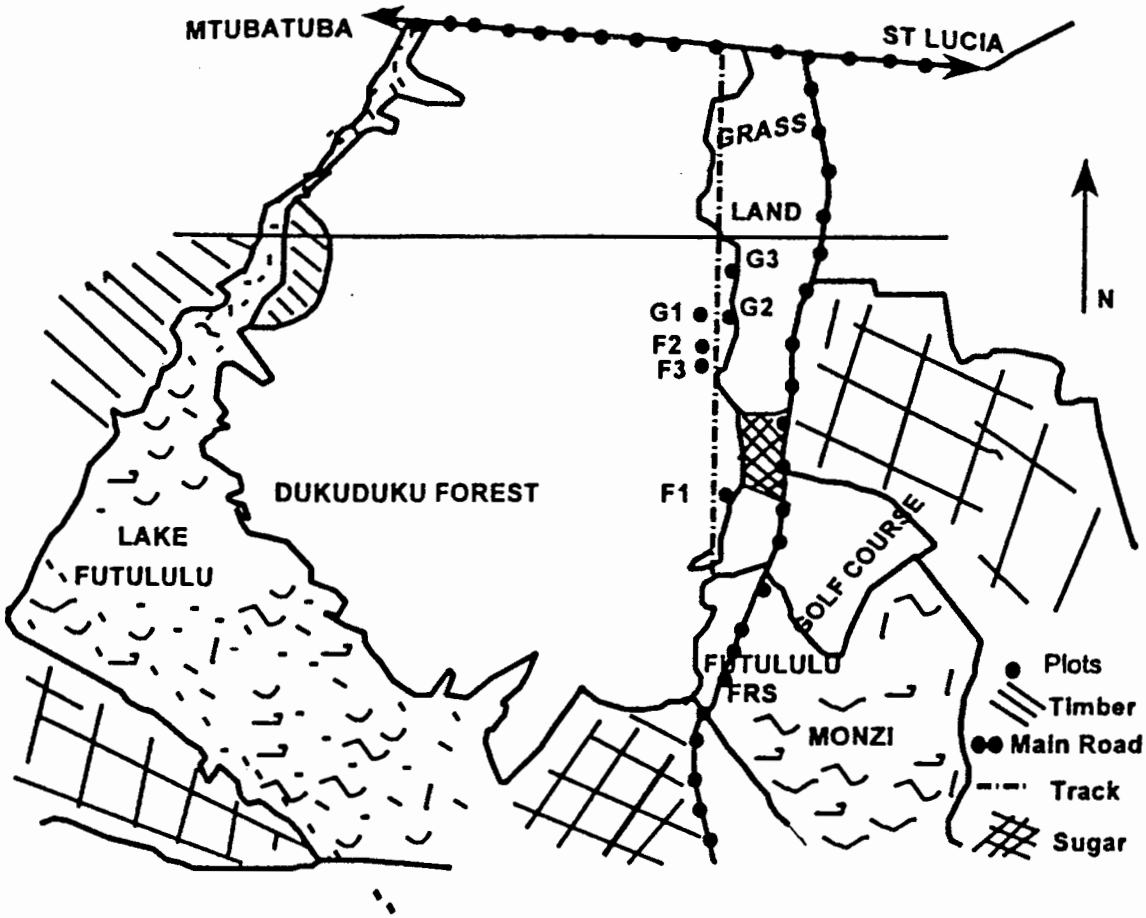

Figure 1. A diagrammatic representation of the western portion of Dukuduku forest showing the location of the experimental plots. Codes are F = undisturbed forest and G = artificially created gaps. (From van Wyk and Everard, 1995).

EXPERIMENTAL METHODS

Herbivory, canopy gaps and understory

Six experimental areas were chosen by van Wyk and Everard (1995) in Dukuduku forest (Figure 1). In three of these areas, the canopy trees were left intact, while in the other three, the canopy trees were cleared to create artificial gaps (Van Wyk and Everard 1995). Wire exclosures were erected in each experimental area (Van Wyk and Everard 1995). The mesh was small enough to exclude browsers such as bush buck and red duiker but not smaller animals such as rodents. The exclosure was divided in

half, each half measuring five metres by five metres. In one half, the herbaceous layer (mainly *I.woodii*) was cleared, while in the other, the herbaceous layer was left intact (Van Wyk and Everard 1995). Any woody shrub, tree seedling, creeper seedling or sapling remained unharmed during the clearing process (van Wyk and Everard 1995). These treatments (clearing of the herbaceous layer and no treatment) were also repeated outside the exclosures (Van Wyk and Everard 1995). Unfortunately van Wyk and Everard (1995) were unable to establish a plot with an intact herbaceous layer outside of the exclosure. This was because the felling of the trees damaged the herbaceous layer. These treatments simulated many of the forest's natural states (i.e. forest canopy with *Isoglossa* underneath, forest canopy after *Isoglossa* had died, canopy gap with *Isoglossa* understory and canopy gap after *Isoglossa* had died). The treatments were then duplicated with and without the influence of herbivores, that is by fencing some of the plots and leaving others unfenced.

During June 1994, van Wyk and Everard (1995) recorded all woody plants in the plots by species and size class. Plants were marked by encircling them with wire and their bearing taken from a set point. This enabled us to identify individual plants and measure their growth over time. Ringed plants and any new plants were then recorded again in June 1996 according to species and size class. In addition to this, the total percentage of herbaceous cover and *Isoglossa* cover was also estimated.

Isoglossa distribution

The *Isoglossa* stem and foliage densities were sampled under a continuum of canopy cover densities. The canopy cover was visually estimated according to the amount of light perceived to be reaching the sub-canopy. Canopy cover values ranged from 5% to 95%. Values closest to zero were usually sampled from areas with little or no forest canopy. Very high percentages of canopy cover were often recorded under the tree *Hypocanthus amoenus* because its crown tended to bend downwards towards the ground, blocking out much of the lateral light source. High percentages of canopy cover were also recorded under trees which were infested with "walls" of creepers. These creepers also had the effect of blocking off much of the available lateral light.

Once the canopy was assigned a value according to the amount of shade cast, a $1m^2$ plot was randomly laid upon the forest floor. *I. woodii* stems and the percentage of *I.woodii* foliage cover were calculated from within the quadrat. In addition, all other woody plants and creepers were recorded by species.

DATA ANALYSIS

Herbivory

The total number of woody seedlings and *Celtis africana* seedlings were recorded and compared between fenced and unfenced plots. Only plants which were unmarked in the 1994 survey were used because they had recruited after the forest treatments had been applied. The forest was divided into three groups, "forest intact," "forest clear" and "gap clear." There were two replicates for the "gap clear" treatment which was protected against herbivory (fenced). All other treatments had three replicates. Comparisons were conducted using Mann-Whitney U tests. Unfortunately the results of statisitcal tests on this set of data are not robust because of the small sample size (n = 3).

Effects of canopy gaps and Isoglossa on seedling recruitment

The forest treatments were divided into four groups: "Forest intact" (i.e. forest canopy with intact *Isoglossa* layer), "forest clear" (i.e. forest canopy with *Isoglossa* layer cleared), "gap intact" (i.e. canopy gap with intact *Isoglossa* layer) and "gap clear" (i.e. canopy gap with *Isoglossa* layer cleared). There were only three replicates for "gap intact" plots as there was not an unfenced version of this treatment. There were supposed to be six replicates of the "gap clear" plots, however two replicates had to be excluded from the analysis. A duiker became trapped in one of the "gap clear" exclosures and damaged most of the seedlings before it died. The other "gap clear" plot was excluded because *Isoglossa* had invaded 80% of the plot. Three methods were used to examine the significance of gaps and *Isoglossa* in determining forest structure.

Method 1

Each seedling species was recorded by number in each plot. Those seedlings ringed in 1994 were excluded from the data set as they had recruited before the gap and *Isoglossa* treatments had been applied. The seedling data was tested for normality using the Shapiro-Wilk's W test. Parametric data was tested using an ANOVA, while non parametric data was tested using a Kruskal-Wallis test.. The grouping variable used was forest treatment (i.e. "forest intact", "forest clear", "gap intact" and "gap clear"). In this way it was possible to observe if any plant species were preferentially recruiting according to any particular forest treatment.

Method 2

The numbers of certain seedling species were compared before and after forest treatments were applied. Before forest treatments, all plots would have been in the "forest intact" state (i.e. intact forest canopy and intact *Isoglossa* sub-canopy). These comparisons made it possible to establish if any new species had recruited or if recruitment values had changed for certain species because of the forest treatment. "Before and after" values were tested for *Strychnos decussata, Ochna natalitia, Celtis africana* and *Albizia adianthifolia* using t-tests. These particular species were tested because they were the only seedlings common enough on which to perform reliable statistical tests.

Method 3 (multivariate techniques)

Multivariate techniques were also used to group plot replicates according to the species composition of the plots. Classification was performed using the hierarchical classification package, TWINSPAN (Hill, 1979a). Stems per plot were used as importance values. Only unringed stems were used for this data analysis because these stems would have recruited after the forest treatments had been applied. All options were set to default for the TWINSPAN algorithm, except the pseudospecies cut levels which were set at 0, 2, 5, 10, 20 and 40. The data set was then ordinated using a detrended correspondence analysis (DCA), which is a subroutine of the program DECORANA (Hill, 1979b).

Isoglossa distribution

The effect of canopy cover on the abundance of seedlings and on the density of *I.woodii* was examined using correlation matrices. Correlations measure the relation between two variables and the coefficient of variation represents the strength of the relationship.

RESULTS

HERBIVORY

Comparisons indicated no significant differences between the number of woody seedlings in fenced and unfenced plots (Table 1). Thus herbivory is not a significant factor in determining the numbers of woody plants in a given area ($p = 0.27$, $p = 0.28$ and $p = 0.51$; see Table 1). Similarly, the exclusion of herbivores has no effect on the abundance of *Celtis africana* ($p = 0.36$, $p = 0.19$ and $p = 0.56$; Table 2).

Table 1. The number of woody seedlings counted in fenced and unfenced plots. Forest clear = closed canopy with no *I. woodii* sub-canopy, forest intact = closed canopy with an *I.woodii* sub-canopy and gap clear = canopy gap with no *I. woodii* sub- canopy.

	FOREST CLEAR		FOREST INTACT		GAP CLEAR	
	fenced	unfenced	fenced	unfenced	fenced	unfenced
n	3	3	3	3	2	3
average	52	30	46	33	15	18
std dev	28	12	69	31	15	1
p	0.27		0.28		0.51	

Table 2. Total number *Celtis africana* seedlings counted in fenced and unfenced plots. Forest clear = closed canopy with no *I. woodii* sub-canopy, forest intact = closed canopy with an *I. woodii* sub-canopy and gap clear = canopy gap with no *I. woodii* sub-canopy.

	FOREST CLEAR		FOREST INTACT		GAP CLEAR	
	fenced	unfenced	fenced	unfenced	fenced	unfenced
n	3	3	3	3	2	3
average	14	7	0	2	1	2
std dev	6	4	0	3	2	4
p	0.26		0.19		0.56	

EFFECTS OF CANOPY GAPS AND *ISOGLOSSA* ON SEEDLING RECRUITMENT

Method 1

Celtis africana and *Abizia adianthifolia*

Celtis africana and *Albizia adianthifolia* were recruiting maximally in areas with an intact forest canopy but no *Isoglossa* layer (figures 3 and 3). The numbers of seedlings recruiting in other forest phases are minimal. There is a significant difference between the numbers seedlings counted in each of the forest treatments ($p = 0.01$ for *C. africana* and $p = 0.006$ for *A. adianthifolia*, Table 3). Thus, the recruitment for *A. adianthifolia* and *C. africana* is greater in cleared forests than in any of the other forest treatments.

Ochna natalitia

Ochna natalitia seedlings also seem to show specific light requirements (Figure 4) and found recruiting mainly in canopy gaps which had been cleared of *Isoglossa.* Results from the Kruskal - Wallis test (Table 3) indicate that the recruitment differences seen in the Figure 3 are significant ($p = 0.004$).

Strychnos decussata

Strychnos decussata was the most commonly occurring seedling but did not show any specific requirements for recruitment regarding the presence or absence of gaps or *Isoglossa* (Figure 5). Seedling recruitment was similar throughout all forest treatments ($p = 0.25$).

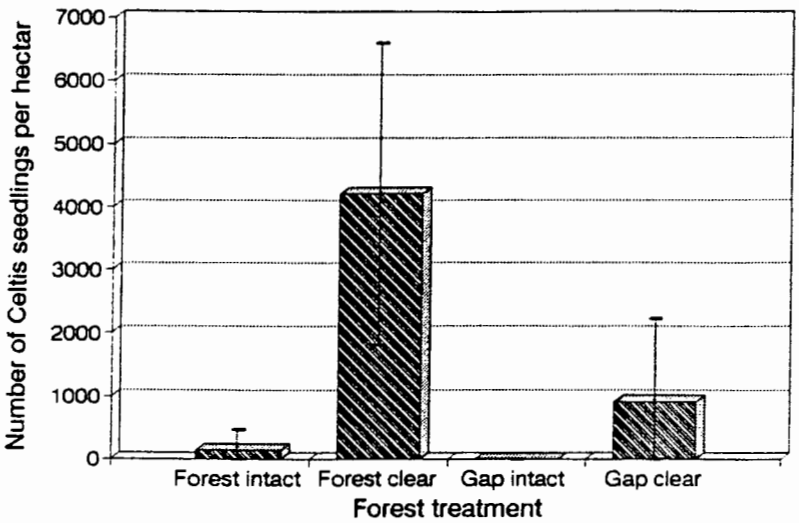

Figure 2. The effect of forest treatment on *Celtis africana* recruitment. Forest intact = closed canopy with an intact *Isoglossa* understory, forest clear = closed canopy with *Isoglossa* sub-canopy removed, gap intact = canopy gap with intact *Isoglossa* sub-canopy, gap clear = canopy gap with *Isoglossa* sub-canopy removed. Values displayed are seedlings which recruited after the forest treatments in 1994.

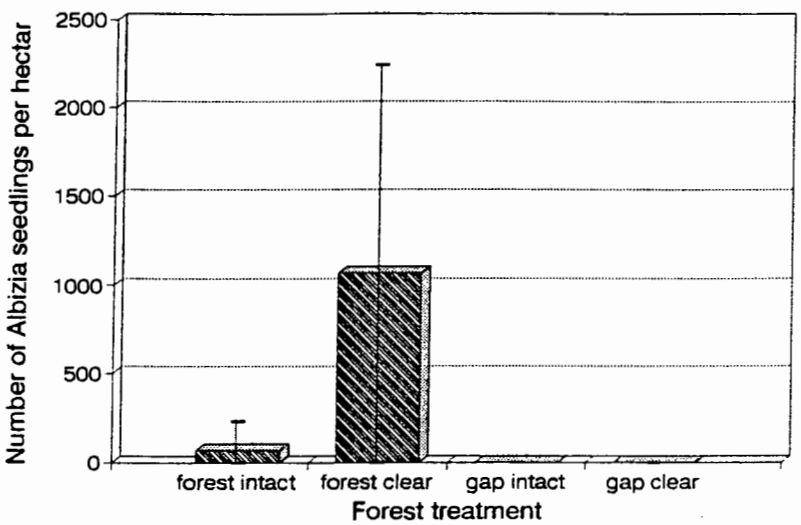

Figure 3. The effect of forest treatment on *Albizia adianthifolia* recruitment. See Figure 2 for meanings of the different forest treatments.

Table 3. Comparisons of the recruitment of several species after different forest treatments.

	significance value (p)
ANOVA	
Landolfia kirkii	0.056
herbaceous cover	**0.0003**
KRUSKAL WALLIS	
Albizia adiathifolia	**0.006**
Celtis africana	**0.01**
Ochna natalitia	**0.004**
Strychnos decussata	0.25
Uvaria caffra	0.13

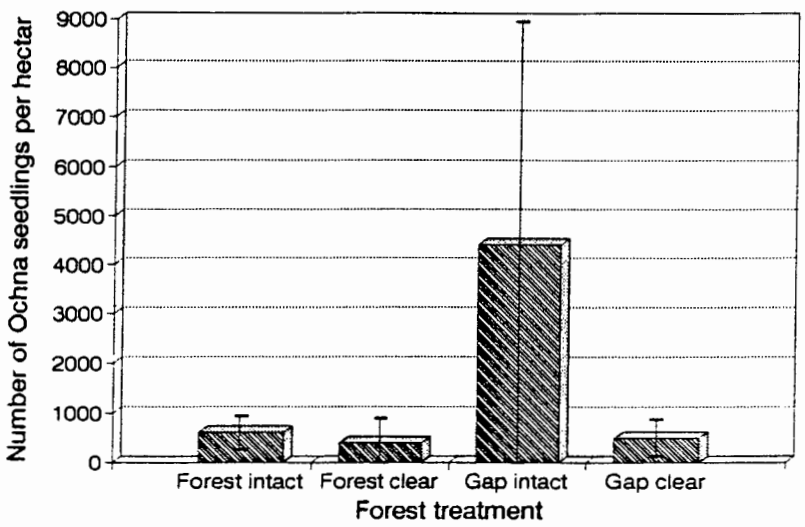

Figure 4. The effect of forest treatment on *Ochna natalitia* recruitment. See Figure 2 for meanings of the different forest treatments.

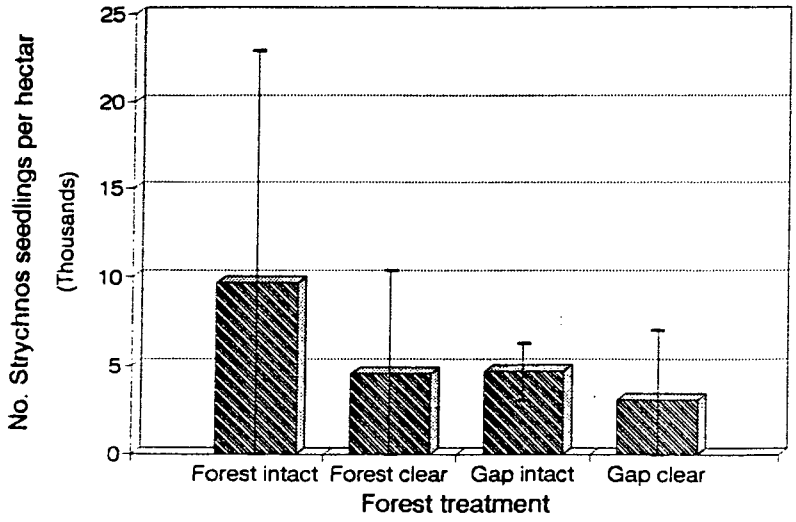

Figure 5. The effect of forest treatment on *Strychnos decussata* recruitment. See Figure 2 for meanings of the different forest treatments.

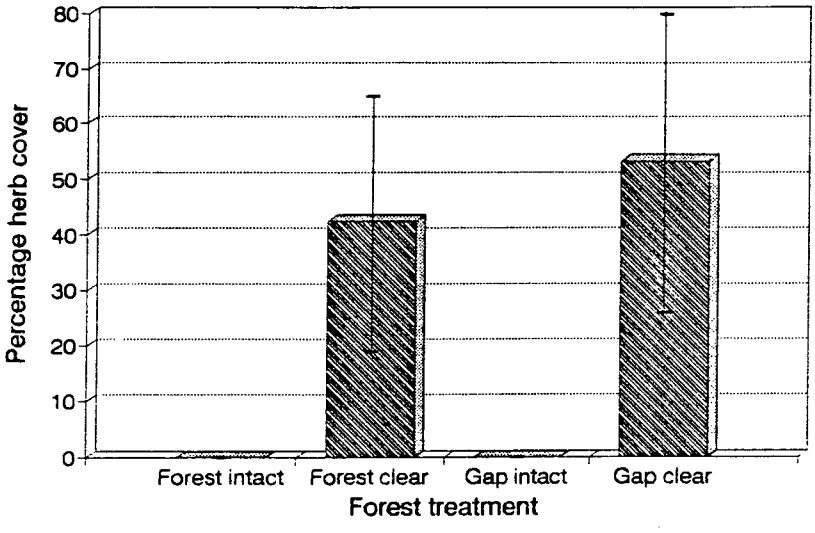

Figure 6. The effect of forest treatment on the amount of herbaceous cover. Plants sampled were all herbaceous plants excepting *I.woodii*. See Figure 2 for the meanings of the different forest treatments.

Herbaceous cover

Herbaceous cover (excluding *Isoglossa*) was dependent on the absence of *Isoglossa* (Figure 6).The percentage herbaceous cover was large in both canopy gaps and intact canopies as long as the *Isoglossa* layer had been cleared (Figure 6). The herbaceous cover was very sparse in plots which had not been cleared of *Isoglossa.* These results were statistically significant ($p = 0.0003$, see Table 3).

Creepers

The two most common creeper species were *Landolfia kirkii* (Figure 7) and *Uvaria caffra* (Figure 8). Both species showed little difference in where they recruited in greatest numbers. Statistically, the differences in recruitment for both species were insignificant ($p = 0.056$ and 0.13 respectively, see Tabe 3).

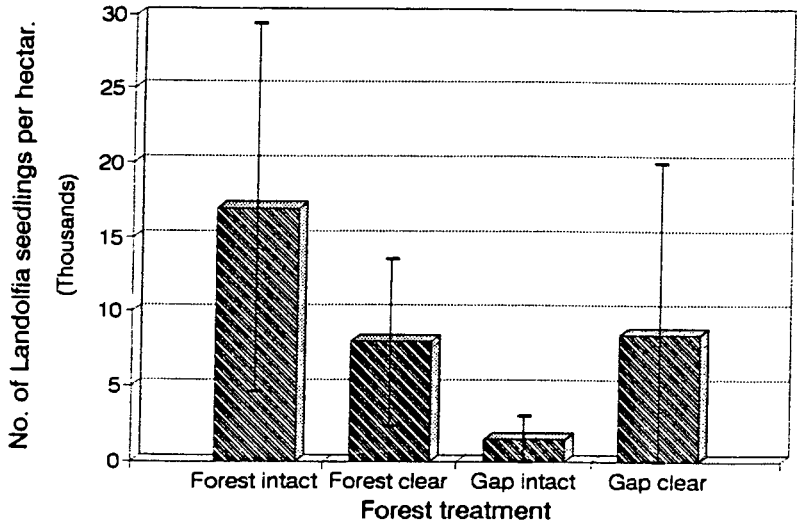

Figure 7. The effect of forest treatment on *Landolfia kirkii* recruitment. See Figure 2 for meanings of the different forest treatments.

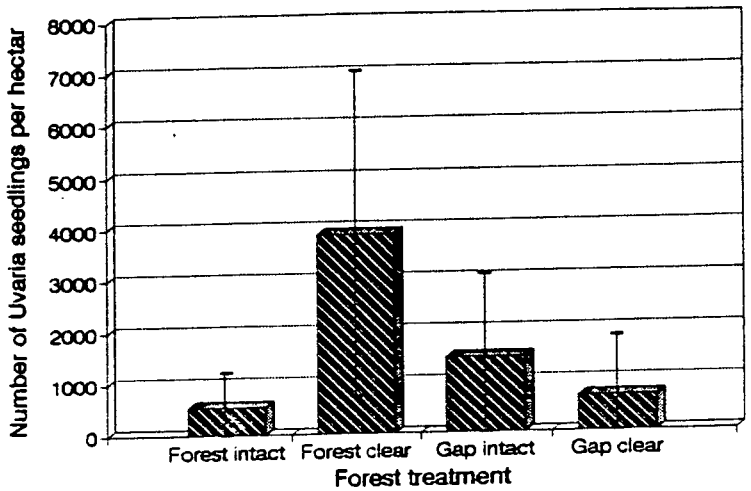

Figure 8. The effect of forest treatment on *Uvaria caffra* recruitment. See Figure 2 for meanings of the different forest treatments.

Method 2

Celtis africana and *Albizia adianthifolia*

Important results were obtained for the recruitment of *C. africana* and *A. adianthifolia* in forests cleared of *Isoglossa* (Table 4 and 5). Both of these plants had significant recruitment only after the *Isoglossa* was removed from under the closed canopy. Before the *Isoglossa* was cleared, there were no *C. africana* or *A. adianthifolia*. However, two years after the *Isoglossa* was cleared, 63 *C. africana* and 16 *A. adianthifolia* seedlings were counted. These "before and after" values were found to be significantly different ($p = 0.0008$ and $p = 0.05$ respectively, Table 5).

Ochna natalitia

The recruitment of *Ochna natalitia* before and after the forest was treated is also very interesting. Figure 4 shows *O. natalitia* to be recruiting mainly in forest gaps which are devoid of *Isoglossa*. However, Table 4 indicates that *O. natalitia* recruitment actually dropped from 56 to 33 seedlings after gaps were created and the *Isoglossa* was removed. Table 5 indicates that there was no significant difference in *O. natalitia* recruitment before and after forest treatments were made ($p = 0.65$). This indicates that the high values for *O. natalitia* seedlings in "gap intact" plots (see figure 4) is probably due to the fact that recruitment *of O. natalitia* is not spatially homogenous. There was probably a parent tree very nearby!

Strychnos decussata

The numbers of *S. decussata* did not change significantly after forest treatments were applied (Tables 4 and 5). *S. decussata* seedlings increased five times in number since the start of the experiment in the "Forest intact" plots (Table 4), however this increase was insignificant ($p = 0.18$, Table 5). The largest increase in *S. decussata* numbers was found in plots cleared of *Isoglossa* (Table 4), however this increase was also insignificant ($p = 0.12$). Thus, *S. decussata* is able to recruit approximately equally throughout the forest, irrespective of the light conditions.

Table 4. A comparison of seedling numbers before and after forest treatments. Values outside of the brackets are numbers of seedlings sampled before forest treatments, those values within brackets are the numbers of seedlings sampled after forest treatments.

	FOREST INTACT	FOREST CLEAR	GAP INTACT	GAP CLEAR
S. decussata	29 (145)	10 (69)	15 (35)	20 (31)
O. natalitia	13 (9)	8 (9)	56 (33)	15 (5)
C. africana	0 (2)	**0 (63)**	0 (0)	0 (9)
A. adianthifolia	0 (1)	**0 (16)**	0 (0)	0 (0)

Table 5. Significance values (p) obtained using t-tests. T - tests compared the numbers of seedlings before and after forest treatments.

	FOREST INTACT	FOREST CLEAR	GAP INTACT	GAP CLEAR
S. decussata	0.18	0.12	0.29	0.62
O. natalitia	0.54	0.86	0.65	0.26
C. africana	0.34	**0.0008**	1	0.22
A. adianthifolia	0.34	**0.05**	1	1

Method 3 (multivariate techniques)

The first TWINSPAN division (eigenvalue 0.49) was divided according to the presence of *Celtis africana, Albizia adiathifolia, Ziziphus mucronata, Strychnos decussata, Trema orientalis* and *Hypercanthus amoenus.* This was the most robust division which separated the "forest clear" plots from the rest of the plots (Figures 9 and 10). These plots with their intact canopies and cleared *Isoglossa* layers were characterised by the presence of *Celtis africana, Albizia adianthifolia* or *Ziziphus mucronata.*. Reasonably strong separation is also shown for the "gap clear" plots (Figures 9 and 10). "Gap clear" plots were separated at TWINSPAN division five (eigenvalue 0.48). These plots were characterised by the plants *Clausena anisata, Erythrococca berberidea* and *Trema orientalis.* None of these plants were found

recruiting in great densities. The most common of these species was *Trema orientalis* of which only eight individuals were found. All eight were found distributed among three of the "gap clear" plots. Other TWINSPAN divisions grouped "forest intact" and "gap intact" plots together. This implies that a gap on its own, is not sufficient disturbance to change the woody seedling recruiting community. The composition of the woody seedling recruiting community only changes after the elimination of the *Isoglossa* layer either in closed canopy or open canopy areas.

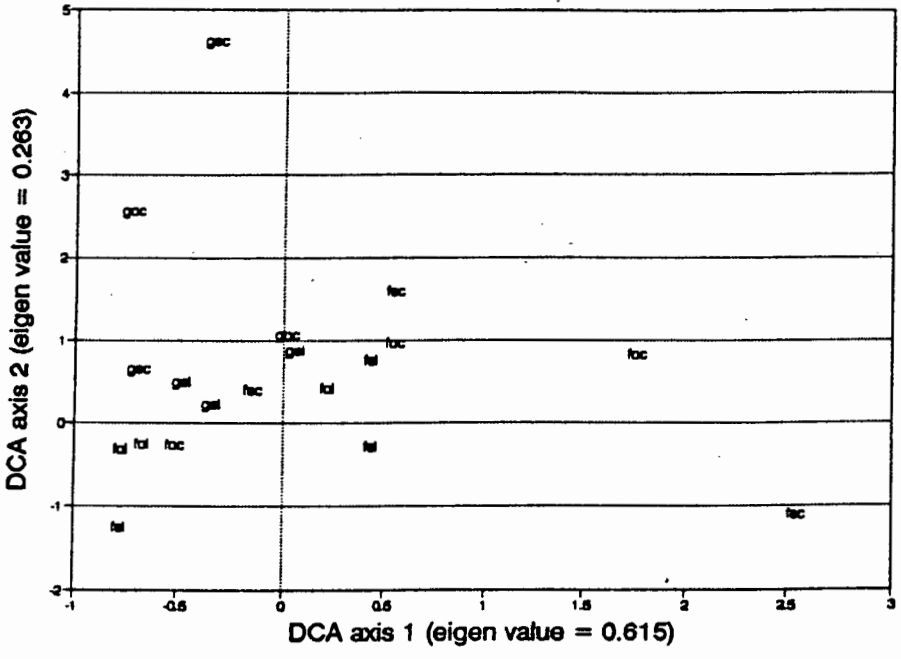

Figure 9. An ordination diagram (DCA) of the different plots in Dukuduku forest. Letters refer to the different treatments applied to the vegetation of each plot. **f** = forest (i.e. closed canopy), **g** = gap (in the forest canopy), **e** = enclosed (i.e. fenced), **o** = open (i.e. unfenced), **I** = intact (i.e. Isoglossa layer intact) and **c** = cleared (i.e. Isoglossa layer cleared).

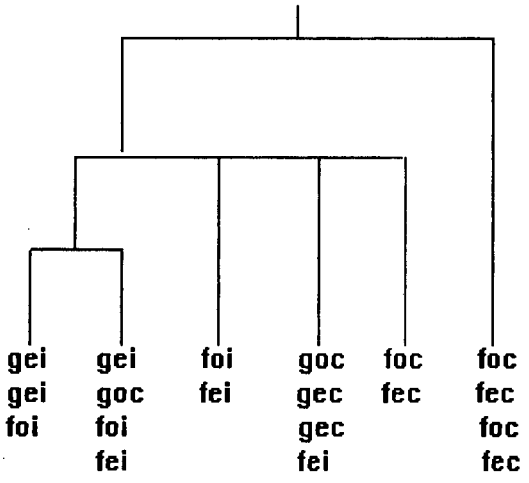

Figure 10. A dendrogram displaying the plot divisions supplied by TWINSPAN. The forest canopy), **e** = **e**nclosed (i.e. fenced), **o** = **o**pen (i.e. unfenced), **I** = **i**ntact (i.e. Isoglossa layer intact) and **c** = **c**leared (i.e. Isoglossa layer cleared).

ISOGLOSSA DISTRIBUTION

Percentage cover and number of *I. woodii* stems over the light continuum (Figures 11 and 12 respectively) both increase as more light permeates through the forest canopy. Coefficients of determination (R^2) are reasonably high for the number of *I. woodii* stems and the percentage *I. woodii* cover (R^2 = 0.67 and R^2 = 0.66 respectively). Thus, there is a strong relationship between percentage canopy cover and the number *of I. woodii* stems and also with the percentage cover of *I. woodii*. Significance values calculated for correlations (Table 6) are also high for the number of *I. woodii* stems and the percentage *I. woodii* cover (p = 0.000 for both), indicating that the correlations are very reliable. The numbers woody seedlings and creepers were not related to the percentage canopy cover (Table 6). None of the coefficients of correlation were close to the value one (Table 6) and the significance levels calculated for the correlations were all greater than 0.05 (Table 6).

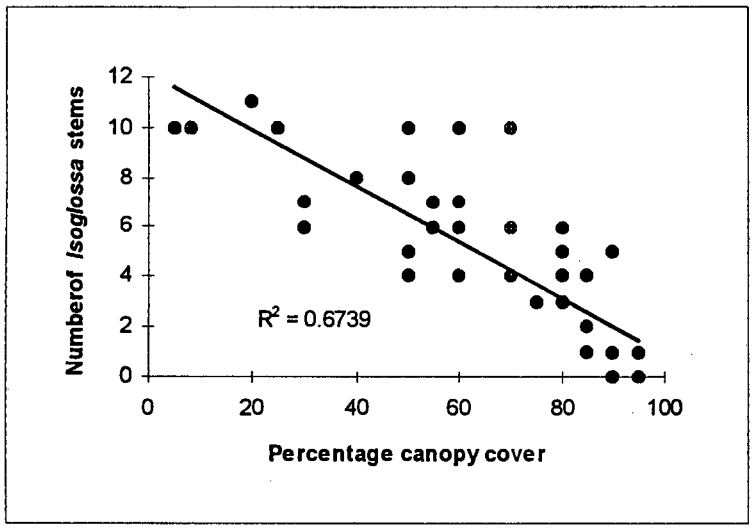

Figure 11. The number of *I. woodii* stems sampled in $1m^2$ plots over a light continuum in Dukuduku forest.

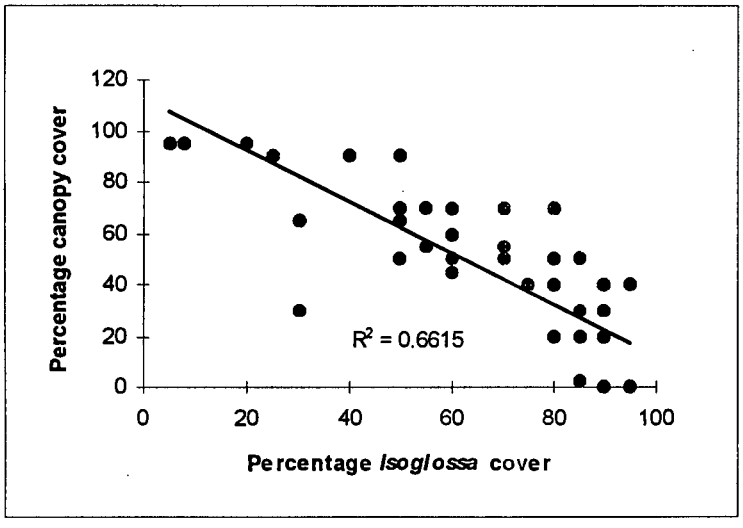

Figure 12. The percentage of *I. woodii* foliage cover sampled in 1 ± 1m plots over a light continuum in Dukuduku forest.

	Significance value (p)	Coefficient of determination (R^2)
No. *I. woodii* stems	0.000	0.67
% *I. woodii* cover	0.000	0.66
No. woody plants	0.097	0.05
No. *O. natalitia*	0.051	0.08
No. *S. decussata*	0.731	0.003
No. *U. caffra*	0.876	0.0004
No. *L. kirkii*	0.081	0.06

Table 6. The relationship of the numbers of seedlings and *I. woodii* with the percentage canopy cover.

DISCUSSION

HERBIVORY

Comparisons between fenced and unfenced plots indicated little or no difference in the total numbers of woody seedlings. This suggests that herbivory is not impacting on the general seedling recruitment in the forest. Differences in the numbers of *C. africana* seedlings between fenced and unfenced plots were also insignificant. However the small sample size in these experiments make the statistical results unreliable as indicators of herbivory. Naturally, the best method to circumnavigate this problem is to create more replicates but this is costly in terms of time and materials. Although statistical results showed no significant difference between seedling recruitment in fenced and unfenced plots, there were twice as many *C. africana* in fenced plots as there were in unfenced plots in the "forest clear" treatment (Table 2).

The period since the plots were fenced has only been two years, which is a short time when trying to examine the effects of herbivory. Data from herbivory experiments conducted in northern hardwood stands were only collected several years after the experiments were set up [15 years (Webb *et al.* 1956), 10 years (Curtis and Rushmore, 1958), 9 years (Tierson *et al.* 1966) and 5 years (Tilghman 1989)]. Thus, perhaps given time and more replicates, it may be possible to observe a significant difference in the number of *C. africana* seedlings between fenced and unfenced plots in

the "forest cleared" treatment. However, even if a significant difference were found, herbivory would be unimportant as factor creating of the forest patterns of Dukuduku. The reason for this is that even with the impact of herbivory, there are still relatively large numbers of *C. africana* seedlings found in fenced plots (Table 2).

EFFECTS OF CANOPY GAPS AND *ISOGLOSSA* ON SEEDLING RECRUITMENT

Methods 1 and 2

Celtis africana and *Albizia adianthifolia*

All results (Figures 2 and 3, Tables 3, 4 and 5)show conclusively that in Dukuduku forest, these two species are preferentially recruiting in areas with intact forest canopies but no *Isoglossa* layer ("forest clear" plots). They may be dependent on the periodic death of *Isoglossa* for their recruitment. The apparent lack of seedlings could be because significant numbers of these seedlings are only able to recruit once the *Isoglossa* dies (every 5 to 10 years). Unfortunately there is not much literature on the life history of *Isoglossa.* However, *Isoglossa* is a herbaceous plant and its re-establishment probably takes less than two years. This is the length of time that the Dukuduku plots have been cleared. I would predict that the *Isoglossa* would re-establish fairly quickly after its mass death and overshade all but the fastest growing, shade-intolerant plants. Thus these experiments only show that *Isoglossa* inhibits the regeneration of shade intolerant-seedlings. This does not necessarily mean that shade-intolerant seedlings would be able to keep up with and survive the regrowth of *Isoglossa.*

From the height of seedlings measured, it seems that *Celtis africana* has a very fast growth rate. Some seedlings were found to be over one metre in height after only two years of growth. Given this growth rate, it seems probable that *Celtis africana* could keep its leaves above the regrowing *Isoglossa* layer. On the other hand, the largest *Albizia* seedlings found after the experimental period were just 30cm high. These seedlings would probably be rapidly overtaken by the *Isoglossa* re-growth.

Ochna natalitia

Two different methods were used to determine where *O. natalitia* is recruiting. Both showed conflicting results. One method showed *O. natalitia* to be recruiting in "gap intact" plots (Figure 4), while the other showed that *O. natalitia* recruited equally throughout the forest (Tables 4 and 5). When comparing the numbers of seedlings in plots after different treatments, one of the assumptions is that seed dispersal is approximately equal throughout the forest. However, this is not always true. The reason for the abundance of *O. natalitia* in "gap intact" plots (Figure 4) is probably due to abnormally high recruitment in some of these plots. Comparing numbers of seedlings before and after forest treatments showed no difference in the numbers of *O. natalitia* (Tables 4 and 5). This method did not make the assumption of spatially homogenous seed dispersal. Thus *O. natalitia* probably does not require canopy gaps for recruitment.

Strychnos decussata

Both experimental methods showed *Strychnos* to recruit more or less evenly throughout the different forest treatments (Figure 5 and Table 4). *Strychnos* was the most common woody plant found in most of the plots regardless of the plot treatments. Although being able to recruit in areas of fairly high light intensity (e.g. "gap clear" plots), *Strychnos* is a fairly slow growing plant and would not be able to outcompete fast growing, shade-intolerants such as *Celtis africana* in areas of intense light.

Method 3 (multivariate techniques)

The strongest grouping was for "forest clear" plots (Figures 9 and 10). These plots are floristically different to the other plots examined in this survey. The main difference is that many shade-intolerant plants are recruiting in "forest clear" plots, whereas few shade-intolerant seedlings are recruiting in other plots. "Gap intact" plots do not have many shade-intolerant recruits. The reason for this is because after the forest canopy is removed, the shade cast by *Isoglossa* is still too dense for shade-intolerant seedlings to grow. Alternatively, after the canopy is removed, the *Isoglossa* is able to grow more densely, thus intercepting the new available light before the shade-intolerant seedlings are able to grow through the understory.

However, there are also very few shade-intolerant tree seedlings in the gaps which are cleared of *Isoglossa*, even though there is excess light in these plots. There was one unique species in the cleared gaps and that was *Trema orientalis* which was found in very low densities in three of the four "gap clear" plots. Van Wyk and Everard (1995) surveyed the same plots six months after the plot treatments were applied and also found that shade-intolerant plants were apparently lacking from these plots (even though there was little shade). They reasoned that severe drought conditions during the duration of the experiment had caused unfavourable conditions for *C. africana* in the cleared gaps. They found that cleared gaps looked particularly dry because sunlight was able to penetrate right to ground level. However, these unfavourable conditions did not seem to affect the abundance of the shade-tolerant plants *S. decussata* and *O. natalitia* (Van Wyk and Everard 1995) which I would have expected to be more adversely affected by the dry conditions.

It was noticed in the 1996 survey that the herbaceous cover in the cleared gaps was often extremely dense and formed a thick, choking mat which probably competes with woody seedlings for both light and space (Brereton-Stiles and Kruger, pers. comm. and pers. obs.). The herbaceous cover in "gap cleared" plots was on average of 52%. This was not significantly different to the 41% herbaceous cover in "forest clear" plots. However the differences in herbaceous cover were visually very different and this was not portrayed properly by the statistical results. The herbaceous layer was visually more dense and choking in "gap clear" plots than it was in "forest clear" plots. This may be because of the greater light intensity in "gap clear" plots. There is no canopy or sub-canopy in these plots, whereas the canopy in "forest clear" plots filters much of the light before it reaches the ground. The dense, choking herbs in "gap clear" plots may suppress many of the shade-intolerant plants such as *C. africana* and *A. adianthifolia*.

ISOGLOSSA DISTRIBUTION

Isoglossa was found growing over a large range of the available light conditions. In the most illuminated parts of the forest, *Isoglossa* flourished. However, *Isoglossa* was never found far away from forested areas (pers. obs). Presumably they are not suited to

totally open, more illuminated conditions, or they are out competed by grasses in these areas. In the forest, the only areas which did not support dense stands of *Isoglossa* were those areas of intense shade. Areas of intense shade and sparse *Isoglossa* were relatively uncommon in the forest and were small in their dimensions (about five by five metres, pers. obs.). Thus, there were few naturally occurring areas without a dense *Isoglossa* understory. However, the only plants able to recruit there are shade tolerant species such as *Strychnos decussata*. Consequently, the seedling flora in these shady areas was very similar to the flora found under the *Isoglossa* layer. If there were tree falls in these intensely shady areas, it may be possible for shade-intolerant seedlings to recruit. Many of these shady areas are found under *Hypercanthus amoenus* because of its down bending branches. However, this plant reaches a maximum height of just eight metres (Pooley, 1993). Consequently it is seldom exposed to strong wind and is probably seldom the cause of tree fall gaps. The chances of tree falls in the few remaining areas of dense shade are very remote. Thus, the regeneration of shade-intolerant plants in these *Isoglossa* free patches is probably a rare event and is insignificant in contributing to the present population of shade-intolerant plants.

The seedling numbers and seedling composition were similar in all the plots sampled, regardless of the percentage canopy cover or number of *Isoglossa* stems. Thus, the amount of light reaching the ground is similar regardless of whether the canopy is intact or if there is a canopy gap. The reason for this is that the more light filtering through the forest canopy, the denser *Isoglossa* sub-canopy will grow (Figures 11 and 12).

The numbers of seedlings did not differ between plots. Therefore, seedling density is not limited by the presence of *Isoglossa*. It may have been expected that fewer seedlings would be able to exist in areas of dense *Isoglossa* because of root competition for nutrients, however this was not observed. It would have been interesting to measure seedling height in areas of dense *Isoglossa* and areas of sparse *Isoglossa*, as this would have been a better method of gauging whether competition is occurring between *Isoglossa* and seedlings. However, the fact that seedling numbers

are similar in areas with and without *Isoglossa* implies that the numbers of shade-tolerant seedlings are not limited by nutrients (i.e. competition with Isoglossa). Instead, they may be limited by other factors for example, parental seed set.

CONCLUSION

The most distinct flora was found in the plots with a closed forest canopy and no *Isoglossa*. These plots had several shade intolerant plants such as *Celtis africana* and *Albizia adianthifolia*. The next most distinct community was found in forest gaps which had been cleared of *Isoglossa*. The similarity between these two plot types is that they had both been cleared of *Isoglossa*. Thus *Isoglossa* is the factor which must be eliminated in order for shade-intolerant plants to recruit. Gaps and closed canopies with an *Isoglossa* layer were floristically very similar. This suggests that gaps on their own play a very small role in driving forest processes. Thus, gap makers, such as elephants or woodcutters, may not have contributed much to the Dukuduku forest structure in the recent past.

If *Isoglossa* were to die on mass every 5 to 10 years, it could facilitate the recruitment of many shade-intolerant seedlings. However, I believe that the success of these seedlings would be very limited because many would soon be swamped by the newly emerging *Isoglossa* layer. Seedlings need a longer head start than the time offered by the periodic death of *Isoglossa*. One way to gain a substantial head start on *Isoglossa* is through fire. If fire were to sweep through an area, it would kill the *Isoglossa* layer. The *Isoglossa* would only be able to recolonise these areas after adjacent stands of *Isoglossa* set seed. This only happens every 5 to 10 years. A fire early in the *Isoglossa* reproductive cycle could leave large areas of land devoid of *Isoglossa* for considerable periods of time. However, a fire would also eliminate most canopy species, inducing substrate conditions similar to those found in "gap clear" plots. These plots were dry and highly illuminated, but perhaps more importantly, they were very choked with a thick mat of herbaceous plants. As a result, "gap clear" plots were unable to support *C. africana* or *A. adianthifolia* seedlings. I would expect resprouters to grow in these areas and perhaps *Trema orientalis* which was found in three of the four "gap clear" plots. This plant is described as a pioneer species which often frequents the forest

margins (Pooley, 1993). The shade cast by resprouting species and *T. orientalis* would soon thin the choking herbaceous layer. This would ultimately facilitate the generation of plants characterised by the "forest clear" plots such as *Celtis africana* and *Albizia adianthifolia*.

Thereafter, the adjacent stands of *Isoglossa* would set seed and regenerate. The shade cast by these plants would make it impossible for the recruitment of shade-intolerant plants such as *C. africana* and *A. adianthifolia*. These conditions are reserved for the regeneration of shade-tolerant plants like *Strychnos decussata* which are characteristic of mature forest.

Until recently, the role of gaps has remained unchallenged as being the major factor in driving forest processes. Lieberman *et al.* (1989) question the role played by gaps in driving forest processes and also the methods used by researchers in determining the roles played by gaps. The gaps concentrated on by many papers have been tree fall gaps, (Connell, 1989; Runkle, 1989 and Whitmore, 1989) with little regard for the role played by the understory sub canopy.

The results of this paper highlight the fact that tree fall gaps are not the only gaps which must be considered when studying forest dynamics. Two types of gap were identified in this study as being important in changing community structure. The first is a gap in the understory which allows more light to penetrate to the forest floor. The second type of gap is really a double gap consisting of a canopy gap and a sub-canopy gap. Different gap types create a continuum of light intensities. Each gap type facilitates the growth of a different flora. As these plants mature, they change the nature of the gap, enabling a new guild of plants to recruit. Fire may be the factor which creates the initial gap. From this point, there is a successional change in the light intensity reaching the ground. It is this succession of light intensities which drives the forest cycle in Dukuduku as we know it.

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