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THE IMPORTANCE OF ANIMALS IN THE SURVIVAL OF A CANOPY TREE,
POD MAHOGANY (*Afzelia quanzensis* WELW) IN THE
ARABUKO - SOKOKE FOREST, KENYA

BY

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SATISFACTION OF THE REQUIREMENTS OF A MASTERS DEGREE
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1992.

Declaration.

I hereby declare that the work presented in this thesis is a result of my own investigations and has not been presented for a degree in any other university.

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Dedication.

Dedicated to my parents Moses Gathua
and Elizabeth Warukira.

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ABSTRACT

Field research was conducted between September 1990 and July 1991 in the Arabuko-Sokoke forest. The study involved a detailed investigation of the importance of animals for the survival of the pod mahogany, Afzelia quanzensis (Welw). Four mammals, one bird, two insects and fungi were observed to have strong relationships with this tree at various stages of its fruit development. The red-legged sun squirrel Heliosciurus rufobrachium (Waterhouse), yellow baboon Papio cyanocephalus (Linn), a beetle Caenocara weisii and an unidentified weevil consumed the seeds at the immature stage.

Primates were found to be the major seed dispersers with the white throated monkey Cercopithecus mitis albogularis (Schwarz) and yellow baboon dispersing the seeds. Ad lib. data collection revealed that the crowned hornbill Tockus alboterminatus was a rare and unreliable disperser.

A nocturnal rodent, the giant Gambian rat, Cricetomys gambianus (Ogilby) was found to be the sole seed predator after dispersal. Observations and seed removal experiments revealed seed survival to be low in the range of C. gambianus.

Seedling density was observed to be highest below and around adult trees. There was variation in the density of seedlings between habitats with the open Brachystegia woodland having a higher density than the thick forest. The vigour of seedlings increased with distance from conspecific adults. All seedlings found 7m and beyond the

adults exhibited good growth which was even up to 100% survival.

The adult *A. quanzensis* population structure exhibits an inverse J-curve. This was analysed by use of belt transects and measuring diameter at breast height (dbh). There was a decline in the number of stems with 55cm dbh which corresponds with the stem size desired by loggers. The tree is still logged illegally and forms a source of timber with 12.4 % of the adults having been cut. The adult tree population shows a regular dispersion pattern as shown by the nearest neighbour technique used to test for nonrandom dispersion.

A. quanzensis dominates the thick forest range. The data obtained from converting diameter at breast height (dbh) to cross sectional area at breast height (CABH) and importance value index (IVI) were used, and 16 canopy trees associated with *Afzelia quanzensis* were enumerated. The vertical stratification of the canopy was analysed by sketching profile diagrams. The forest exhibits layering with distinct upper, middle and lower canopies.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

In spite of high biodiversity and endemism in Kenyan forest ecosystems, there has been little effort in understanding the ecological functions and interactions in comparison to the savanna ecosystems.

Forest ecosystems in Kenya range from montane types, for instance, the Aberdares; riverine, for example, Tana river forests; subtropical rain forest in western Kenya and the low-land forests (these are scarce in Kenya and the Arabuko - Sokoke is the only major surviving type of this forest). The Arabuko-Sokoke is the largest persisting forest on the East African coast (Stuart 1985). There are, however, several small forested patches along the Kenya coast. Kaya forests are also common along the Kenya coast. These are patches of indigenous forests which represented clans of the Mijikenda and today they are protected as they are treated as sacred groves (Robertson, pers. comm.)

The international recognition of the Arabuko-Sokoke forest derives from wildlife conservation (Kelsey and Langton 1983, Moomaw 1960, Brown et al. 1982). The forest is made up of distinct vegetation zones with plant species showing restriction in their range. Animals also show a similar pattern in the forest being restricted to their habitats which then determine their distribution pattern.

The distribution of birds and mammals can act as a habitat type indicator. The Sokoke Scops owl Otus iranae, an endemic species in this forest, is confined to the

Cynometra thickets. The East coast Akalat, Sheppardia gunningi, favours uncut Afzelia forest (Kelsey and Langton 1983). The red bush squirrel, Paraxerus palliatus (Peters), is uncommon in the Afzelia forest in contrast to the red legged sun squirrel of which mostly occurs here.

The importance of tree species in the Arabuko - Sokoke forest lies in their utilisation by animals and the local people. The animals are directly dependent on the trees for survival as evidenced by herbivory and frugivory. The animals are also dependent on the tree for shelter, nesting and perching. Thompson (1988) found love birds in Naivasha to nest exclusively in tree holes. In the Arabuko - Sokoke forest squirrels nest in tree holes (pers. observ.). Also birds which are hole nesters such as the drongos, Dicrurus adsimilis, were seen in the forest.

This study had the major objective of getting quantitative information on the predators and vertebrate seed dispersers in this forest ecosystem using A. quanzensis as a model. Natural regeneration and logging rates of this tree were also determined.

The use of forest trees and shrubs by wildlife especially the seeds needs detailed studies as it would very much influence the forest dynamics. The consumption of seeds theoretically must have an upper limit as it would lead to the extinction of some trees if this were not so. The entire seed crop produced should not be consumed so that the plant population may be maintained. Though this is of great importance, the movement of the species through dispersal is also important so that colonisation of newly created sites may be possible. The study of seed

consumption is thus essential for the forest ecologist would like to know the proportion of seeds being destroyed before maturity. Animal species involved using the seeds and their foraging behaviour have to be understood for one to know their importance in maintaining the forest ecosystems.

The answers will be important in the conservation and management of those pivotal resources. Such studies being important in conservation, data is very scanty. The sole reason for that in my view is that most ecologists study either animals or plant ecology separately. Those studying foraging behaviour in animals follow it up to a time when it plucks a fruit, the fate of seeds being unimportant to them.

Trees and shrubs invest a lot of energy and resources on fruit and seed production yet most of the fruits are consumed by animals. Howe (1980) found that 94% of the fruits of a Panamanian rain forest tree were removed by mammals. In a Gabonese forest, nine squirrel species are frugivores (Gautier-Hion et al. 1980) and they preferred seed to entire fruits. In Kakamega forest, Cords (1984) found that the blue monkey's, Cercopithecus mitis diet comprised of seeds and fruits in a proportion of about 70 %. Emu, Dromaius novae-hollandiae, in Australia has been found to feed on the seeds of the nitre bush, Nitraria billardieri, 90% of the crop and proventriculus content being comprised of fruits (Noble 1975). In Kibale forest, mangabey's, Cercocebus albigena (Lydekker) diet comprised on average 59 % fruit in different months of the year

(Waser 1975)

The reproductive effort, that is, the total energy allocated to reproduction, is markedly high in relation to other life history activities organisms (Begon, Harper and Townsend 1986). The reproductive strategy of plants whose reproductive parts are consumed by animals has to be related to the benefit they gain from the frugivores. Optimisation theories predict that the duration and timing of an activity are determined by its profitability. The obvious question is, what ecological and ultimately evolutionary advantages exist between fruiting trees and the fruit consuming animals which are termed as frugivores? However, coevolutionary and ecological implications of variations on seed survival have remained largely unknown due to the lack of empirical studies.

The consumed fruits or seeds are regurgitated, defecated or dropped, either in a viable condition or having been adversely affected. Such adversely affected seeds do not germinate. Several frugivores that interact with seeds have varied effects on them. Seed ecologists have shown that passage of seeds through the vertebrate gut enhances germination in some species (Howe 1980, Lieberman et al. 1979, Mwangi unpub., Rowell pers. comm.).

The fate of seeds after flowers drop is complex with insects and vertebrates being the major determinants of their fate. This, however, depends on tree species. Tsingalia (1989) found that a bulbul is the main disperser of Olea welwitschii, a canopy tree of Kakamega forest. The seeds of this tree are also consumed by monkeys and rodents. In Panama, for instance, 26 species of vertebrates

ate or attempted to eat the fruits of Tetragastris panamensis (Howe 1980).

The plant-frugivore relationship has been thought to be mutualism (Deshmukh 1986) as both the plant and animal are benefiting. If there is no such relationship, the plant species involved may become extinct. The frugivore will also be affected by the fact that a food resource has become extinct and is no longer available.

Tropical ecologists argue that the major benefit the plant gains is the dispersal of its offspring while the animal obtains food (Howe 1980). Fruits have unique attributes as food sources. Relative to other "prey", fruits have evolved to attract frugivores by being accessible, conspicuous, easily digestible and of great nutritive value. In this context, fruits are attractive prey to their predators due to the reduced searching time and ease of handling.

On the other hand, primary consumers have gone a step further in specialising on fruits. Frugivores differ in behavioural and ecological traits that affect their suitability as dispersers (Smith 1970). For practical purposes, dispersal is here defined as manipulations of seeds without harmful effects.

In many tropical tree species, it is advantageous to disperse the seeds into light gaps where offspring mortality is lower (Augspurger 1983) and growth of seedlings (Garwood 1983) and saplings (Whitmore 1984) is enhanced. The seeds must be moved by the dispersal agent for seedlings to be established away from the parent plant.

There is ample information about morphological adaptations that mediate seed and fruit dispersal but little is known about the selective forces that produce them. Fruit and seed morphology often indicate the means of dispersal. The common milkweed plant, for instance, produces plumed seeds adapted to wind dispersal (Sacchi 1987). Vertebrate-dispersed seeds show various adaptations of colour, scent, shape and nutritional value (Howe and Smallwood 1982). The presence of accessory parts, for instance the aril, which is coloured red like in Afzelia quanzensis indicate vertebrate dispersal.

There are alternative advantages to dispersal. Howe and Southwood (1982) argued for three hypotheses in favour of seed dispersal. The first, which is the escape hypothesis, invokes the disproportionate success of seeds that escape the vicinity of the parent as compared to those under the crown. Most seeds fall in leptokurtic distributions in relation to the parent with the seed density being inversely related to distance from the parent tree. Germination success for some species, however, increases with distance from the tree. This is due to seed mortality either by seed predation (Janzen 1970) or competition among seedlings. Distance response seed predators will search for food only in the immediate vicinity of the fruiting trees, ignoring seeds only a few metres away. The cotton stainer Dysdercus fasciatus attacked more seeds of Sterculia apetala near the parent, and mortality reduced to zero at 30 - 40m away Janzen 1972a). Howe and Primack (1975) found higher densities of Casearia corymbosa seeds were found under fruiting trees than away, and up to three times as

many seedlings survived 10 - 30 m away. The destruction was caused by localized rodent herbivory on seedlings. Augspurger (1983) found that seeds of Platypodium elegans escaped fungal pathogens by being dispersed from the conspecific adult. He viewed dispersal as an adaptation to increase the probability of survival of offspring.

The second hypothesis involves colonization. It assumes that habitats for establishment of dispersed seeds vary in space and time. This may allow a tree species to reproduce offspring capable of taking advantage of uncompetitive environments, as they open. In tropical areas some canopy trees are shade intolerant and their seeds remain dormant awaiting the opening of a forest gap. Trees disseminate their seeds so widely that some may encounter favourable conditions as they may occur. This is more effective in plant species which are dispersed by animals traversing large areas as they forage. The hypothesis can be tested by determining the survival of seeds and establishment in different habitats. This hypothesis applies to gap regeneration documented in tropical forests such as Kakamega forest.

The third directed dispersal hypothesis argues that establishment of seedlings in special habitats by plant species requires specific edaphic conditions. Dispersal agents, normally vertebrates, take seeds to nonrandom places that are well suited for establishment and growth. Tsingalia (1988) demonstrated that seedlings of Olea are well established below Combretum molle bushes where soils are well mixed by termites. The dispersal of seeds in Olea

is by bulbuls which perch on C. molle. A classical example is the dispersal of the Australian salt bush shrubs, the ant dispersed shrubs have a notably poor growth off ant mounds (Davidson and Morton 1981).

Of importance is the understanding of animals which remove seeds from parent trees and how they distribute them in space. This, however, is poorly documented. Vertebrates seem to be the major dispersers in forest ecosystems. Seeds of Casearia corymbosa are bird dispersed, the yellow green vireo (Vireo flaeoviridis) being the most reliable disperser throughout the season (Howe and Kerckhove 1979). The blue jay disperses oak (Johnson and Adkinson 1986). Bats are major dispersers of Mutingia calabura (Fleming et al. 1985). Lieberman et al. (1979) found that baboons dispersed 59 tree species in Shai Hills in Ghana. Monkeys disperse several species in Kakamega forest (Mwangi unpub.). In Panama, monkeys moved 74% of seeds of T. panamensis and all seeds extracted from their faeces were viable (Howe 1980). Hornbills also play a role in the dispersal of Maesopsis eminii in Kakamega forest (pers. observ.).

Frugivores do not merely pluck fruits but show a variety of anatomical and behavioural traits. Squirrels are very agile, possess sharp gnawing incisors and have very strong mandibular muscles. Baboons have strong jaws to crack open hard nuts and pods. In primates cheek or gular pouches are common, and are used to carry fruits and other food materials to desired areas.

Animals migrate long distances to track food. In the Serengeti and Masai Mara ecosystem, large herbivores migrate depending on food availability (Wambugu 1990).

Birds also migrate over long distances to track fruit seasons. Fodgen (1972) reported that a frugivore dove, Chalcophaps indica, was common during fruiting seasons in Sarawak. There were great fluctuations in densities after fruit depletion, with no dove netted or heard in this period. In bats, the reproductive period is related to the fruiting season of canopy trees (Howe and Southwood 1982). In cercopithecines the gular pouches are used to carry food material and especially fruits.

The transit times, that is the time lapses or contact times between the seed and animal, are diverse. It takes 10 - 20 minutes for small birds to swallow and defecate or regurgitate seeds. In large herbivores it takes hours to several days for the seeds to pass through the gut. This temporal variation depends on the manner of handling, the utilizable material on the fruit and the animal concerned.

Two broad categories of fruit handling by vertebrates can be distinguished. The first involves swallowing (ingestion) and passage of the seed or fruit through the animal gut. This is termed as endozoochory. The second category, exozoochory, involves carriage of seeds by external features or mouth.

Large distances can be covered while seeds are still in the gut of the animals. Birds and bats can carry seeds for great distances. The blue jay makes round trips between territory and food patches covering 8 km (Johnson and Adkisson 1986). These birds and bats are capable of helping regeneration in cleared areas by dropping seeds as they pass over.

Seed predation, as well as dispersal, is important in the continuing survival of plant species. There is an argument that the predation - dispersal interactions maintain high biodiversity in the tropics. Specialized seed eaters concentrate around the host tree and consume all seeds falling in the vicinity (Janzen 1970). As a result conspecific individuals are not close and other species can occupy the vacant spaces. Thus even spatial distribution of trees is also attributed in part to predation - dispersal phenomena. Seed predation has been known to prevent regeneration: (Boucher 1981) found that the number of acorns produced by isolated oak (Quercus oleoides) is far too low for regeneration. Predation by mammals was high and acorns only survived where trees occurred in clumps such that predators were satiated. Boucher further demonstrated that acorn survivorship is inversely proportional to the apparent mammal density in particular areas of study sites.

Human impact on forest ecosystems is common. In Arabuko - Sokoke, small mammals are hunted for bush meat. These animals are known to be dispersers and their occurrence is high in most forests. A. quanzensis is logged indiscriminately for timber (Moomaw 1960, Kelsey and Langton 1983). Arabuko - Sokoke an indigenous forest, was a refugium during the Pleistocene period and it is one of the largest persisting forest patches on the East African coast. These factors will allow an ecologist to consider this forest an ideal conservation area.

CHAPTER TWO

STUDY AREA

2.1 Location, climate, soils and topography .

The Arabuko-Sokoke forest is situated just near the Kenya coast. It lies between the latitudes $3^{\circ}30' S$ $3^{\circ}10' S$ and longitude $39^{\circ} 50' E$, $40^{\circ} E$ (Figure 1). The forest extends from Kilifi to near Malindi. The forest has been described in detail by Britton and Zimmerman (1979), Moomaw (1960) and Kelsey and Langton (1983).

The total rainfall during the one year study period was 1224 mm. Rainfall is seasonal with peak in May and a dry season in January and February (Figure 2).

The temperature is mild all year round with a mean of $26.5^{\circ}C$. Seasonal variation is small, and even less within the forest ecosystem (Rathbun 1976) .

The forest is low lying, barely rising over 60m above sea level. The soils are mainly of two types; the typical white sands along the coast and the magarini red sandy soil (over 60 % of the forest lies on this type).

2.2. General ecology.

The Arabuko-Sokoke is one of the few remaining indigenous forests in Kenya. It is a lowland rain forest, encompassing an area of about 400 km^2 . It is a very varied forest with regards to plant community structure. The vegetation formations are quite distinct and can be related to edaphic factors and rainfall distribution from the coast line (Moomaw 1960).

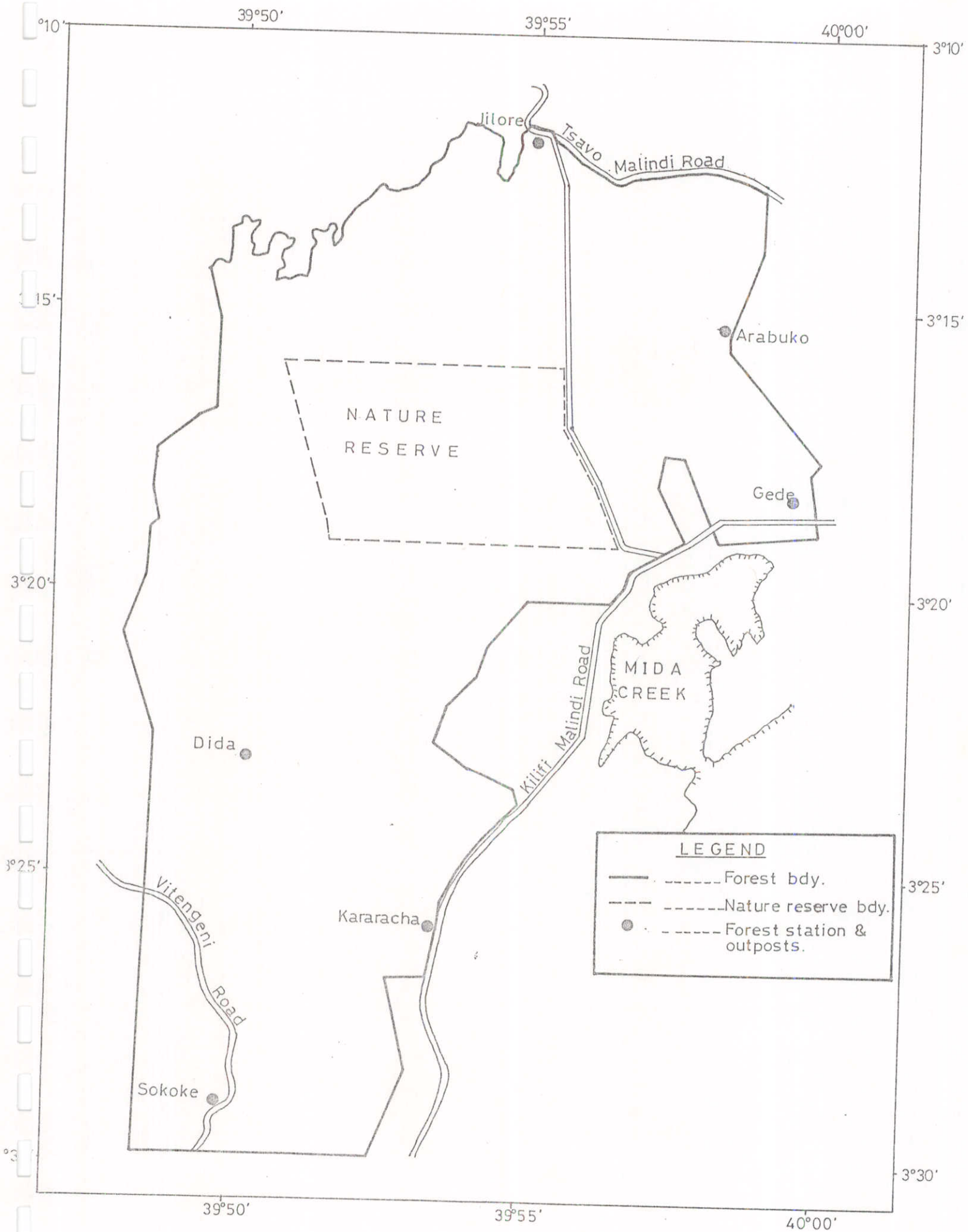


Fig1. The location of the Arabuko-Sokoke forest.

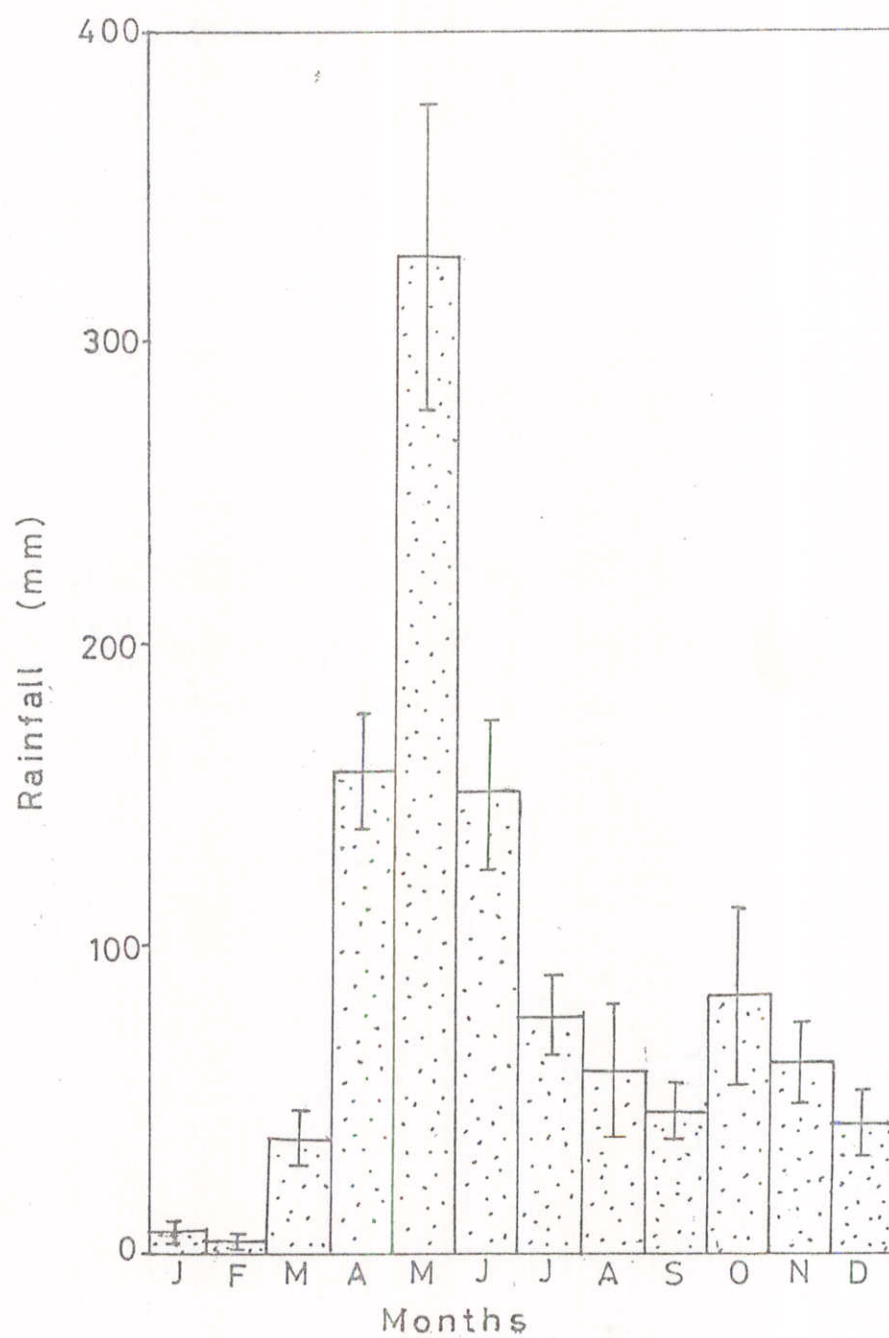


Fig. 2. The mean (\pm SE) monthly rainfall for Arabuko-Sokoke Forest taken at Gedi Forest Station, July 1981 – June 1991 inclusive.

Britton and Zimmerman (1979) recognized four major zones, namely;

- i) thick evergreen forest; the Afzelia forest (plate 1),
- ii) lowland rain forest (plate 2),
- iii) Brachystegia woodland (plate 3), and
- iv) Cynometra - Manilkara forest (plate 4).

The study tree occurs in (i) and (ii) and hence these zones comprised the study area. The two zones cover 50 and 20 km², respectively, totalling 70 km² (17.5%) of the whole forest. However, in some instances A. guanzensis was recorded together with Brachystegia, and it was incorporated in the study area. As well as being distinct in appearance, each vegetation harbours its own distinct fauna (Kelsey and Langton 1983). Subsequently the vegetation zones shall be referred to as mentioned above.

The importance of the forest lies in its conservation value, being a low-land tropical forest refugium, with a high diversity of flora and fauna. Of great importance to conservation is the occurrence of endemic birds and mammals. The forest is home to two endemic bird species, the Sokoke scops owl, Otus irenea, and Clarke's weaver, Ploceus golangi, which are found nowhere else in the world. The Ader's duiker, Cephalophus adersi, Sokoke bushy tailed mongoose, Bdeogale crassicauda omnivora, and the Golden-rumped elephant shrew, Rhynchocyon chrysopygus, are nearly endemic occurring in the thickly forested areas of the forest and the duiker also in a forest in Zanzibar.

Plate 1. Afzelia forest. The photograph was taken in the study area. Note the destruction at the foreground.

Plate 2. Lowland rain forest. Note the closed canopy, this vegetation zone is comprised of mixed tree species. The lower canopy is also closed.



Plate 1.



Plate 2.

Plate 3. Brachystegia woodland. Note the openness and the grass cover. The soil is the white sandy soil.

Plate 4. Cynometra thicket. Note that the soil is red in colour contrasting that of other vegetation zones.



Plate 3.



Plate 4.

Coastal forests, like any other forest areas in other parts of the world, have been a source of commercial timber for many centuries. The Arabuko-Sokoke forest has been logged since the 1920's by European sawmill operators (Moomaw 1960). A. quanzensis and Brachylaena hutchinsii were selectively logged. The latter is an important tree in the wood carving industry and was largely ferried to Nairobi. Despite the total ban on indigenous forest exploitation the trees are still being illegally exploited to date (pers. observ.).

CHAPTER THREE

DISPERSAL AND PREDATION OF THE SEEDS OF *Afzelia*
quanzensis BY ANIMALS

3.1 Introduction

Behavioural ecologists have data on fruits and seeds on which vertebrates forage. This, however, does not describe the process of dispersal, which is the location and fate of the seeds (Janzen 1983), which vary in time and space.

The consumption of fruits or seeds by animals commences at the early stages of fruit development. Animals use seeds in a successional manner, a kind of resource partitioning. They not only leave a certain proportion to germinate but also disperse them to suitable germination sites.

Animals interacting with seeds do so with different impacts. The relationship can either be advantageous, neutral or can be adverse to the seeds. This can also be important in stability and composition of the ecosystem in which those animals and plants occur.

Some plant-animal interactions are known to be mutualistic, and have probably occurred through coevolution. The relationship between *A. quanzensis* and animals using it is probably mutualistic. The Arabuko - Sokoke, an indigenous forest, has persisted for 10,000 years since the Pleistocene period when it was a refugium (Stuart 1985, Britton and Zimmerman 1979). In this context, the results are expected to show the typical patterns of predators and dispersers interacting with *A.*

quanzensis. The fate of seeds as determined by these animals and hence the continued survival of this canopy tree was investigated.

3.2 Methods

3.2.1 Predispersal seed predation

It was essential to first establish which animals were opening the green pods. Focal trees were selected in the forest. Observations were made from a hide-out and animals visiting the focal trees and their activities were recorded. The observation sessions were made systematically in September and October. Observations commenced at 5.30 a.m. (0530 hours) and continued to 8 p.m. (2000 hours) but were not continuous. A pair of binoculars was used for this exercise for animal identification during the day. The second part of the observations involved the use of forest roads and paths. Walks were taken through the forest and fruiting A. quanzensis trees were scanned. Whenever an animal was encountered the identity and activity of the animal were recorded. There were practical problems in the use of this method as the animals were easily frightened. Habituation is necessary in behavioural ecology and in this case I was interested in the foraging behaviour of the animals.

The same data was collected on an ad lib basis. Altmann (1974) argued that this sampling method is important in the study of animal behaviour.

All these methods, coupled together, brought to light which animals opened the pods for seeds and how. The kind

of destruction was used throughout the study to identify and quantify which animals had consumed the seeds (see Plates 7 and 8). This seed destruction method has also been used in the study of predation of cones in pines by squirrels (Smith 1970). Larvae that were found in pods were taken to the house and reared in a can or polythene bag for adults to emerge. The emerging adults were preserved and taken to the National Museums of Kenya for identification.

To quantify the data, focal trees were randomly selected. Ten sample trees were monitored during the fruiting season. The trees were marked by painting a number on the stem.

Each tree was sampled once per week. The sample trees were marked by painting a number on the stem. When a tree was visited all the pods on the ground were collected and put in polythene bags. The tree crown was then scanned for pods which had been opened by animals between the sampling sessions. Those pods were plucked for analysis which was accomplished by either climbing up the tree or by use of a long fork-tipped stick depending on the position of the pod.

The pods were heaped and the following recorded on the data sheet:

- i) age; the pod was either recorded to have grown that season (90/91) or the previous (89/90).

The former were green in colour while the latter were relatively dry and black in colour.

- ii) total seeds; these were the seeds a pod was supposed to have had, since the cavities were very

clear due to the strong interseptum between the seeds (Plate 5).

iii) number of seeds destroyed and the animal responsible; animals were categorized by the use of the criteria illustrated in plates 7 and 8. Insect and fungal infestation of the seeds was also recorded.

3.2.2. Dispersal.

Dispersal is defined as the dissemination of mature seeds. For practical purposes, a seed was categorized as dispersed when it was removed from the pods by vertebrates after maturity. In this study several methods were applied to determine the agents of dispersal. The presence of arils on seeds potentially suggests dispersal by vertebrates (Howe 1980). The seeds of A. quanzensis are vertebrate dispersed since they have a red edible aril removal of which does not affect germination.

The same focal trees sampled at predispersal stages were sampled in the dispersal period. They were visited once per week from October 1990 to January 1991. The ground was searched for pods after which the tree top was scanned. Pods on the tree were plucked by use of a forked stick or by climbing. As in the predispersal stage, direct observations were made where vertebrates and their mode of manipulating the seeds were determined. Pods were analysed for tooth marks. In some cases the dispersers separated the pods into halves during the seed extraction process. Those halves were

matched to form whole ones.

The yellow baboons opened the pods leaving broad tooth marks; the pods were scratched all over (see Plate 8). The white throated monkeys wait for a slight opening of the pod. They opened the pods leaving canine bites on pods and seeds. In a few cases, baboons and monkeys carried pods about 3 metres away from the crown edge, where they extracted and carried seeds away. The red legged sun squirrels also opened some pods and their tooth marks were narrower and at the tips of pods. They were observed carrying seeds. In some cases, the pods were left without a scratch and it were not possible to assign any of the vertebrates. Ad lib. data were also collected, whereby any animal found interacting with seeds was recorded.

During the dispersal period, once a pod opened slightly, the seeds were removed within 24 hours. In contrast, seeds remained in pods in areas where the vertebrate dispersers were absent, such as near human habitation. In all cases vertebrate dispersers removed the red aril which formed a food source and dropped the black part of seed.

Once an animal was found, it was followed for some distance to see where the seeds were dropped. This section had major practical problems due to the animals disappearing since they were very shy.

3.2.3 Postdispersal interactions

Once seeds are on the forest floor they can either be eaten at that point (post-dispersal predation) or some parts are removed and the viable part of the seed left intact sometimes at a further distance (secondary seed dispersal).

Seeds were placed on the forest floor and monitored for removal. Coloured plastic markers were placed 3 cm from each seed. The seeds were monitored twice a day, at dawn and dusk, up to the time that all were removed. The areas were searched for short distances in case the seeds were moved. In most cases seeds were marked with a marking pen. Some seeds were placed when they were still arillate, while others either had the arils removed mechanically or seeds whose arils were already removed by vertebrates at the dispersal stage were used. Time was spent watching those seeds from a hide-out.

After the above basic study, it was established that seeds were being removed at night. A method for establishing the nocturnal predators was therefore necessary. Great difficulty was experienced in searching for the animals responsible for post dispersal predation. Seeds were placed on the forest floor and monitored in the evening immediately after the night fall. Some seeds were also placed at the holes of suspected rodents.

Rodent holes were searched for and seeds placed there during the early hours of nightfall (6.30 - 8.00 p.m.). More seeds were placed under the crown of fruiting trees and also monitored at the evenings. Observations were then made from a hide-out. Using a flashlight, the seeds

were checked for their presence at intervals of about 15 minutes. Animal sounds were also listened to.

Trapping of rodents was attempted using cage, break back traps and local snares. The trapping was unsuccessful. On one occasion, a giant gambian rat was trapped by a local snare but it was out of the fruiting season. On dissection there were no *A. quanzensis* seeds recovered from the stomach.

3.2.3.1. Seed removal experiments

Survival of seeds up to germination is influenced by many factors. Janzen (1970) simulated a model which predicted that seeds which have been moved away from a source would have dramatic increases in survival chances.

Experiments were conducted to verify the optimal dispersal distances of *A. quanzensis*. At such distances, seed survival and establishment would be expected to be the highest in comparison with other distances. Four focal trees were selected. From the base of each tree, two transects were made. The transects varied between 30° - 90° from one another. The transect lengths were 50m. After every 10m, a small post was pushed through the soil and marked by ink. This was defined as a seed station. A sixth station was established under the crown ranging from 3 to 5 metres depending on the crown diameter. Five seeds were placed at each station. The seeds were monitored every week and the number remaining recorded. Once all seeds were removed or the remaining ones were not removed for one month the experiment was discontinued. One transect on each tree was selected and

the experiment repeated, so that on each tree, 3 replicates were made in total. Each transect had 6 stations with 5 seeds per station. In all there were therefore 360 seeds.

The transects were set on the basis of habitats. Each vegetation formation represented different habitats. In this study, 4 ecological zones were used; the Afzelia forest, the lowland rain forest, the Afzelia/Brachystegia ecotone and the Brachystegia woodland. The first three shall be referred to as the thick forest and Brachystegia woodland will be open woodland.

3.2.4. Distribution of the giant Gambian rat (Cricetomys gambianus)

This rat is nocturnal and lives in holes. The holes were said to be actively used if there was an indication of animals continuing to use them. Foot marks or actual observations were used in this respect. Two methods were used, the first involving opportunistic recording of holes. Once a hole was encountered, it was recorded and the type of habitat it was found in noted.

The second method involved the use of transects. These were the same transects used during the vegetation analysis (Section 4:2:2). Holes found on the transects were recorded together with the vegetation type where they occurred.

3.2.5 Phenology of trees and shrubs used by frugivores

Phenology can be defined as the study of periodic ecological phenomena on a seasonal time scale or over a few years (Newton 1986). In this study the fruiting

phenology over a season was covered. Both mature and immature stages were important since frugivores exploit fruits at every stage in the development process.

In each month of the year since the study commenced, the fruiting was recorded for plant species used by frugivores. Then stages of fruit development (mature, green or flower) were recorded.

3.3 Results

3.3.1 Predispersal seed predation

The red legged sun squirrel Heliosciurus rufobrachium gnaws dorso-laterally on the placental side of the immature pods where the arils are attached (Plate 7). The squirrels are very agile, an adaptation for arboreal animals. This allows them to manipulate the pods and leave them intact on the tree. Two insect species attacked the seeds that were left by squirrels.

The yellow baboon, Papio cyanocephalus, also opens the pods but unlike in the squirrels all the pods were found on the floor of the forest under the tree. The baboons open the pods using incisors and in a manner opposite to that of squirrels (Plate 8). Using the finger nails, they dig out the soft seeds and drop the pod. In most cases they ate the whole seed.

Monkeys, unlike squirrels and baboons did not directly consume seeds but instead plucked the pods in an attempt to extract the arils which was usually unsuccessful.

In the 1990/1991 season, 4180 seeds were categorized in terms of fate. A mean number of seeds for each tree

Plate 5. Immature seeds of *A. guanzensis*. Note the purple colour. The yellow part is the aril, the whole seed is consumed at this stage. Also note the strong septum between the seeds.

Plate 6. Mature seeds of *A. guanzensis*. Note the conspicuous red aril which is a food resource for vertebrate dispersers. The black part which germinates is avoided by them but it is consumed by *C. gambianus* after dispersal.



Plate 5.

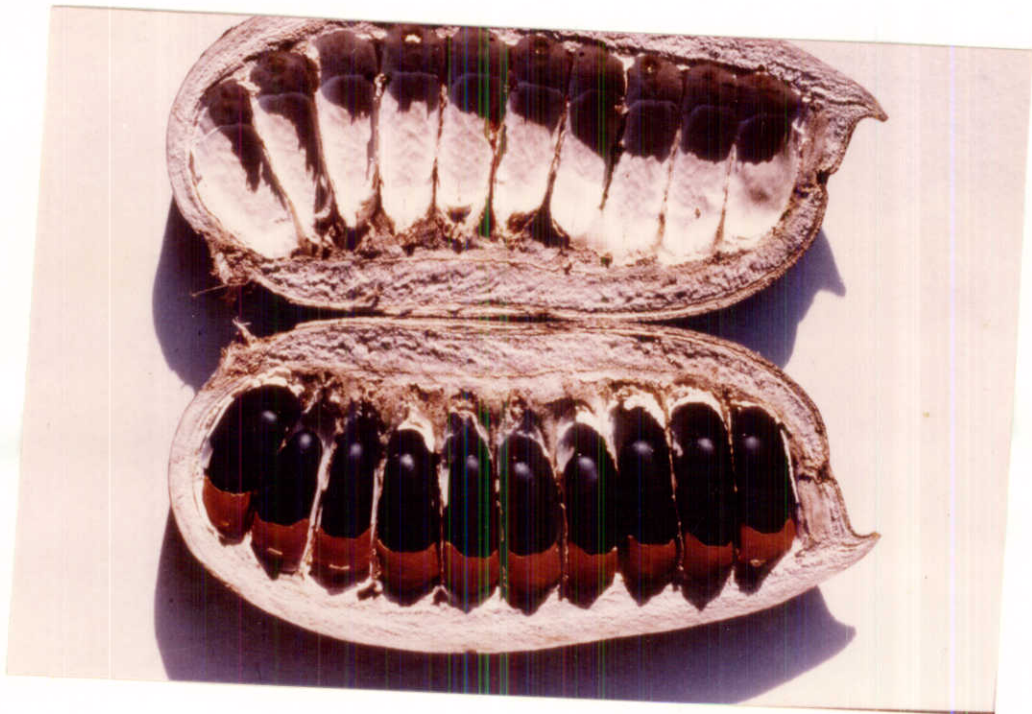


Plate 6.

Plate 7. Immature pods opened by squirrels. The upper one was attached to the tree while the lower was collected from a tree hole. Note that the stalk of the lower one was cut by sharp teeth; also note the neat extraction of the seeds. The red bush squirrel Paraxerus palliatus was responsible (see text).

Plate 8. Immature pods opened by the yellow baboon.
Note the tooth marks. The baboons open one side and extract seeds leaving cavities.

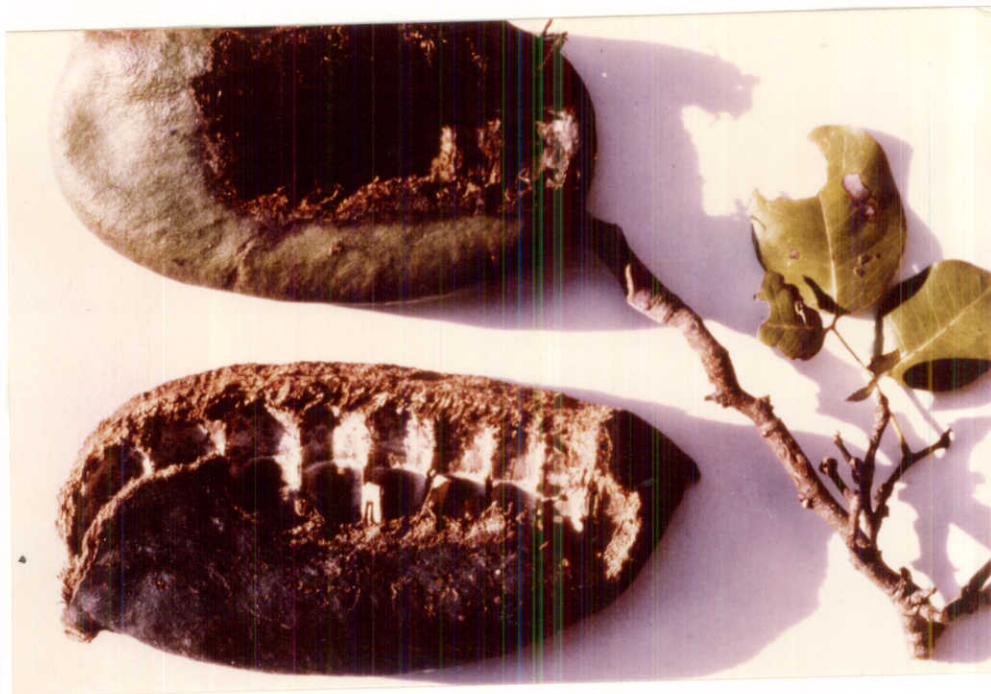


Plate 7.

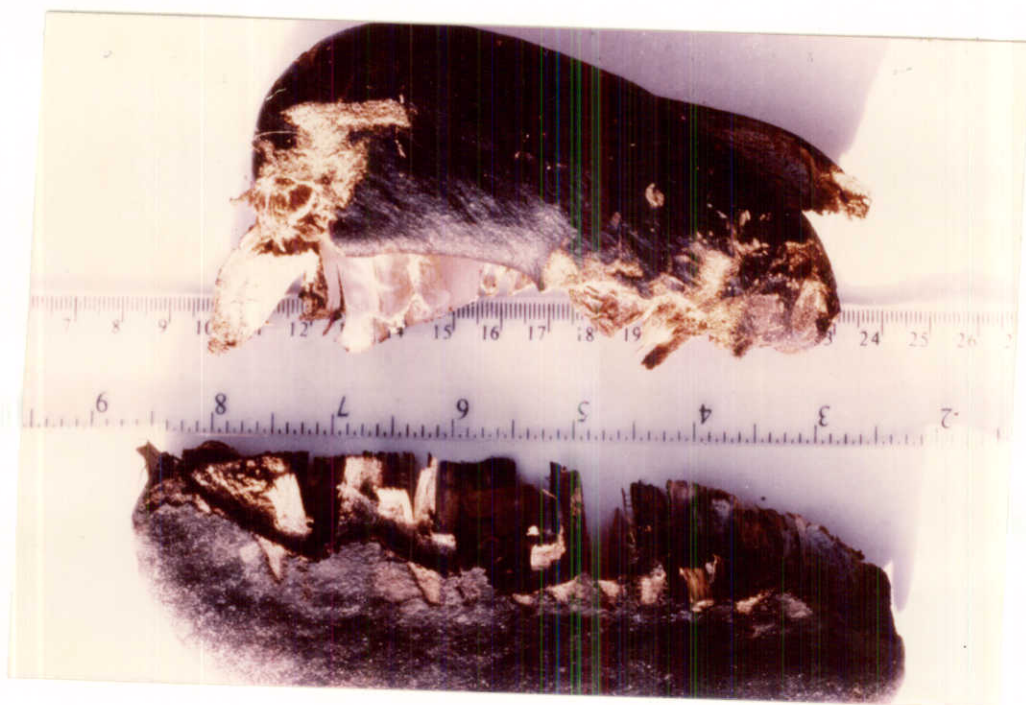


Plate 8.

(n=10) of 157.7 (range 35-478) were consumed before maturity. The total percentage of seeds consumed before maturity was 37.5% (Appendices 3 a and 3b).

Figure 3 shows the animals which consumed the seeds and the respective proportions. A Kruskal Wallis one way Anova with ranks (Zar 1984) was used to test for the differences in seed predation amongst the animals. A significant difference was detected ($H = 23.12$, d.f. = 5, $p < 0.05$). The red legged sun squirrel was the major seed predator while the yellow baboon, Papio cynocephalus, ranked second. Compared to these two mammals seed destruction by insects, fungal attack and the white throated monkey, Cercopithecus mitis albogularis, was less. Beetles were the insect seed predators including Caenocara weisii of the family Anobiidae. A unidentified weevil belonging to the family Curculionidae was also found to be a seed predator. The seed attacking fungi were not identified but could have been seed attacking fungi common in other forests such as Rhizopus spp., Pencillium sp and Sporangium sp.

Infestations of seeds by insects and fungal attack was secondary damage. In all pods where they were present, there was an opening made by squirrels. In some instances squirrels were opening the pods feeding on a few seeds and the rest either matured or were secondarily infested. Intact pods were however safe from damage by insect and fungal species.

In the previous season (1989/90) red legged sun squirrel still ranked first in seed predation. There were practical problems in assigning the animals that

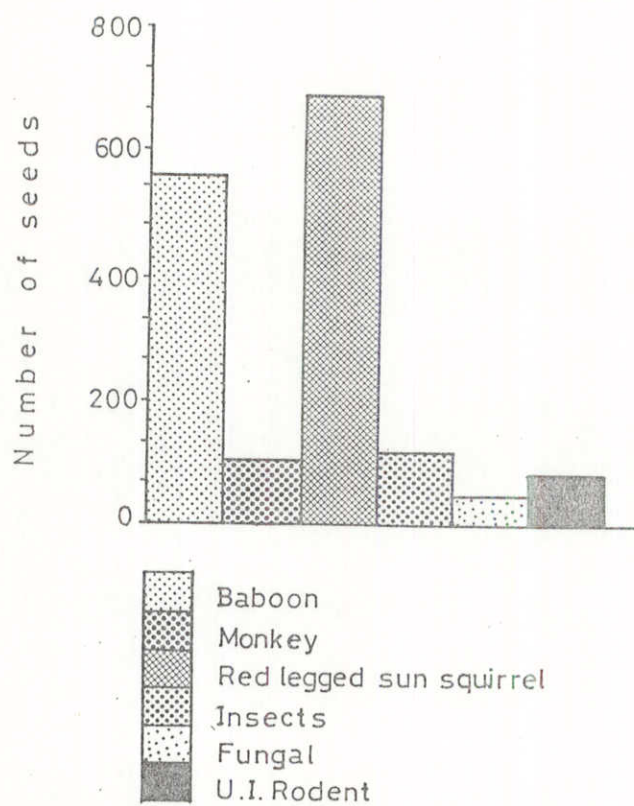


Fig. 3 : Predispersal seed predation in 1990/91
(Where U.I. is unidentified)

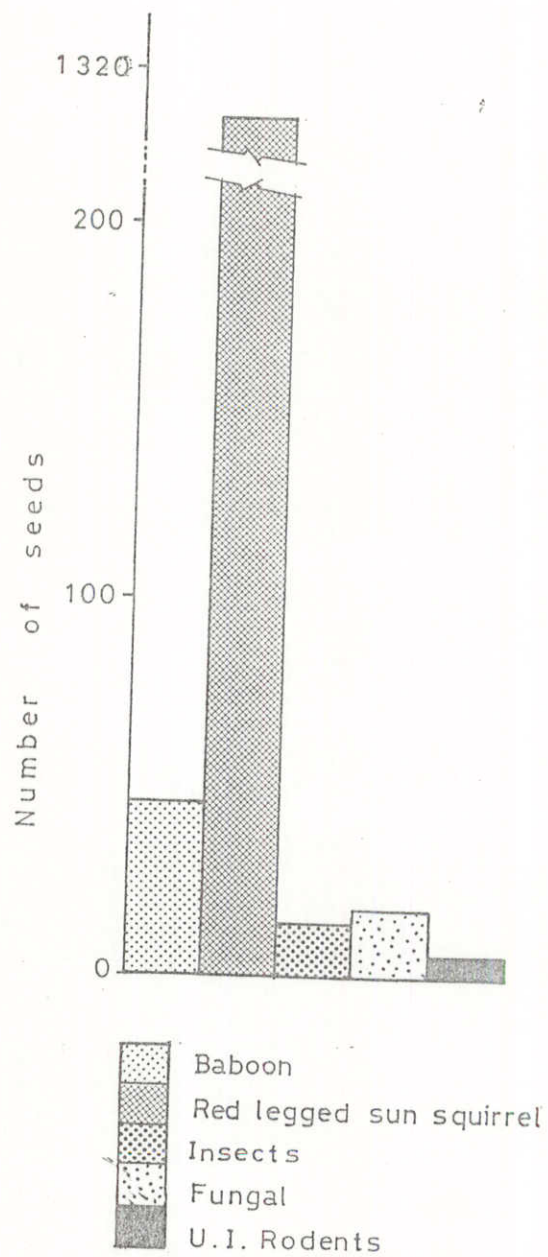


Fig. 4: Predispersal seed predation in 1989/90

manipulated the pods in this season. Figure 4 shows the probable fate of the seeds at the immature stage, but should be taken with caution.

In the unidentified category, the seeds were found cached in holes below one of the focal trees. It was believed that the red bush squirrel was responsible as inferred from its foraging behaviour. The kind of destruction showed a rodent to be responsible and the tree was also in the range of the red bush squirrel. However this does not out rule the presence of other rodents.

3.3.2. Dispersal

Figure 5 shows the vertebrate dispersers and the proportion of seeds dispersed by them. Primates were the major and reliable dispersers throughout the fruiting season. A statistically significant difference was found in the proportion of seeds dispersed by different vertebrates (Kruskal Wallis, $H = 9.76$, d.f. = 2, $p < 0.05$).

The white throated monkey, C. m. albogularis (Plate 9), was the main disperser while the yellow baboon ranked second, and the red legged sun squirrel third (fig. 5). There was a proportion which was not fully assigned to those animals due to practical problems. Some pods had no tooth marks and could therefore not be directly assigned and the seeds were presumably extracted with ease.

The study seeds are cylindrical in shape with a mean length of 2.7 ± 0.05 cm ($n=14$), orange at an early stage of maturity (Plate 5), turn purple, then black when mature

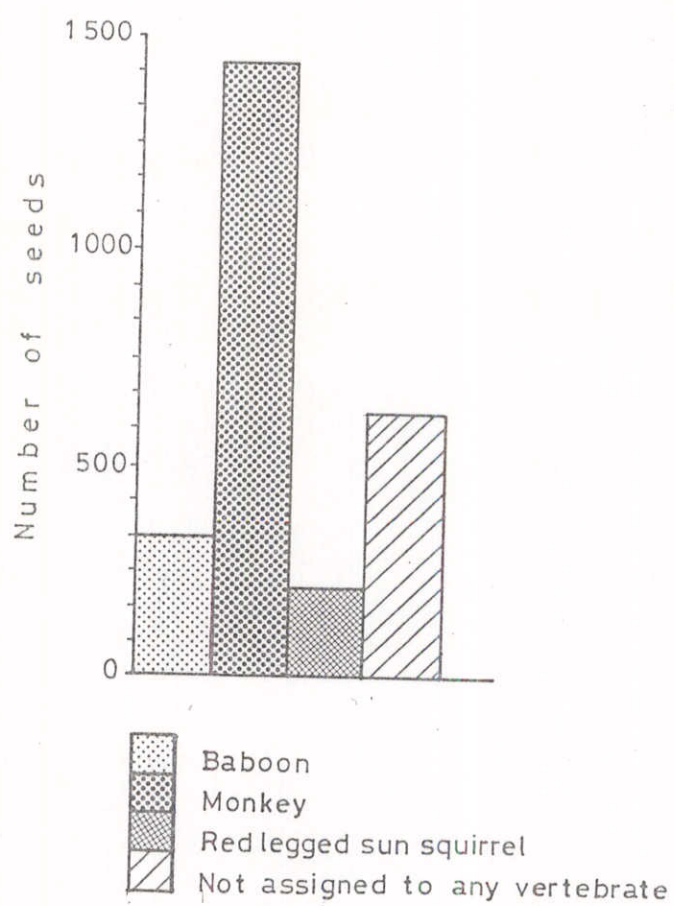


Fig. 5: Seed dispersal by vertebrate

and have an aril which is red in colour (Plate 6). It is the aril that animals consume at the mature stage when the pods open slightly, revealing them. Dispersal occurred immediately after the seeds matured in October up to December. The seeds were removed 24 hours after the pod opening.

The fourth potential disperser could be the crowned hornbill Tockus alboterminatus. It was observed on rare occasions in the forest station and Brachystegia woodland four months after the main dispersal duration. The hornbills were unable to remove the aril as it was quite hard, dry and firmly embedded on the seed. During the dispersal period Oct-Dec, this bird species was not recorded dispersing seeds.

3.3.3. Postdispersal interactions.

Once on the forest floor, seeds were noticed to be removed by a nocturnal rodent. All the 76 seeds placed at different places and time, monitored at dawn and dusk were removed at night. The giant Gambian rat (Cricetomys gambianus) was found to be the sole seed predator at this stage. The experimentally placed seeds were found to be consumed after 7.00 p.m. The removal of the experimentally placed seeds mostly occurred from the first night to three nights later. This however varied and seeds could stay for as long as two weeks before disappearing overnight.



Plate 9.

White throated monkey Cercopithecus mitis albogularis,
a seed disperser.

3.3.3.1. Seed removal experiments.

The Arabuko-Sokoke forest has a great variety of habitats within it and this may affect seed removal due to the different types of animals using the habitats. Figure 6 (Appendix 3d) summarises the results of the seed removal experiment. The data was analysed by first regressing seed removal by C. gambianus against the distance of the seed station to the source and the slope tested for significance from zero (Figure 6).

Seed removal by C. gambianus is a function of distance in the Afzelia forest. There was a significant negative slope, so that as distance increased fewer seeds were removed. In the lowland rain forest, Afzelia-Brachystegia ecotone and Brachystegia woodland, the slopes were not significantly different from zero.

To test for differences in seed removal between habitats, two-factor ANOVA was performed. There were statistically significant differences between the habitats ($F = 7.28$, d.f. = 3,15 , $P < 0.05$).

A range test was carried out to detect the location of the differences in seed removal between the habitats. Seed removal was significantly lower in Brachystegia woodland as compared to the other 3 habitats while no differences were detected among the Afzelia, LRF and Afz/Brachy ecotone habitats. (Tukey test after ANOVA)

Comparison	q	d.f.	
LRF vs Brac.wld	6.23	15,4	$p < 0.05$
LRF vs Brac/Afz Ecot.	1.78	"	$p > 0.05$
Afz vs Brac.wld	4.83	"	$p < 0.05$
Brac/Afz Ecot.vs Brac.wld	4.45	"	$p < 0.05$

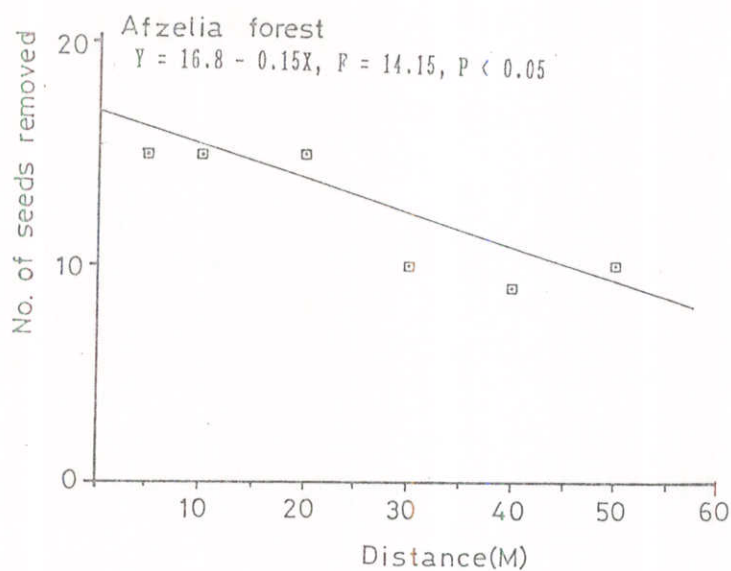
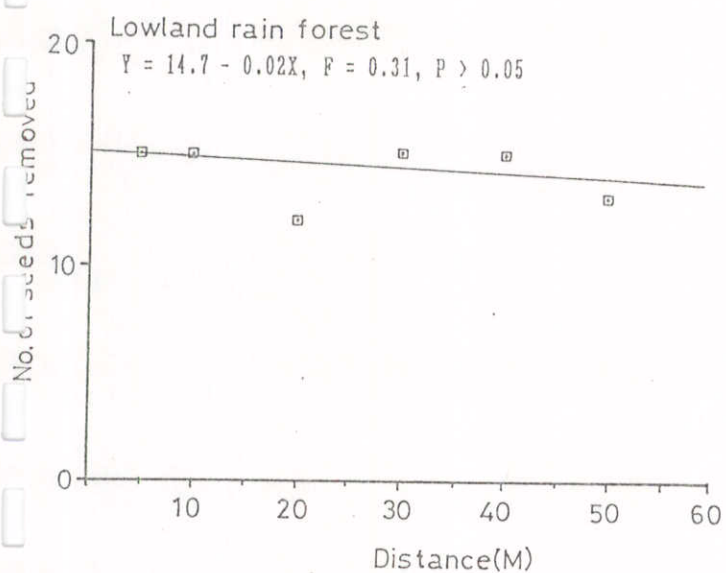
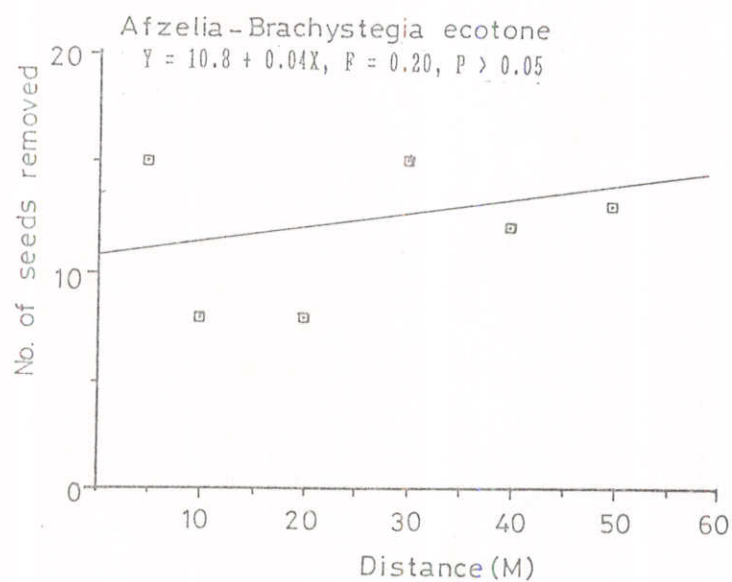
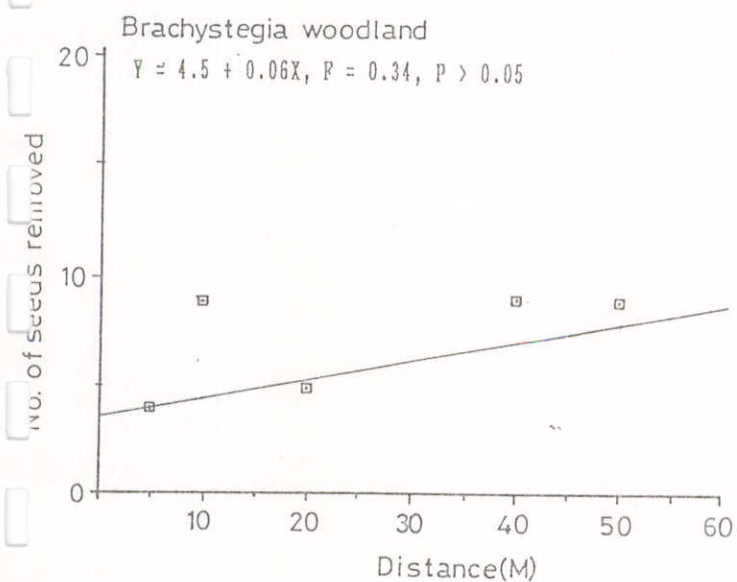


Fig: 6: Relationship between distance of the seed source and number of seeds removed by Cricetomys gambianus

3.3.4. Distribution of the giant Gambian rat (Cricetomys gambianus)

The frequencies of occurrence of the holes which were in use in the two types of forest varied. Of the 13 holes recorded during the study period, 12 were in thick forest and only 1 in the open Brachystegia woodland. This single hole was dug under a shrub. The giant rat was thus an inhabitant of the thick forest habitats.

3.3.5. Phenology of trees and shrubs used by frugivores

There is a seasonal variation in the fruiting phenologies of trees and shrubs in the Arabuko-Sokoke forest (Figure 7). The seed and fruit eating animals are concentrated on a few or one fruiting tree at a time.

In the months of May to September, A. guanzensis has green pods and is a food resource for the red-legged sun squirrels and yellow baboons. In relation to other plant species it is a key species at that particular time of the year. In January to February, Manilkara sansibarensis, a widespread tree, produces thousands of seeds and is exploited by a variety of frugivores including the African civet Viverra civetta, monkeys, rodents and even human beings.

Tamarindus indica is a popular tree with white throated monkeys immediately before seed maturity. The tree is very scattered and rare (Section 4.3.5.2.). Strychnos deccusata is an important shrub, uncommon in A. guanzensis forest but occurring in other zones and widely consumed by primates.

Fruits of climbers (lianas) were consumed by monkeys

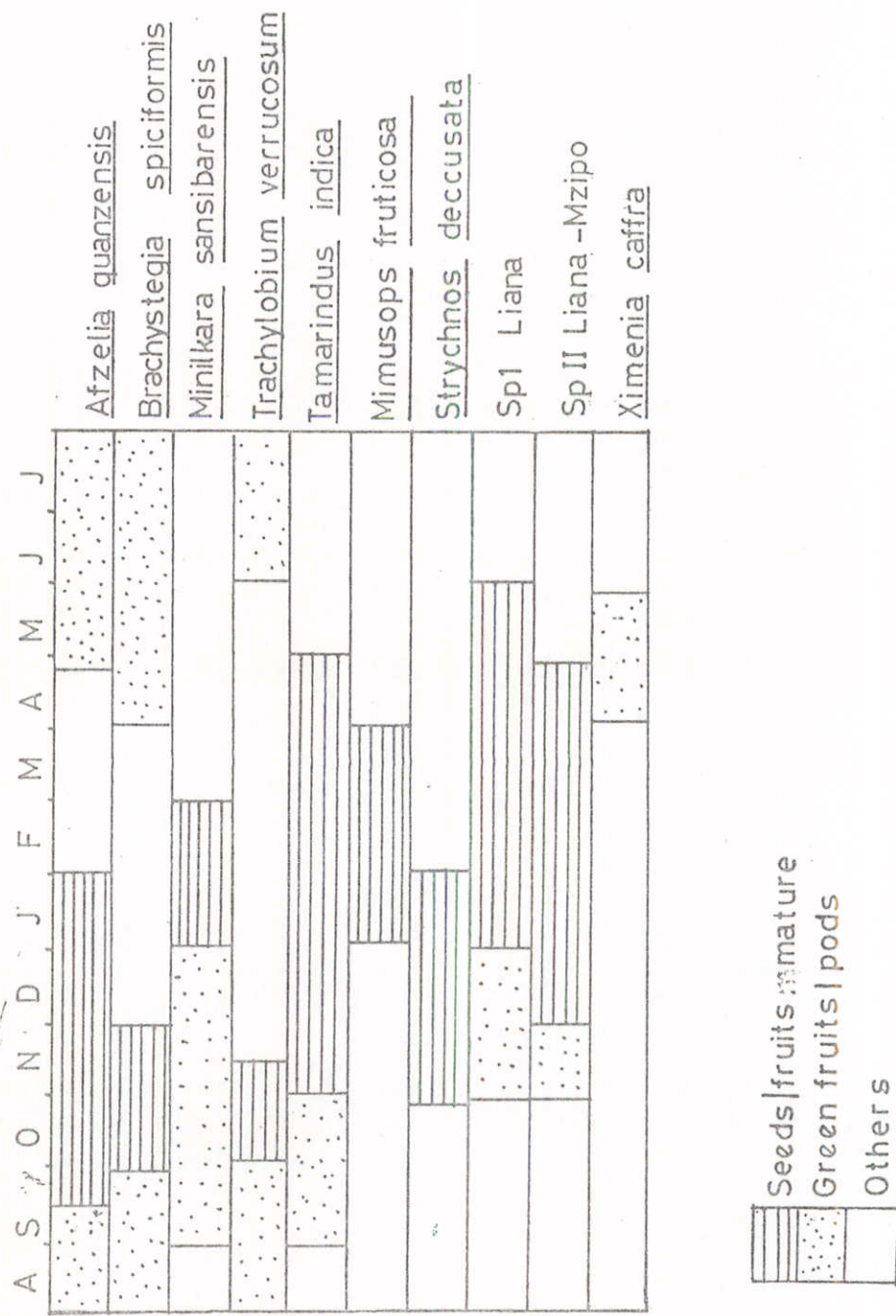


Fig.7. The flowering and fruiting phenologies. The 7 trees, 1 shrub and 2 lianas were commonly used by frugivores during the study.

in the Afzelia forest. One species is Ladorphia.

3.3.6 Discussion

The results clearly show that there is an interaction between the primates, rodents, insects and A. quanzensis as they use the seeds at different developmental stages. The data illustrates the animals as factors affecting the survival of the tree in an ecological time scale. In summary the results can serve as a model describing the interrelationships between A. quanzensis and the animals.

Squirrels, baboons and monkeys played a key role in determining the fate of seeds of this tree as they do in other forest ecosystems and in various plant species. In the Kakamega forest, the blue monkeys (Cercopithecus mitis) and red tailed monkeys (C. ascanius) disperse the majority of seeds (Mwangi 1989 unpubl). In Ghana baboons dispersed 59 plant species (Lieberman et al 1979). In Arabuko-Sokoke forest, squirrels and baboons consumed a large proportion of seeds before maturity. This can greatly affect the dynamics of a tree depending on the seeds available for dispersal along with post dispersal seed predation (Janzen 1970). There must be a compromise on the fate of seeds since if all seeds were to be destroyed before germination, then the tree species would become extinct. This would adversely affect the dispersers and predators which depend on the tree as a food resource (Terborgh 1986). At another level other animals using the plant for other resources such as perching and nest sites will be affected. A. quanzensis was found to be an important habitat for geckos which

occupied the loose old bark, monkeys were found to rest under this tree during hot afternoons.

The survival of trees is highly dependent on the dispersal of its propagules which is a complex process especially where vertebrate dispersers are involved. The food value of the propagules, their structure, the number of seeds produced in a season (Howe 1980, Sork and Boucher 1977) and the foraging behaviour of the dispersers are all of critical importance. It is widely believed by tropical rain forest ecologists that dispersal of seeds reduces competition between seedlings and conspecific adults as well as between members of the same cohort (Connell 1978). A second advantage for dispersal is that once seeds are dispersed specialist seeds predators will not find them (Janzen 1970, 1972a).

In this study the importance of the primates in seed dispersal derives from the long distances covered while foraging. The yellow baboon cover large distances as they forage. They were frequently sighted in the Brachystegia woodlands and occasionally in other vegetation types whereas monkeys were mostly found in the thick forest. In Amboseli wild living yellow baboon females cover upto 9 km / day (Muruthi 1989).

The importance of dispersal of seeds away from the parent tree was verified in this study where it was found that in the Afzelia zone dispersal even to 20 m resulted in high survival while in others many seeds disappeared regardless of the distance (Fig. 6). Probably of importance is the total seeds which survive in a particular habitat not their distance relative to

conspecific adults. In this context the movement of seeds from a habitat where survival was tending to zero was necessary and in this case it was from the other habitats to the Brachystegia woodland. The seed predation after dispersal was related to the density of the seed predator C. gambianus. In the Brachystegia woodland seed survival was quite high (Fig 6), there were no holes of C. gambianus and the woodland floor was covered by a grass species (Panicum spp) which covered the seed if they fell on the tufts. The two factors, absence of seed predators and grass cover exerting their effects together would result in a tremendous increase in seed survival.

Ecotones are habitats of great ecological importance where forest and woodland animals share resources. A high density and biodiversity is expected in this area. Ecotonal communities may contain animals characteristic of each of the overlapping communities in addition to species living only in the ecotone area. This is the edge effect (Odum 1971). Similarly high rates of seed removal were expected in this area. Seed removal, however, in this habitat was found to be intermediate to the other two vegetation types. Host-specificity and density of C. gambianus explains the observation. Seeds were found to be consumed by this rat, thus it is expected that where their population density is high, seed predation will be high. In the ecotone an intermediate population density was expected as densities were high in the thick forest and lowest in the open woodland.

The dispersal of seeds and the availability of some

seeds or parts of them to animals as food resources clearly indicates a mutual relationship. Beneficial relationships may or may not result from coevolution of particular taxa. It is the production of arillate seeds which are probably of high nutritive value that may have resulted in the Afzelia-vertebrate relationship. The development of muscular jaws in the squirrels probably arose due to the opening of hard fibrous fruits (Smith 1970). The seeds of A. quanzensis are contained in a hard pod, yet the squirrels extract the largest proportion by neatly gnawing them; a foraging feat which monkeys are incapable of.

The production of seeds by this tree has resulted in a higher level of interaction among animals. The opening of pods by squirrels provides a niche for secondary infestation by a beetle, Caenocara weisii; females oviposit eggs on such opened pods. The larval instars and emerging adults consume the seeds which remain after the squirrels open the pods. The foraging behaviour of squirrels in this forest thus has a direct effect on the life history of this beetle. If the squirrels become locally extinct in this forest and the beetles are rare as in this case, then there will be no opened green pods for the beetle infestation on the assumption that there is no alternative food plant for the beetle. The parasitoids of the beetle would also be affected thus setting in motion a cascade of local extinctions.

Seed size is important in dispersal as small seeds are more likely to be swallowed and defecated while still viable. Large seeds have limited dispersal though this

depends on the foraging behaviour of the dispersers. In A. quanzensis the seeds are not swallowed.

The attachment of the seed to the aril is critical with respect to the contact time between the seed and the disperser. During the dispersal period, the aril is loosely attached to the seeds and little effort is required by dispersers to detach them. In addition the pod has a slight opening during that period even exposing the seeds to the dispersers. Dispersal can also be enhanced when the animals are in transit and using the cheek pouches. White throated monkeys were seen to carry seeds to more than 20m away from the source tree. Baboons were observed carrying the pods and extracting seeds 5 - 10 m away from the tree and to carry seeds even further.

The dispersal of A. quanzensis seeds is strictly by external means as seeds were not swallowed, though the use of gular pouches was common. As a consequence the results of this study cannot be easily compared with others since ecologists have largely dealt with seed dispersal through the gut of vertebrates.

There is a high possibility that the black part of a mature seed is avoided by animals due to the presence of toxic chemicals. This is a defence mechanism widespread in the plant kingdom. Seigler (1979) found that lipid secondary metabolites deter general predation on seeds, especially in the legume family to which A. quanzensis belongs. From this it can be inferred that the giant Gambian rat is either tolerant to the toxic chemicals or can effectively detoxify and use them, a phenomenon that

may be the result of a long period of coexistence hence coevolution.

The results show a clear partitioning in the exploitation of the A. quanzensis seeds in time and space. When the tree flowers, the forest duikers consume the flowers that drop on the forest floor (Ngala pers. com.). When the seed stage is attained consumption by squirrels starts, up to September when the pods are almost maturing. Baboons also exploit the seeds at this stage and on maturity the monkeys join in the consumption of the arils. The giant Gambian rat continues with the consumption of seeds even up to the germination stage.

CHAPTER FOUR

THE NATURAL REGENERATION OF *Afzelia quanzensis*

4.1 Introduction

It is often assumed that plant communities are stable in composition and structure at seral stages. On the contrary, forest ecosystems are continuously changing as trees grow and die. In the tropics the mortality factors are winds, storms and logging where gaps are created in the forests and seedlings emerge (Whitmore 1984). Thus a forest is a living entity in a state of dynamic equilibrium.

Regeneration in plants is a complex process involving a lot of factors but can however be divided into two major categories - seedling recruitment and mature phase. Regeneration depend on the tree species and type of ecosystem, for instance some trees are pioneers, for example *Trema sp* in African forests. They are mostly shade intolerant and they will colonise newly created gaps and give way to secondary colonizers later. In the tropics tree regeneration is important and occurs when gaps are opened up. There are normally seed banks in the soil from which seeds germinate in response to changing conditions. Alternatively seeds are dispersed into the gap and become established (Whitmore 1984).

The recruitment phase is vital in regeneration as it is the period that seeds are dispersed, germinate and establish themselves. Whether in animals or plants juvenile recruitment is necessary for the maintenance of a viable population as they replace the dying adult members.

Several factors are involved in regeneration with

edaphic, climatic and biotic factors being important. In the tropics biotic factors play a key role. Tsingalia (1988) found that bulbuls disperse seeds of Olea in Kakamega forest. In the Galapagos, a near extinct tree, Bursera graveolus, was dispersed by animals to suitable regeneration sites (Clark and Clark 1981).

Animals on the other hand can arrest regeneration and this happens when they destroy seedlings and saplings. In the Amboseli ecosystem, Acacia have shown poor regeneration. There has been controversy amongst ecologists as to what factors are responsible with the main arguments split between the hydrological cycle and herbivory and destruction of seedlings especially by elephants.

Deshmukh (1986) argued that the savannahs have not reached climatic climaxes and would evolve into different vegetation types if released from fire and grazing pressure. He even argues that closed canopy forest would replace savannahs if these pressures were removed. Oweyegha - Afunadula (1982) working in the Tsavo ecosystem found that tree density increased when elephants were excluded.

This part of the study was aimed at investigating how A. quanzensis regenerates and the role of animals.

4.2. Methods

In this study regeneration was considered from seedling up to the adults. Data on seedling demography, population structure and dispersion patterns was collected.

Human disturbances through extraction of A. quanzensis and others was quantified. The association of A. quanzensis and other trees was also quantified and the IVI (importance

value index) was used towards this end.

4.2.1 Seedling demography

Juveniles of A. quanzensis less than 3m in height were extensively searched for in the selected study sites where adults were selected as the base and a circular area around them searched for the seedlings. The forest was divided into zones in a systematic random sampling manner and each site was sampled. Equal effort was allocated where equal time was spent on searching for seedlings or taking data when a seedling was encountered. In areas of high seedling density fewer adult trees would be sampled and vice versa. The search area was limited to 50m, a distance beyond which seedlings were never seen. 64 adult trees were focally sampled and more data obtained opportunistically during the study where other trees were encountered. Several parameters were recorded as follows:

- i) age,
- ii) height,
- iii) diameter at base just above the soil surface which was measured using a vernier calliper,

- iv) vigour which was categorized as very good, good or bad,

Very good - The seedling had not lost leaves and no stem damage,

Good - Some destruction had occurred but the seedling was recovering,

Bad - Seedling was dead,

- v) distance to conspecific adult tree. The edge of the nearest branch was taken as the shortest distance

for dispersal, (Clark and Clark 1981),

- vi) the last fruiting season for the adults sampled,
- vii) crown diameter and DBH of the adult.

The study was done after the seed drop in order to take germination into account. Detailed studies were done in each study site, where various microhabitats were sampled such as road sides, logged areas, forest gaps and areas cleared of conspecific adults. Some seedlings were tagged for future monitoring.

Active searching for seedlings is a better method of studying regeneration than taking transects (Clark and Clark 1981).

4.2.2. Size class structure of adult *A. quanzensis*.

The forest was divided into blocks Arabuko, Gedi/Mida, Nature Reserve, Kararacha and within them transects were randomly taken. The forest exhibits a high degree of variation and to obtain a representative sample, the distribution of transects between blocks was essential .

Belt transects with a length of 100m and width of 10m were used in the study. This kind of transect is ideal for vegetation analysis in forests (Derhammen et al. 1989). Fifteen such transects were taken and therefore an area of 1.5 ha was covered. Roads and paths in the forest reserve were used as base lines . The wide distribution of transects between habitats reduces errors which may arise from the heterogeneity of the vegetation types.

Once a transect corner was established, a straight line was cut along the length of the transect. This was accomplished by one person using a compass and directing

the second person who was clearing. To maintain the straight line and to guide the sampler, a sisal string was laid on the cleared line. Ten metre width was maintained by taking a perpendicular length from the string.

The size class structure was obtained by characterising plant species by diameter at breast height (dbh) (the height is about 1.3m from the ground). Individuals more than three metres in height were sampled. The unidentified species were pressed for later identification.

4.2.3. Afzelia quanzensis as a source of illegal timber.

The transects used in characterising the population structure were also used in this aspect of the study. When a logged tree was encountered the following information was recorded:

- i) whether the stump was old or recently cut.
- ii) status (either coppicing or dead),
- iii) stump diameter (data obtained will indicate desired stem size).
- iv) Natural mortality (a tree was classified in this category if it was found dead and still standing with no signs of human disturbance).

4.2.4. Dispersion pattern.

The nearest neighbour method (Pielou 1959, Laessle 1965, Turner and Franz 1985) was used. Laessle (1965) found that narrow strips simplify the determination of nearest neighbour. In each transect distances between the adults was measured using a tape measure. This was defined as the nearest neighbour distance and the data was used for determining the dispersion pattern. An index (a_i) was

computed and was used to identify non random distribution .

$$a_i = Dw\pi$$

Where,

w is the mean square of the distances from the individual to the nearest neighbour;

D is the density as estimated from the strips sampled. (It is expressed in m^2 , which is also termed as the number of individuals per unit area).

If there is a random distribution, the expected value of a_i will be equal to $(n - 1)/n$. Where n is the number of distances recorded.

$a_i > (n - 1)/n$ indicates regularity.

$a_i < (n - 1)/n$ indicates clumped dispersion.

4.2.5. Vegetation analysis

4.2.5.1. Profile diagrams

Typical strips which represented Afzelia forest were selected. The first profile was taken in the nature reserve and was 100 by 10m. All species were sketched to scale. A second profile diagram was sketched for a plot taken in Kararacha (Fig. 1). In this area there is a small patch of Afzelia mixed forest. The plot size was 60 by 20m.

The plant species found were identified, then their height and crown diameter estimated. The sketch was done in the field and later transformed into representative sketches.

The profile diagrams are important when an ecologist needs to know the kind of layering or stratification of canopy in forest ecosystems. When coupled with population structure by stem sizes, a good description of the forest

where *A. quanzensis* occurs will be realized.

4.2.5.2. Importance value index

The use of density to represent plant populations does not fully describe the plant communities. For example, a forest may have a few large sized trees with numerous shrubs or small trees. To solve such a problem, the use of the importance value is of great importance (Newton 1986).

$$IVI = \text{Relative dominance} + \text{Relative frequency} + \text{Relative density}$$

Dominance is obtained by converting the diameter at breast height of all stems into area. Thus dominance can be visualized as the area of the stump tops left if the forests were cleared at breast height. Relative dominance is obtained for each species as follows;

$$\text{Rel. dominance} = \frac{\text{Basal area of the } i^{\text{th}} \text{ species} * 100 \%}{\text{Total basal area}}$$

(Newton 1986).

Density is obtained by counting the number of stems in all transects. Relative density is similarly calculated.

$$\text{Rel. density} = \frac{\text{Individuals of the } i^{\text{th}} * 100 \%}{\text{Total individuals (N)}}$$

Frequency is obtained by recording the presence or absence of a species in a transect regardless of number.

$$\text{Rel. density} = \frac{\text{Frequency of } i^{\text{th}} * 100 \%}{\text{Total frequency}}$$

In this study, the IVI was calculated for the canopy tree species only, also those newly recruited juveniles of

those canopy species and greater than 3m in height were included.

4.3 Results

4.3.1. Seedling Demography

4.3.1.1. Size class distribution

Figure 8 summarizes the distribution of size class structure in seedlings classified by diameter at base. A sample of 234 seedlings was taken. Over 85% were found to be less than 1.5 cm in diameter. There were significant differences in seedling size distribution (Kolmogorov-Smirnoff test for continuous data, d_{\max} , d.f = 234, $P < 0.05$).

4.3.1.2 Distance of seedling from conspecific adults.

Figure 9 shows the distances at which seedlings were found to the nearest adult. Most of the seedlings were between the tree base and 6 m away. The zero distance was classified as under the canopy and at the crown edge where the actual measurement commenced. That means seedlings were abundant below the crown and up to 6m away from the crown edge. There was a decrease in seedling number from 20 m with occasional records up to 50 m away. The curve shows the general distribution of all seedlings regardless of vigour.

Figure 9 also shows the distribution of the viable seedlings which represent the category very good and good. Seedlings under the canopy tree suffered high mortality. The mortality was reduced after 7 metres, where all the seedlings were in good vigour. Despite the low numbers at

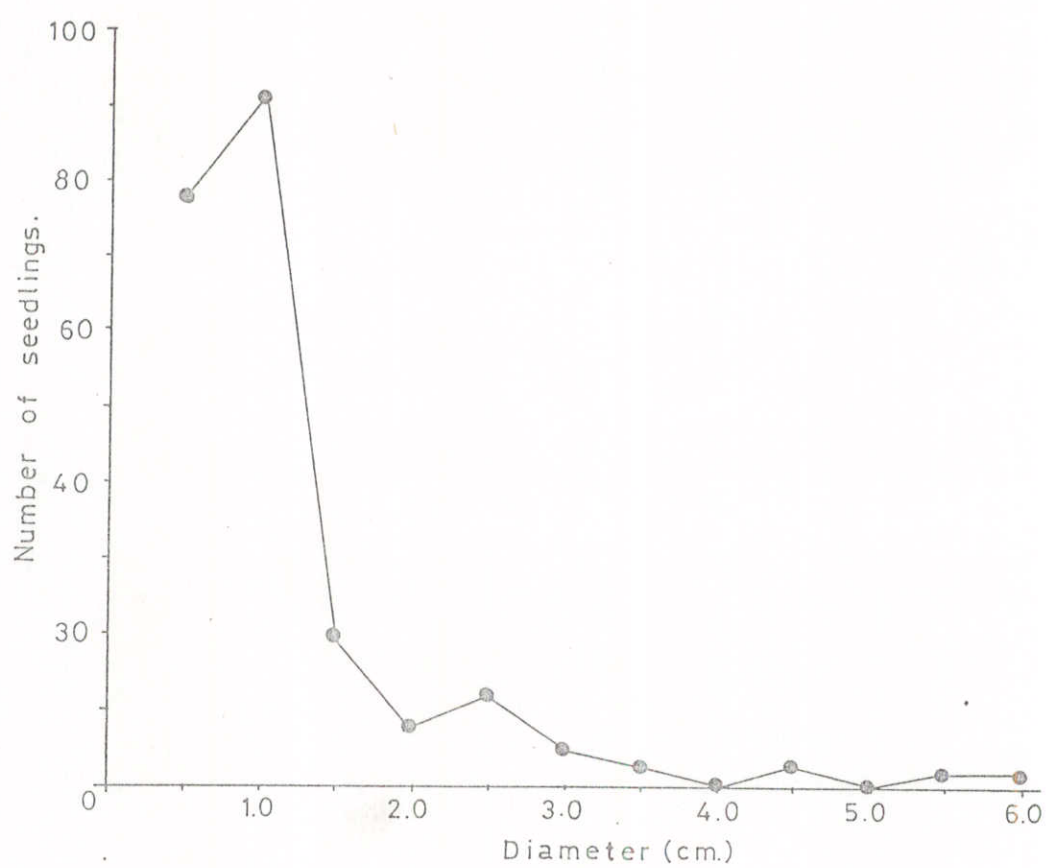


Fig.8: Seedling size distribution

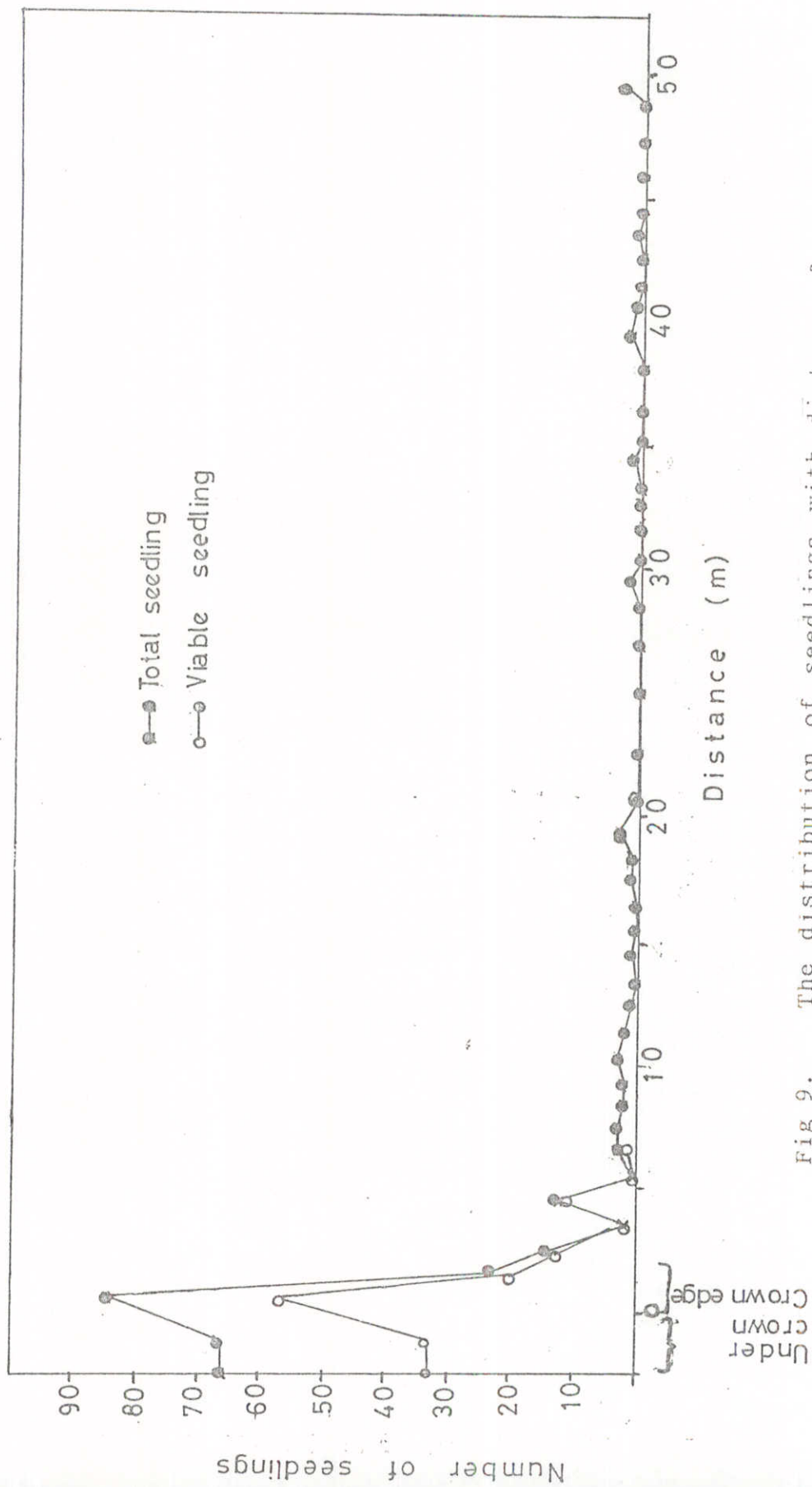


Fig 9. The distribution of seedlings with distance from the nearest conspecific adult.

that distance there was a good chance of a seedling becoming established away from a conspecific adult.

The distribution of seedlings was significantly different between habitats ($\chi^2 = 143.9$, d.f.=2, $p < 0.05$), (see Appendix 5).

4.3.1.3. Seedling Mortality.

The mortality factors involved at seedling stages are varied depending on tree species. Herbivory by insects and competition (stunted growth) are the major factors in this study (Table 1). Both factors caused the death of more than 50.7% ($n = 77$) of seedlings. 15.6% of the seedlings mortality resulted from desiccation. Destruction by mammals was not found to be of great significance. Amongst the mammals, the African elephant, Loxodonta africana, caused destruction by breaking saplings and trampling. The giant Gambian rat caused death by removing the cotyledons and the first leaves after germination. A. quanzensis germination is epigeal, where the radicle elongates and pushes the cotyledons out of the soil before they open, and it is after that that they are destroyed. Elephant shrew (Rhyncocyon chrysopygus) were found to have destroyed one seedling. When foraging they scratch for insects and it is then that seedling can be uprooted. For 18 seedlings none of the above factors could be held responsible as their mode of destruction was unclear.

The data presented showed the dynamics of A. quanzensis seedlings in Arabuko - Sokoke forest for one year. For key factor analysis, inter year variations would be needed for factors to be ranked on the basis of their magnitude.

Table 1. The mortality of seedlings in A. quanzenis and the proportion of each mortality factor. (See text for explanation).

	Insect herbivory	Dessication	Damage by mammals	Stunted growth	Stem rot	Unidentified
seedlings	18	12	6	21	2	18
Percent	23.4	15.6	7.7	27.3	2.6	23.4

4.3.2 Population structure of the adult A. quanzensis

The population structure of the adult trees is an inverse J- curve. Figure 10 indicates that the sapling / pole size or young trees which have been recruited recently into the canopy are rare. However at dbh 20 - 50 cm, the species is well represented with the majority of the trees between 45 - 50 cm dbh.

There was a drastic decrease in the number of individuals above 55 cm in dbh. The graph levels and there were no trees recorded with a dbh of 90 - 95 cm. The maximum dbh was 100 cm above which no individual was recorded.

4.3.3 Afzelia quanzensis as a source of illegal timber.

In the Arabuko - Sokoke forest, Afzelia quanzensis and Pleurostyliia africana are being cut illegally (Plate 10). Table 2 shows the general status of Afzelia quanzensis with 12.4% illegally logged while 76.5% of trees are viable. Natural mortality of adult trees was 11.1% (n = 81, dead trees found standing). The selective logging was expected to be zero after the ban on indigenous forest exploitation in 1983. The policing of forests has however been relaxed and exploitation has resumed. Natural mortality was found in the nature reserve with mature standing trunks rotting.

The A. quanzensis tree has an ability to coppice depending on the height of the stump left standing after the logging. Stumps 15cm in height were found coppicing, though in some cases the logger was found to dig up to 30 cm below the soil surface to maximize on the timber yield. Such stumps did not coppice and were found mostly dry or

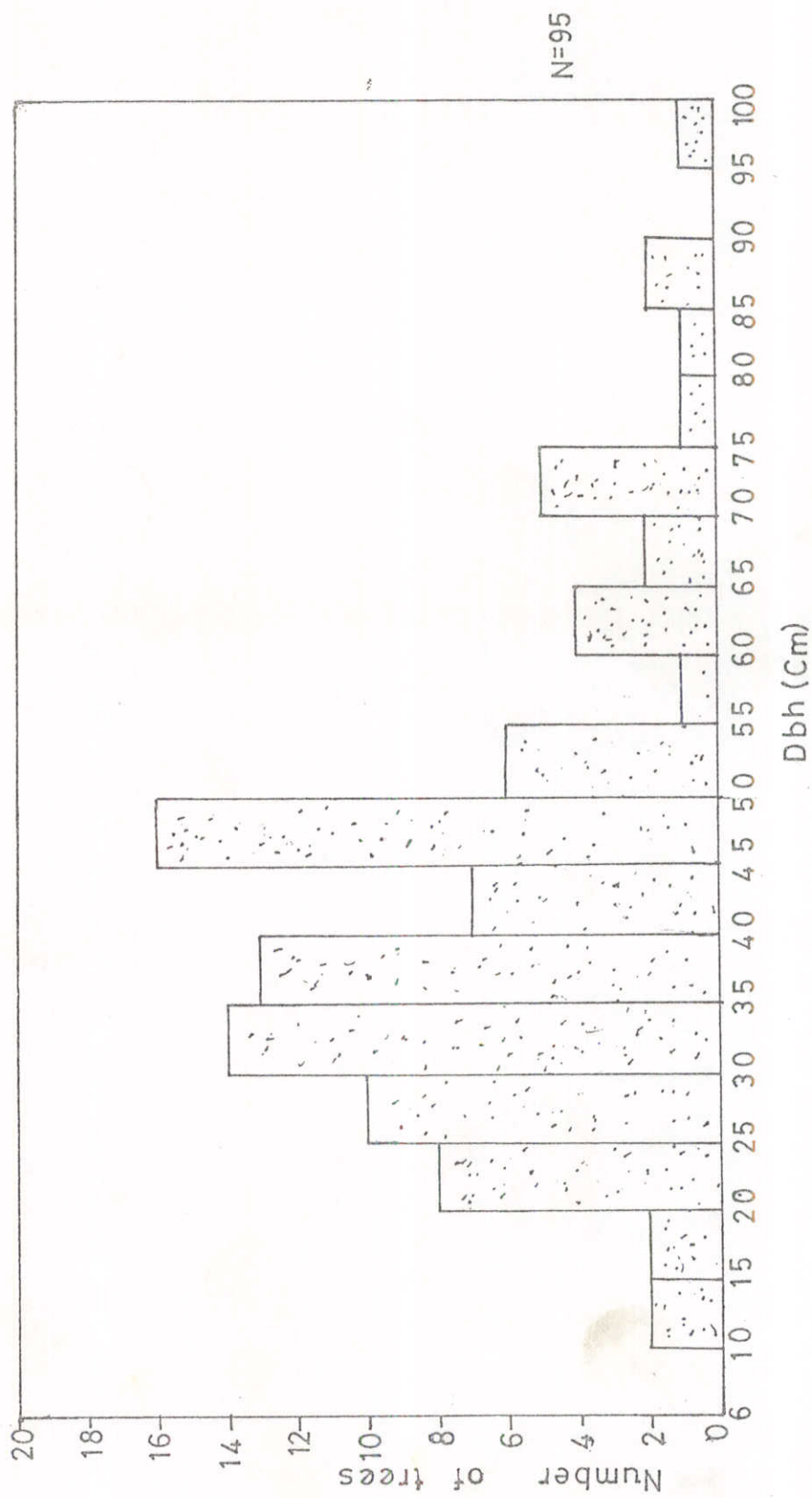


Fig. 10. The size class distribution of adult *Afzelia quanzensis*, Diameter at breast height (Dbh) was used as a measure of size.

Table 2. General status of the adult *A. quanzensis*

	Logging	Natural death	Viable trees
Number of trees	10	9	62
Percentage	12.4	11.1	76.5



Plate 10.

Logged *A. quanzensis*. This is done illegally inside the forest by the local people for timber.

rotting. Out of 10 logged trees, only 3 were found coppicing while the rest had died.

The diameter of the stump was measured to get an idea of what size of trees are logged, and a mean diameter of 60.9 ± 4.6 (SE) cm was found. Assuming that the diameter of the stem approximates dbh which should be true for a species without a buttress, then this explains the decline in abundance of trees with dbh 55cm (Figure 10).

4.3.4 Dispersion pattern.

Dispersion pattern results indicate how natural populations of plants are spatially arranged. Three types of distribution are distinguished : random, aggregated and regular. Random distribution occurs when each individual plant occurs independently of others. Aggregated populations are those where individuals occur in clumps, and in regular distribution individuals are evenly spaced.

A formula developed by Pielou (1959), Laessle (1965) and Turner and Franz (1985) was used to identify nonrandom distribution.

Observed $a_i = 6.59$

$$\text{Expected } a_i = \frac{n - 1}{n} = 0.98$$

n = number of measurements = 50 (Appendix 6).

Thus $6.59 > 0.98$.

This indicates regular distribution.

4.3.5 Vegetation analysis

4.3.5 Vegetation analysis

4.3.5.1 Profile diagrams.

Figure 11 represents a typical Afzelia forest which is extensive around the nature reserve. Figure 12 was taken in Kararacha. Forest structure is conventionally depicted by profile diagrams, the importance being its three dimension representation of height, length and width. Kararacha site In the nature reserve, Afzelia forest is quite thick with undergrowth, in contrast, in Kararacha the forest is open at the ground level with a lot of stems of woody species.

The vertical stratification of the plant community is evident. In the Kararacha site, the top canopy is dominated by Brachystegia spiciformis and Manilkara sansibarensis. The middle canopy is where Afzelia quanzensis dominates, Trachylobium verrucosum is also represented. The lower canopy is dominated by Securinega virosa and Memecyclon sansibaricum, both being shrubs. In the nature reserve the three layers are not very distinct. However T. verrucosum, Mimusops fruticosa, A. quanzensis form the upper canopy. The middle canopy is formed by Drypetes reticulatus, Mytenus undata and Ludia mauritanicus. The common shrub at the lower level is Polysphaeria parvifolia, and it holds several climbers.

4.3.5.2. Importance value index.

Sixteen woody species which comprise the upper canopy were considered in this section. 1.5 ha was covered in 15 transects where 417 stems of the 16 species were enumerated.

Considering relative dominance alone A. quanzensis leads with 51.5% (12.1 m^2), Trachylobium verrucosum

Figure 11. Profile of a typical Afzelia forest taken in
the Nature reserve (size, 10 * 100m).

Figure 12. Profile of forest in Kararacha (size,
60 * 20m).

Legend

B.S. *Brachystegia spiciformis*

Af.q. *Afzelia quanzensis*

T. *Teclea trichocarpa*

c.d. *Euphorbia candelabrum*

c. *Cassipourea*

T.V. *Trachylobium verrucosum*

Pl. *Polyathia stuhlmanii*

s.d. *Strychnos deccusata*

M.v. *Maytenus undata*

o.o. *Ozora obovata*

D.r. *Drypetes reticulatus*

G. *Grewia plagrophylla*

T.b. *Terminalia bovinii*

M.f. *Mimusops fruticosa*

S.v. *Securinega virosa*

D.o. *Dialium orientale*

P. *Pysadrax sp.*

L.M. *Ludia mauritanus*

L. *Lonchorpus sp.*

M. *Memecylon sansibaricum*

P.P. *Polysphaeria parvifolia*

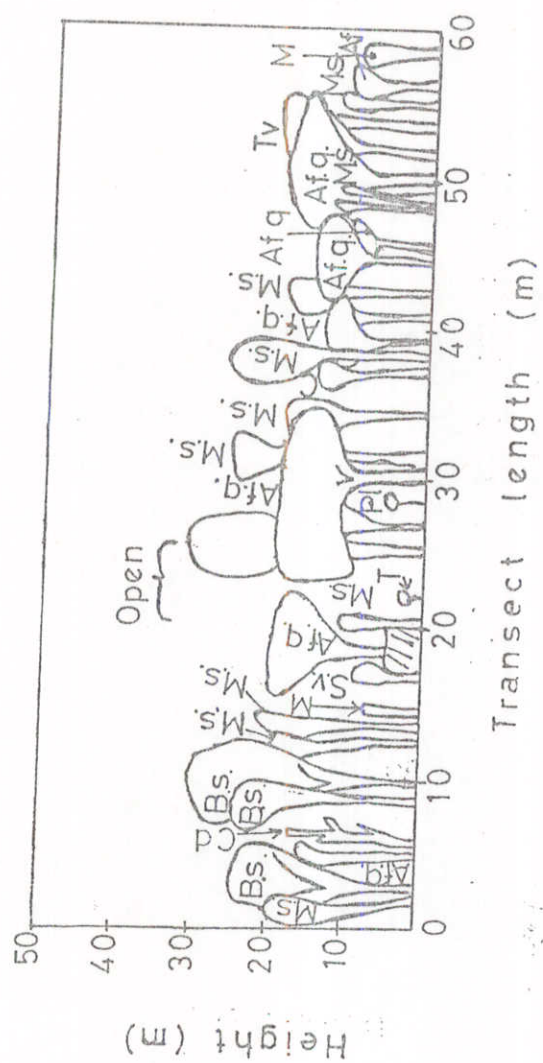
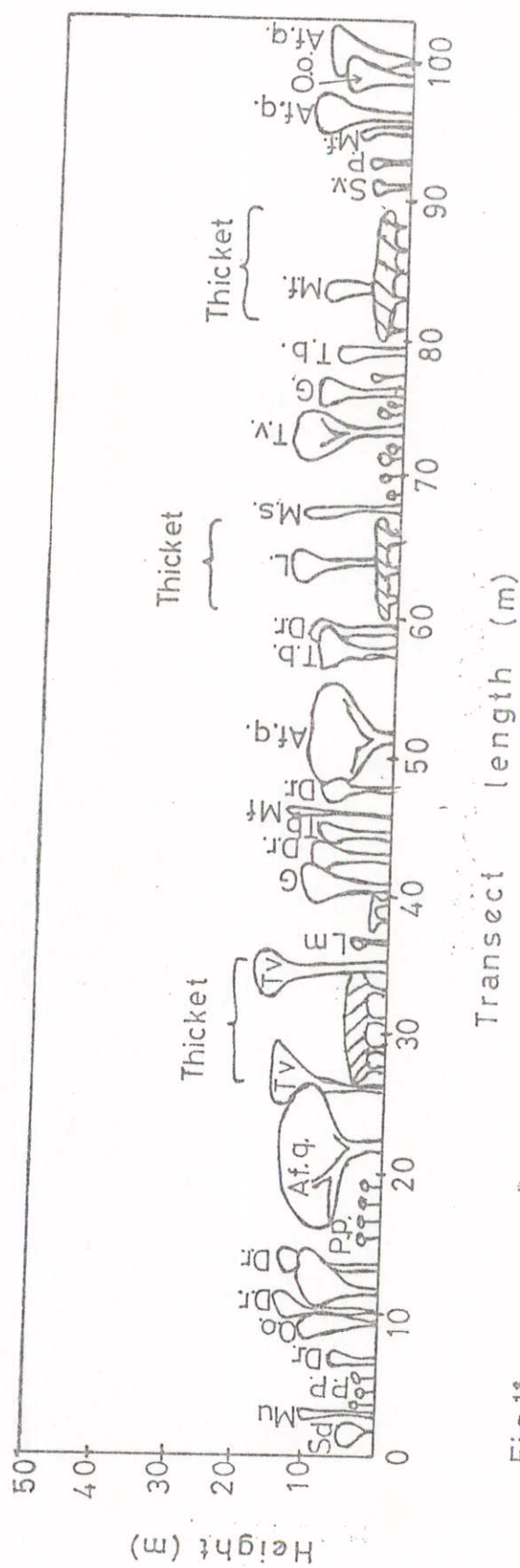


Table 3. The importance value of 16 plant species associated with *A. quanzensis* in 1.5ha

TREE SPECIES	Dominance (m ²)	Relative dominance	Density	Relative density	Frequency	Relative frequency	Importance value	Rank
<i>Afzelia quanzensis</i>	12.1	51.5	63	15.0	15	14.4	80.9	2
<i>Trachylobium verrucosum</i>	5.0	21.3	99	23.7	15	14.4	104.3	1
<i>Manilkara sansibarensis</i>	2.6	11.1	103	24.7	14	13.5	49.3	3
<i>Tamarindus indica</i>	1.2	5.1	3	0.7	3	2.9	8.7	9
<i>Mimusops fruticosa</i>	0.4	1.7	20	4.8	8	7.7	14.2	7
<i>Strychnos decussata</i>	0.2	0.9	21	5.0	7	6.7	29.8	4
<i>Dialium orientale</i>	0.35	1.5	16	3.8	8	7.7	13.0	8
<i>Pluerostylia africana</i>	0.17	0.7	7	1.7	4	3.9	6.3	11
<i>Terminalia bovinii</i>	0.31	1.3	29	7.0	9	8.7	17.0	5
<i>Balanites wilsoniana</i>	0.12	0.5	2	0.5	2	1.9	2.9	16
<i>Diospyros consolatae</i>	0.02	0.1	4	1.0	3	2.9	4.0	14-15
<i>Brachylaena huichinsii</i>	0.03	0.1	4	1.0	3	2.9	4.0	14-15
<i>Combretum schulmanii</i>	0.48	2.1	27	6.5	8	7.7	16.3	6
<i>Paramacrolobium</i> sp	0.29	1.2	12	2.9	1	0.9	5.0	12
<i>Fagara chalybea</i>	0.17	0.7	5	1.2	3	2.9	4.8	13
<i>Lannea schweinfurthii</i>	0.05	0.2	2	0.5	1	0.9	6.4	10

ranked second with 21.5% (5.0 m^2), while relative dominance of other species was low (Table 3).

Density was highest in Manilkara sansibarensis. This is a widespread tree and it was expected. A. quanzensis ranked third after T. verrucosum. Balanites wilsoniana and Lannea schweinfurthi ranked the lowest, with 2 stems each. A. quanzensis, T. verrucosum and M. sansibarensis were the most frequent trees. They were recorded in all transects apart from M. sansibarensis which was absent in one transect. Paramocrobium coeruleum was recorded only in Kararacha.

In terms of IV T. verrucosum ranked the first with a value of 140.3, A. quanzensis second (80.9) and M. sansibarensis third. Strychnos decussata, a shrub, had a value of 26.8.

4.4 Discussion

It is important to concentrate attention on the ecology of the forests. There is a need for studies on the conservation of the indigenous forests and the status of the ecologically and economically important species.

The requirements for seed germination and seedling establishment differ from one species to another. However the basic requirements are high moisture content, light and nutrients in the soil. In most tropical forests these abiotic factors are present but biotic factors also play a key role. Seedling destruction by herbivores and seed predation by insects and rodents are important (Janzen 1972b and Connell 1978). In A. quanzensis seeds must escape the destruction by a rodent (C. gambianus) at maturity, not

to mention seedling mortality after germination.

Rodents are known to have impact on regeneration elsewhere. Boucher (1981) found that the acorns of an isolated oak were depleted by the pocket mice (Liomys salvini) and squirrels (Sciurus variegatoides).

The establishment of seedlings does not entirely represent the future population structure. This is realized by the continued mortality of seedlings with age. In Prunus africanus abundant seedlings were recorded in early stages of germination (Tsingalia 1988). Subsequently, seedling herbivory by the grazing duikers reduces the number of seedlings to be recruited into the next stage. Connell (1978) presents the same argument for herbivory.

The same pattern of distribution was found in this study, where seedling numbers decreased with size. For practical purposes diameter of seedling at base was used as the best measure of size. In the Arabuko - Sokoke forest herbivory was also a major factor on A. guanzensis in this respect though insects were the main herbivores in contrast to duikers on Prunus africanus. Competition, which was considered to cause stunted growth, desiccation and damage by mammals, elephants and C. gambianus were found to be of great importance in A. guanzensis. Desiccation caused 15.6% mortality (it is a mortality factor in dry lands and even in savannahs).

In A. guanzensis, some seedlings were chopped off by C. gambianus immediately after germination. At this stage, destruction of the meristematic apex and removal of cotyledons, which are photosynthetic, leads to death. The seedlings at this stage are dependent on the food reserves

in the cotyledons (Crawley 1983). The seedlings are tender at this stage, and with their food reserves still intact, are an attractive resource to the herbivores. The elongation of the hypocotyle during germination has the effect of exposing seeds which previously had escaped predation and thus enhancing seedling mortality.

Although seed predation in the Brachystegia woodlands was low, germination conditions were also better with more light penetration through the more open canopy (Plate 3). Afzelia quanzensis seedlings found in the Afzelia forest were found either along the roads or open patches which could not be described as gaps. In one sample tree, the area under the crown appeared to have been cleared a couple of years back and more seedlings were recorded here than in any other sample tree in this vegetation type. Afzelia can therefore be described as a shade intolerant tree requiring light for it to be established.

Afzelia quanzensis is associated with other canopy trees, herbs and shrubs such as T. verrucosum and Manilkara sansibarensis which are broad leaved trees and have the effect of lowering canopy light penetration. Brachystegia spiciformis in contrast is narrow leaved and the trees are widely scattered and thus more light reaches the ground and if the argument for shade intolerance holds, then A. quanzensis would germinate in this woodland.

A. quanzensis could be described as invading the open Brachystegia woodland and can be described as a colonizer at secondary level. The explanation being that more seedlings were recorded in this woodland, and were in good

vigour. Adult trees in the woodland were smaller in size than in the thick forest showing colonisation to have been a recent process. Similar results were found in Bundongo forest in Uganda (Eggeling 1947). In colonizing stands very few adult species dominated, but the juveniles on those stands were of entirely different species (Eggeling 1947).

In coloniser and shade intolerant tree species, 'waiting' for gap formation is an important part of life history strategies. Once seeds are dispersed, they remain dormant for a long duration for favourable conditions to commence. In *A. quanzensis*, predation of seeds after dispersal by *C. gambianus* is quite heavy and dispersal is limited. This in effect reduces the probability of a seed falling on a patch with optimal condition for germination and survival. That means the colonization can take decades.

Seedling survival has been reported in other studies to vary with distance from the conspecific fruiting adults (Janzen 1970, Augspurger 1983, Tsingalia 1989, Howe 1989). In *Platypodium elegans*, the survival was high as distance increased (Augspurger 1983), fungal pathogens being the cause of mortality. Howe (1989) reported that 99.6% of the seedlings of *Virola surinamensis* under adult trees die. As the distance increases, survival increases, and at 40m away, more than 30 times as many seedlings survived.

In *A. quanzensis*, seedling number was high at the edge of the crown, those under the tree ranked second. From the crown edge up to 6m away, density decreased and there was a dramatic decline in numbers up to 50m away. A leptokurtic seedling distribution similar to other species was found

(Hubbell 1980). Seedling vigour was also found to improve with distance from the adult tree with all seedlings being in good vigour and 100% survival from 7m and beyond. The reason for this may be the reduction in competition for nutrients and other resources between seedlings and adult trees. Since the density of seedlings decreased inversely with distance from the parent tree seedling competition is also in effect reduced.

In summary, seedling survival is a result of an array of factors. In the presence of adverse factors, such as seedling destruction as in oaks (Boucher 1981), seed dispersal and hence seedlings survival is obligatory. In the Arabuko - Sokoke, primates and especially the yellow baboons are vital to the survival of the A. quanzensis. The baboons move across the forest while foraging and show a great preference for the Brachystegia woodland where seed survival is also highest. The white throated monkey solitary males were also found in the Brachystegia woodland and no monkey troops were recorded in Brachystegia woodland. However monkeys are important in the thick forests where they transverse the thick areas. Baboons were however observed to follow the forest paths. The monkeys do a great deal of seed dispersal though there is severe seed mortality in their range as mentioned in the section of seed removal. Dispersers are vital for the continued recruitment of seedlings of the study tree.

The dispersion pattern of adult trees is a result of seed dispersal (Howe 1989, Hubbell 1980). The presence of an adult tree indicates a safe site where a seedling became

established. Conditions are, however, dynamic since conditions that can be measured today are not necessarily those pertaining at the time the tree became established. In this context, long term monitoring is necessary to describe the optimal establishment sites and physical environment.

Adult A. guanzensis trees were regularly distributed. At the adult and sapling stage one would expect clumps because seedling density is very high around adults as observed in some sample trees. Laessle (1965) found that departures towards regular distribution in pines was realized as vegetation stands age. Regular distribution occurs if individuals are not distributed by chance and as such there must be factors acting, and as a consequence a pattern arises.

Intraspecific competition between individuals is an explanation for spacing of individuals in a population (Laessle 1965, Pielou 1959). They argued that competition is more common in natural populations. In animals it results in territoriality to control resources such as food or mates. In plants space acquisition may be equated with territoriality (Begon and Mortimer 1986).

The explanation for the regular spacing observed in this study may be that regular spacing may occur due to capturing of space or rather intraspecific competition where establishment of seedling and growth to maturity occurred in individuals with adequate growth conditions.

A. guanzensis dominates its range when the cross sectional area at breast height (CABH) is considered. However, on the importance value index, it ranks second

(Table 3). The population structure of adult *A. quanzensis* shows that it exhibits an inverse J - shaped curve. However, there are few large-sized trees, which can only be explained by logging of individuals when they grow up to 55cm in dbh (Fig. 10)

CHAPTER FIVE

GENERAL DISCUSSION, CONSERVATION IMPLICATIONS AND RECOMMENDATIONS

5.1 General discussion

The results obtained in this study indicate that animals are important in the survival of the pod mahogany, A. quanzensis. The interactions commence at the immature, then to mature stages of seed development, and continue to the germination and seedling levels. This then means that the animals involved and A. quanzensis have strong associations at crucial levels of their life histories. This finding calls for a detailed explanation.

The consumption of seeds and seedlings should not always be viewed as adverse on the plant species involved. In some instances, it may be even an ecological requirement to reduce the density of juveniles for survival of a few individuals. Organisms produce large numbers of offspring to ensure the survival of a few individuals. Thus this tree loses 37.5 % of seed at premature stages and a second proportion after maturity and dispersal. A third proportion of offspring die at seedling stage. Mortality leaves few offspring to survive up to the establishment of the seedlings and recruitment to the population.

Different animals use this tree as a food source at various stages of fruit development. At early fruit development, pods are hard and fibrous and it is only baboons and squirrels which manage to successfully open them. At maturity, seeds are available because the pod can easily be opened but the dispersers avoid them, consuming

the aril only.

The dispersed part of the seed which germinates was consumed by the C. gambianus. It is possible that the seeds have a chemical defence at maturity. Baboons and squirrels consume them when they are immature and avoid them when they mature. The extraction of the seeds at maturity when the pods opens is expected to be less energetically expensive so that in the absence of chemical defence the trees might lose hundreds of seeds. The tree probably defends the seeds by concentrating secondary chemical compounds. C. gambianus may have the ability to eat the seeds having the chemicals such that the rodent is not adversely affected.

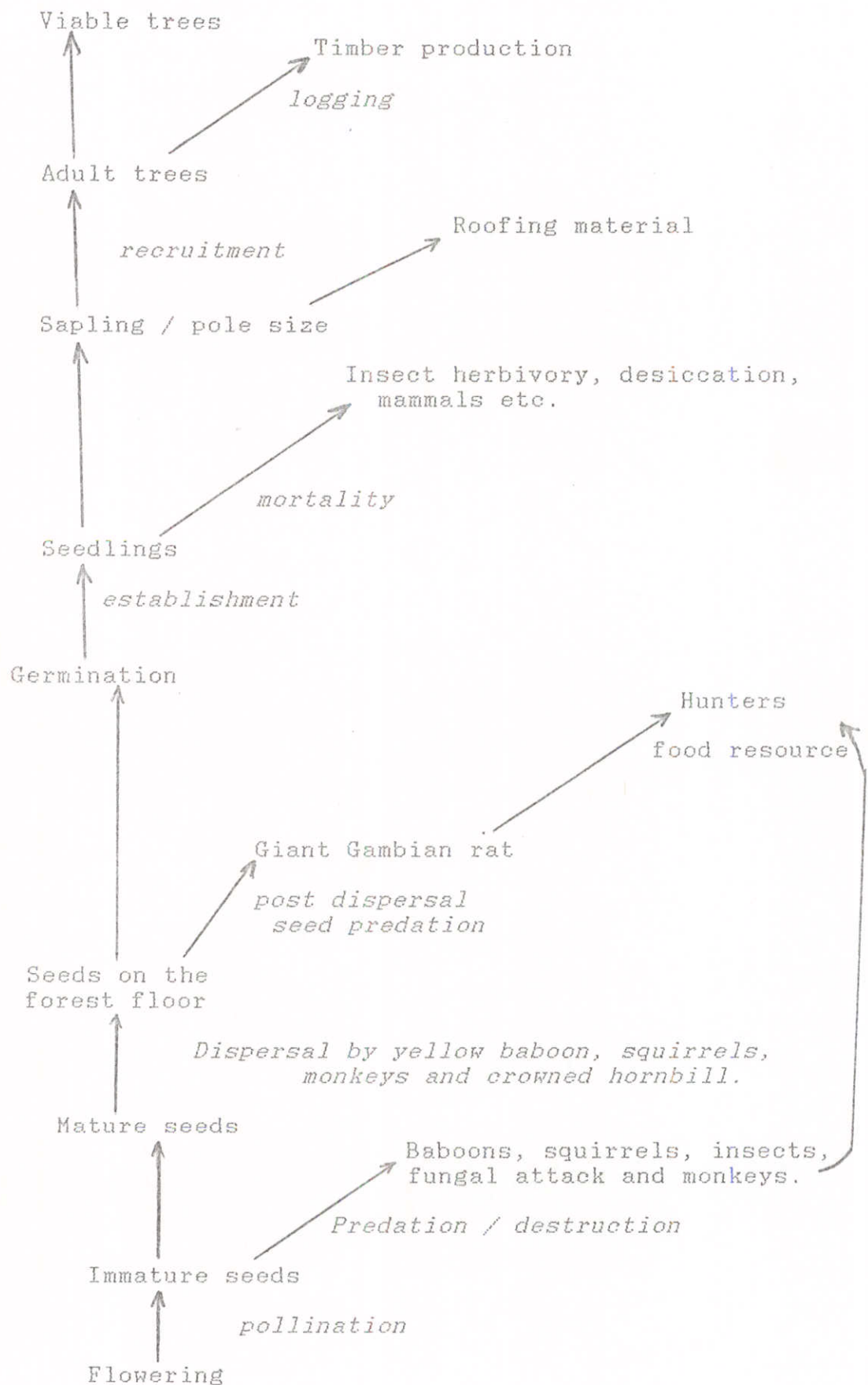
The explanation as to how C. gambianus manages to use seeds probably involves detoxification of the chemicals by enzymes. This rat might have evolved mechanisms that inhibit the toxins. Animals have been known to detoxify toxic materials and use them as food (Siegler 1979).

Dispersal of the seeds is essential because the tree is a coloniser, requiring an open range. For such areas to be reached then dispersers, like the yellow baboon and the white throated monkey, are essential in the life history of this tree species. Figure 13 summarises the general discussion.

5.2 Conservation implications.

Seasonality greatly affects organisms as they have to adapt to the changing conditions. Whole life history strategies are adapted to fit climatic patterns and especially reproduction (Begon and Mortimer 1986). One of

Figure 13. A summary of the direct interactions between animals and Afzelia quanzensis. Man is included because of logging and hunting activities.



these is the fruiting seasonality observed in trees of tropical forests. Seasonality influences the foraging behaviour and life histories of animals that depend on these trees (Fodgen 1972). Terborgh (1986) argues that vertebrate frugivores dominate most tropical forests and even show higher diversity than that of vertebrate herbivores. During the period of fruit and seed scarcity frugivores either migrate or modify their diets. Cords (1984) found that red-tailed and blue monkeys in Kakamega forest use different fruits over a year depending on which plant species have fruited. In Arabuko - Sokoke, a similar fruiting seasonality is evident (Fig. 7).

The seasonality in fruit production has the effect of concentrating fruit eaters on very few or even one tree species at a particular time of the year (Howe and Kerckhove 1979 and Terborgh 1986). For practical purposes those species providing an only food resource at a critical time will be termed as pivotal or keystone species as in Howe (1989) and Terborgh (1986). The pivotal tree species are not only important to animal species of that particular ecosystem but also to migrants.

A. quanzensis is an important tree in the Arabuko - Sokoke forest since it serves as a food resource for the red-legged sun squirrel for a large part of the year. After maturity, the giant gambian rat (C.gambianus) highly use those seeds. In summary A. quanzensis was found to be important to primates, rodents and insects that consumed different proportions of seeds or their parts.

Seasonality in the availability of food has the effect of maintaining animals, especially vertebrates, that act as

dispersers in an ecosystem. When fruits of one species are depleted, the mammals shift to another tree species which can be termed as prey switching.

The role of plant species is to maintain the dispersers in the ecosystem over the year or season. Chance extinction of one tree species will create a gap in food availability. Such critical food resources could cause the local extinction of frugivores that play important roles in the reproductive strategy of other trees at other times of the year. Thus, chains of extinctions are probable, especially at local levels.

People have used forest resources for long. The usage has become excessive after the commercialization of forest and wildlife resources. In the Arabuko - Sokoke forest A. quanzensis and Pleurostyliia africana are trees which are illegally logged for timber. Hunting for small mammals as a source of bush meat is evident. All holes of C. gambianus that were located had a snare at one time or another. Primates are also hunted for bush meat by the local people. Logging and hunting are likely to exterminate animals or plants, consequently increasing chances of local extinction of interdependent species. Unless management plans are drawn and implemented the situation is likely to worsen. Dispersal agents must be conserved otherwise some tree species will continue to be threatened. A. quanzensis requires primates for its survival as it is the only way its seeds can be moved effectively. The limited dispersal observed implies that this tree requires a long time scale to colonise favourable areas. This tree produces large

pods with large seeds and most of these seeds end up in the guts of rodents. If the tree is exploited to extinction, the population densities of these animals will fall or result in local extinction.

Conservation of natural resources would be sound if each ecosystem in the world is represented. In some cases management for restoring nature is essential. It is the detailed study of desired ecosystems that will result in the selection of representative areas. The refugia theory has been advocated as a first step to conserve those persistent areas. Such areas are believed to have higher biodiversity than their surroundings and can be termed as terrestrial habitat islands. Reserves selected in such areas will protect more species than those established elsewhere in the same biome (Deshmukh 1986).

The size of reserves is the next crucial aspect in conservation. This is an aspect of Island Biogeography theory (MacArthur and Wilson 1967, East and Williams 1984). The theory predicts that dynamic equilibria of species number is dependent on size of the area and distance from source of immigrants.

As mentioned earlier Arabuko - Sokoke forest is surrounded by an agricultural land use system. As such it persists like a forest island; ecologically isolated from other forests. Arabuko - Sokoke is a refugium which has persisted for thousands of years, and this has resulted in its selection as a conservation area. The question lies in the designation of the nature reserve to be protected in this forest. This is a political problem because the local people use almost the whole forest. Secondly, the forest

is under the management of forest department and commercial logging continues. There is, however, a nature reserve which covers about 40 km², which is supposed to be protected despite the illegal logging and hunting of desired species.

Restriction areas must be selected on an ecological basis, especially in a heterogeneous forest such as the Arabuko-Sokoke. This will have the effect of reducing chances of exploitation of critical areas. Rebuilding ecosystems is always more expensive than maintaining them. Conservation strategies should also consider other species using such areas in parts of their life history such as migrants.

The boundaries of the nature reserve in Arabuko - Sokoke are ecologically ill situated. First the lowland rain forest which covers 20 km² and inhabited by a lot of wildlife is not included within the proposed boundaries. The proposed boundaries can remain if the buffer zone is managed in a manner in which the ecosystem is not adversely affected. The buffer zone is meant to be a forestry area and there is a potential threat from illegal and legal logging which takes place in the buffer zone. Alternatively the whole of the Arabuko-Sokoke should be put under the national reserve policy of protected areas and sustainable utilisation can be implemented.

From the community ecologist point of view, the distribution of habitats in this forest makes it an ideal conservation area. The habitats are unique and rare elsewhere. Small reserves need to be managed intensively

and large ones are more economical than small ones. In that context, putting the whole of the Arabuko-Sokoke forest into a management plan would be easier than concentrating on the small nature reserve.

Recommendations

Based on the present knowledge of diversification of the Arabuko - Sokoke forest, it should be managed as one unit. The forest covers an area of about 400 km² of which 372 km² is indigenous. The forest is surrounded by human inhabited areas under agriculture and the forest is thus a terrestrial island.

In the Kenya wildlife policy (K.W.S. 1990) frame work, the Arabuko - Sokoke and Kakamega forests have been considered as conservation priority areas. Forests are poorly represented in the national park and reserve systems yet they have high biodiversity, especially of birds, small mammals, insects and flora. Conservation of such animals is important if the forest ecosystems are to remain stable.

The Arabuko-Sokoke forest has been considered a conservation area and its gazettelement as a National park is underway since June 1990. The area occupied by the forest formerly belonged to the local community. Today it is managed by the forest department, and a small portion to the north by the Kilifi county council. In such a situation political problems are inevitable when proposals for other land use policies are drawn.

The restriction of the local people from entering a forest they have traditionally used is a major problem. Talking to the local people one detects a high degree of

animosity to this situation. At the national level other government bodies have other plans for that forest. The county council on one hand has the right to allocate people the land, build schools or undertake other development projects in that forest patch it owns. The forest department may use the forest for timber exploitation or even silviculture. Glass manufacturing companies have carried out mining operations in the forest and there are plans to continue. All these activities have in effect reduced the forest, and especially, mining which took place in the lowland rain forest. The Arabuko - Sokoke forest includes the Mida creek where mangrove trees have been exploited for building poles and roofing materials.

The conservation plans for Arabuko - Sokoke forest should be compatible with other activities. In this kind of situation, a system in which the local people are benefiting is necessary since in the long run they are the guardians of the forest. K.W.S. views the forest as an area which can generate a lot of foreign exchange through tourism.

The following are some of the recommendations for conservation and sustainable utilization of the forest.

1. The forest has a great potential for tourism. As discussed in previous sections the forest is home to some endemic species. Interested visitors may be ornithologists, botanists and primatologists. Nocturnal life is also diverse with rodents, civets and owls being active at night. Dangerous animals are rare and risks are thus considerably reduced. This makes walking safe as risks are

considerably reduced and people without vehicles have a chance.

Today tourists to the forest enter free of charge. Charges should be introduced like in other national parks and a share of the revenue collected used to support community projects in the area. In this way a friendly environment can be created and in the long run this would stop the illegal utilization of the forest. The revenue would be used for health projects, water and schools.

2. The local people should be involved in the propagation of trees of commercial and traditional value. This in the long run would lead to a cessation of illegal logging in the forest. The forest management should start a silvicultural project where they supply to people seedlings at subsidized rates. Currently the forest supplies seedlings of Casaurina equisitifolia at subsidized rates. This tree is popular as a source of roofing material for hotels and has a short maturing period. The local people should be involved in the choice of the tree species they need for which purpose.

3. Non-commercial use of the forest resources should be controlled. Most people around the forest are hunters and use small mammals as a source of bush meat to supplement their protein intake. If such hunting were to be allowed, a detailed study on the biology of the desired animals should be carried out. Materials gathered in the forest without damage to the habitats should not be stopped. Fruits, vegetables and medicinal plants are widely collected in the forest and this should not be discontinued. Some activities such as debarking of trees for strings should be stopped

urgently. In the Kararacha, Paramacrolobium sp is affected while in the nature reserve Brachystegia sp. is exploited in this respect. Fuelwood can continue to be gathered from logging operations. The use of dead trees and branches for fuelwood may affect hole nesters. Thus it requires a detailed study to investigate what can be available to the people .

4. The forest has a great potential for timber and building materials. In the short term people can be given controlled access to the forest until alternative management plans are drawn. The logging of threatened species such as Afzelia, Pleurostylia and Brachylaena should be restricted. Selective logging for Brachystegia spiciformis, T. verrucosum and Manilkara sansibarensis, which occur in relatively pure stands and have good regeneration, can be carried out.

Pole size trees are in great demand as building materials and widely distributed shrubs like Polyathia stuhlmanii, Drypetes natalensis and D. reticulatus can be used. Today Terminalia bovinii and the mangrove forest are heavily used for this purpose, and this should be restricted. Recommendations 3 and 4 call for zonation of the forest, hence design. A strictly protected area should be set aside where no activities are allowed. This area will be surrounded by a buffer zone where local people will be having access.

In summary this study has brought to light the interactions of trees and animals in the Arabuko - Sokoke forest. The interactions are intricate and this study can

serve as a basis for other more detailed studies. The giant Gambian rat was found to be an important seed predator and more investigations of its biology and distribution should be conducted. Primates are the major dispersers of seeds in this forest and no research has been carried out on them in this forest. The forest living yellow baboon has not been widely researched on compared to their savanna dwelling counterparts. Studies should be carried out on the population structure and density of the endemic Ader's duiker in this forest. Community based studies on the use of the forest by local people should commence.

There are other conservation studies that commenced at the same time with this one and the pooled information would be vital for a management plan of Arabuko-Sokoke forest.

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APPENDICES

Appendix 1.

List of mammalian species recorded in Arabuko-Sokoke during the study.

S = sighted.

I = use of indices e.g. dung, footmarks, etc.

Common name	Scientific name	
Yellow baboon	<i>Papio cynocephalus</i>	S
White throated monkey	<i>Cercopithecus mitis albogularis</i>	S
Manda velvet monkey	<i>Cercopithecus aethiops</i>	S
Red legged sun squirrel	<i>Heliosciurus rufobrachium</i>	S
Red bush squirrel	<i>Paraxerus palliatus</i>	S
Giant Gambian rat	<i>Cricetomys gambianus</i>	S
Four-toed elephant shrew	<i>Petrodromus tetradactylus</i>	S
Golden-rumped elephant shrew	<i>Rhyncocyon chrysopygus</i>	S
African civet	<i>Viverra civetta</i>	I
Buffalo	<i>Syncerus caffer</i>	I
African elephant	<i>Loxodonta africana</i>	I
Bush baby	<i>Galago sp</i>	S
Ader's duiker ?	<i>Cephalophus adersi</i>	S
Sokoke Bushy-tailed Mongoose	<i>Bdeogale crassicauda omnivora</i>	S
Suni	<i>Neotragus moschatus</i>	S

Appendix 2.

List of plant species identified during
sampling.

Latin name	Local name
<i>Afzelia quanzensis</i>	Mbambakofi
<i>Strychnos deccusata</i>	Mkwakwa
<i>S. panganensis</i>	Girmacha
<i>Allophyllus previllei</i>	
<i>Securinega virosa</i>	Mkwamba
<i>Psydrax sp</i>	
<i>Annona sp.</i>	Muzambaran mwitu
<i>Rytygnia oligacantha</i>	
<i>Maytenus undata</i>	Muriakitu
<i>Boscia angustifolia</i>	Mlolombuzi
<i>Tarrena nigrens</i>	
<i>Asteranthe asterias</i>	
<i>Cassipourea euryoides</i>	
<i>Xylopiia arenaria</i>	Mbarawa mwitu
<i>X. parvifolia</i>	Mbarawa
<i>Canthium kilifiensis</i>	
<i>C. mombanzenve</i>	Bilcha
<i>Fagara chalybea</i>	Mdungu
<i>Teclea trichocarpa</i>	Mbirandu mtumwa
<i>Suregada zanzibarensis</i>	Mdimu mwitu
<i>Drypetes reticulatus</i>	Magadho, Mbagenambage
<i>D. natalensis</i>	Mwangandamwe

<i>Polyalthia stuhlmanii</i>	Mwanganjini
<i>Ximenia caffra</i>	Mtudu-kula
<i>Ochna mossambicensis</i>	mpamapama, mdahabu
<i>Dialium orientale</i>	Mpepeta, Mtsungwi
<i>Eleodendron schweinfurthiana</i>	Mhumwitu
<i>Haplocoelum inopleum</i>	Mfungatanzu
<i>Ludia mauritanus</i>	
<i>Stadmannia oppositifolia</i>	Mkipulu
<i>Alchornea laxiflora</i>	Mkuyu
<i>Salacia sp.</i>	
<i>Flacourtia indica</i>	Mdunga tundu
<i>Terminalia bovinii</i>	
<i>Lecaniodiscus fraxinifolius scassellatii</i>	Mberenga
<i>Euclea natalensis</i>	Mkipa
<i>Polysphaeria parvifolia</i>	Mangimangi
<i>Diospyros consolatae</i>	
<i>Carpodiptera africana</i>	Mjilore
<i>Paramacrolobium coeruleum</i>	Msahe
<i>Memecylon sansibaricum sansibaricum</i>	
<i>Ozoroa obovata</i>	Mkayukayu
<i>Eugenia sp</i>	
<i>Hunteria zeylanica</i>	
<i>Prema chrysoclasa</i>	Mvuma nyuki
<i>Pleurosyhia africana</i>	Mtangae
<i>Lannea schweinfurthii</i>	Mnyumbumwitu
<i>Tamarindus indica</i>	Mkwanju
<i>Trachylobium verrucosum</i>	Msandarusi
<i>Manilkara sansibarensis</i>	Mngambomaziwa
<i>M. sulcata</i>	Msedzi
<i>Mimusops fruticosa</i>	Mngambo kapehe

<i>Brachylaena hutchinsii</i>	Muhuhu, Muhugu
<i>Combretum schulmanii</i>	Mgurure
<i>Vitex payos</i>	Mfudu
<i>Cynometra webberi</i>	Mfuda
<i>Balanites wilsoniana</i>	Mkonga
<i>Grewia plagiophylla</i>	Mkone
<i>Euphorbia candelabrum</i>	
<i>Croton pseudopulchellus</i>	Myama
<i>Encephalatus hilderbrandtii</i>	Mkisapo
<i>Lonchocarpus sp.</i>	Msumari mbara

Appendix 3 a.

Data on predispersal seed predation in
1990/91 season. Ten focal trees were
sampled.

	Baboon	Monkey	Sun squirrel	Insects	Fungal attack	Unidentified rodent
	0	6	137	7	3	0
	104	2	25	1	4	0
	9	86	329	40	9	5
	89	0	10	0	3	0
	84	0	3	28	3	0
	97	5	25	12	8	0
	42	0	10	0	3	0
	25	0	53	1	1	0
	111	0	71	15	2	74
	0	3	22	4	6	0
Total	561	97	685	108	42	79

Appendix 3b.

Data on predispersal seed predation in
1988/90 season. Ten focal trees were
sampled.

	Baboon	Monkey	Sun squirrel	Insects	Fungal attack	Unidentified rodent
	16	0	16	-	-	0
	0	0	262	3	-	0
	14	0	132	4	0	0
	0	0	144	3	0	0
	3	0	91	-	0	0
	0	0	9	-	-	0
	0	0	84	0	0	0
	0	0	272	4	14	0
	14	0	172	0	1	7
	0	0	136	0	3	0
Total	47	0	1318	14	18	7

Appendix 3c.

Data on vertebrate seed dispersal.

Ten focal trees were sampled.

	Baboon	Monkey	Sun squirrel	Not assigned
	6	33	0	0
	42	119	4	96
	0	430	82	105
	0	31	0	27
	245	393	0	68
	42	102	19	251
	0	9	6	0
	0	150	16	39
	0	167	74	47
Total	335	1434	201	633

Appendix 3d.

Seed removal experiments (see text for explanation).

	Location of transects			
	Low land rain forest	<u>Afzelia</u> forest	<u>Brachystegia/</u> <u>Afzelia</u> ecotone	<u>Brachystegia</u> woodland
Dist. of seed station to tree base (M).				
0 - 5 under crown	15	15	15	4
10	15	15	8	9
20	12	15	8	5
30	15	10	15	0
40	15	9	12	9
50	13	10	13	9

Appendix 4a.

Number of seedlings classified by
diameter at the base.

Class interval (cm)	Number of seedling.
0 - 0.5	78
0.6 - 1.0	91
1.1 - 1.5	30
1.6 - 2.0	8
2.1 - 2.5	12
2.6 - 3.0	5
3.1 - 3.5	3
3.6 - 4.0	0
4.1 - 4.5	3
4.6 - 5.0	0
5.1 - 5.5	2
5.6 - 6.0	2

Appendix 4b.

Size class distribution of the adult
Afzelia quanzensis.

Class interval (cm)	Number of trees
6 - 10	0
11 - 15	2
16 - 20	2
21 - 25	8
26 - 30	10
31 - 35	14
36 - 40	13
41 - 45	7
46 - 50	16
51 - 55	6
56 - 60	1
61 - 65	4
66 - 70	2
71 - 75	5
76 - 80	1
81 - 85	1
86 - 90	2
91 - 95	0
96 - 100	1

Appendix 5.

The distribution of seedling with habitat.

<u>Brachystegia</u> Woodland	<u>Afzelia</u> Forest	Lowland Rain Forest
168	19	60

Appendix 6

Nearest neighbour distances of adult *A. quanzensis*.

Class Interval (M)	Number
5 - 10	11
10 - 15	11
15 - 20	4
20 - 25	12
25 - 30	8
30 - 35	0
35 - 40	2
40 - 45	1
45 - 50	1