

TESTING THE JANZEN-CONNELL MODEL FOR SPECIES DIVERSITY IN A WEST AFRICAN MONTANE FOREST.



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CONTENTS

CONTENTS.....	I
LIST OF FIGURES.....	IV
LIST OF TABLES.....	X
ABSTRACT.....	XIII
CHAPTER 1: BIODIVERSITY AND THE JANZEN-CONNELL HYPOTHESIS.....	1
1.0 GENERAL INTRODUCTION.....	1
1.1 PATTERNS IN BIODIVERSITY.....	2
1.2 THE PREDATION HYPOTHESIS.....	3
1.3 TROPICAL FORESTS AND THE JANZEN-CONNELL HYPOTHESIS.....	5
1.4 RESEARCH FINDINGS SINCE THE JANZEN-CONNELL HYPOTHESIS.....	10
1.5 TESTING THE JANZEN-CONNELL MODEL IN WEST AFRICA.....	15
1.6 OBJECTIVES OF THIS STUDY.....	15
CHAPTER 2: THE STUDY SITE AND STUDY SPECIES.....	17
2.0 THE STUDY SITE: NGEL NYAKI.....	17
2.1 NGEL NYAKI IN AN INTERNATIONAL CONTEXT.....	22
2.2 SPECIES USED FOR MEASURING SURVIVAL AND LEAF HERBIVORY OF NATURALLY OCCURRING SEEDLINGS AT INCREASING DISTANCES AWAY FROM CONSPECIFIC ADULT TREES.....	25
2.2.1 <i>Pouteria altissima</i>	25
2.2.2 <i>Newtonia buchananii</i>	27
2.2.3 <i>Isolona pleurocarpa</i>	29
2.3 SPECIES USED FOR MEASURING SURVIVAL AND LEAF HERBIVORY OF EXPERIMENTALLY PLANTED SEEDLINGS AT INCREASING DISTANCES AWAY FROM CONSPECIFIC ADULT TREES.....	31
2.3.1 <i>Entandrophragma angolense</i>	32
2.3.2 <i>Deinbollia pinnata</i>	34
2.3.3 <i>Sterculia setigera</i>	36

CHAPTER 3: TESTING THE HYPOTHESIS THAT SEEDLING SURVIVAL INCREASES WITH INCREASING DISTANCE AWAY FROM CONSPECIFIC ADULT TREES.....37

3.0 INTRODUCTION.....	37
3.1 METHODS.....	38
3.2 DATA ANALYSIS METHODS.....	40
3.3 RESULTS.....	41
3.4 DISCUSSION.....	46

CHAPTER 4: TESTING THE HYPOTHESIS THAT SEEDLING LEAF AREA LOST TO HERBIVORY DECREASES WITH INCREASING DISTANCE AWAY FROM CONSPECIFIC ADULT TREES.....52

4.0 INTRODUCTION.....	52
4.1 METHODS.....	53
4.2 DATA ANALYSIS METHODS.....	57
4.3 RESULTS.....	57
4.4 DISCUSSION.....	60

CHAPTER 5: TESTING WHETHER OR NOT SURVIVAL INCREASES AND HERBIVORY DECREASES WITH DISTANCE AWAY FROM CONSPECIFIC ADULT TREES FOR EXPERIMENTALLY PLANTED SEEDLINGS.....64

5.0 INTRODUCTION.....	64
5.1 METHODS.....	65
5.2 DATA ANALYSIS METHODS.....	69
5.2.1 Seedling survival.....	69
5.2.2 Seedling growth.....	70
5.2.3 Leaf herbivory.....	70
5.3 RESULTS.....	71
5.3.1 Seedling survival.....	71
5.3.2 Seedling growth.....	74
5.3.3 Leaf herbivory.....	77
5.4 DISCUSSION.....	79

CHAPTER 6: TESTING WHETHER OR NOT TREE SPECIES IN NGEL NYAKI SHOW CLUMPED DISTRIBUTIONS.....	83
6.0 INTRODUCTION.....	83
6.1 METHODS.....	84
6.2 DATA ANALYSIS METHODS.....	84
6.3 RESULTS.....	88
6.4 DISCUSSION.....	90
CHAPTER 7: GENERAL DISCUSSION AND CONCLUSION.....	93
7.1 GENERAL DISCUSSION.....	93
7.2 CONCLUSION.....	98
REFERENCES.....	100
APPENDIX.....	107

LIST OF FIGURES

Chapter 1.	Page
<p>1.1 Graphical representation of the Janzen-Connell model adapted from Krebs (2001). The amount of seeds dispersed per unit area decreases monotonically with distance from parent tree (curve (I)). The probability of seedling survival increases monotonically with distance from parent tree (curve (P)). The product of these two factors determines a recruitment curve that peaks at the distance from the parent at which a new adult is likely to appear (curve (PRC)).</p>	7
Chapter 2.	
<p>2.1 West Africa Maps: (A) Location of Nigeria in West Africa (adapted from: www.africa-expedition.com/rout_nigeria_fr.html), (B) Location of the Mambilla plateau in Nigeria (adapted from: http://hausamissions.org/Images/WestAfricaMap2.jpg), (C) Location of the Mambilla plateau in the Cameroon Highlands (adapted from Borrow & Demey 2001).</p>	19
<p>2.2 The Mambilla plateau and the location of Ngel Nyaki (3). Ngel Nyaki is situated north-west of Yelwa village (center).</p>	20
<p>2.3 The Afro-montane archipelago (shown as solid black areas). Adapted from (White 1983).</p>	24
<p>2.4 (left) - A clump of <i>Pouteria altissima</i> trees growing at the edge of the forest (photo by Arne Matthesius), (right) View of the trunk and root buttresses of <i>P. altissima</i> (photo from Chapman & Chapman (2001)).</p>	25

- 2.5** *Pouteria altissima* seedling (photo by Arne Matthesius). **26**
- 2.6** *Newtonia buchananii* at the forest edge (photo by Arne Matthesius). **27**
- 2.7** *Newtonia buchananii* seedling (photo by Arne Matthesius) (left).
Field assistant Usmanu Abubakar and a *Newtonia buchananii*
sapling (photo by Hazel Chapman) (right). **28**
- 2.8** *Isolona pleurocarpa* adult (left). *Isolona pleurocarpa* seedling
(right). (Photos by Arne Matthesius). **29**
- 2.9** *Isolona pleurocarpa* seed pod (photo by Hazel Chapman). **30**
- 2.10** *Entandrophragma angolense* (photos by Arne Matthesius). **32**
- 2.11** *Entandrophragma angolense* seed pod: (left) apex with seeds
still attached and inside pod, (right) Apex separated from pod
(photos by Arne Matthesius). **33**
- 2.12** *Deinbollia pinnata* (photo by Arne Matthesius). **34**
- 2.13** *Deinbollia pinnata* seedling (photo by Arne Matthesius) **35**
(left). *Deinbollia pinnata* seedling making a new leaf after
having all its leaves and a portion of its stem lost to herbivory
(Photo by Hazel Chapman) (right).
- 2.14** *Sterculia setigera* (photo by Gerd Matthesius). **36**

Chapter 3

- 3.1** Layout of plots for measuring seedling heights. At 0-5m, 5-10m and 10-15m plots were 5mx5m, at 15-20m they were 5mx10m and at 20-25m they were 5mx15m. **39**
- 3.2** *Pouteria altissima*: regression slopes of seedling abundance versus distance, for each height category, changed from being negative for smaller height categories to being positive for the larger height categories. **42**
- 3.3** *Newtonia buchananii*: regression slopes of seedling abundance versus distance, for each height category, changed from being negative for smaller height categories to being positive for the larger height categories. **43**
- 3.4** *Isolona pleurocarpa*: regression slopes of seedling abundance versus distance, for each height category, changed from being negative for smaller height categories to being positive for the larger height categories. **43**

Chapter 4

- 4.1** Layout of plots for seedling leaf herbivory measurements: **55**
There was one 5 x 5m plot at each distance interval: 0-5m, 5-10m, 10-15m, 15-20m, 20-25m.
- 4.2** Diagram depicting method for visually estimating total seedling leaf area lost to herbivory: Calculations were made roughly without the use of a calculator. As 1 entire leaf was lost (only the petiole **56**

remains) out of seven original leaves, approximately 15.0 % of total leaf area was lost through the loss of that leaf. Additionally, two leaves out of the seven original leaves suffered 30 % leaf area loss. Therefore, approximately 5 % of the total leaf area had been lost through the leaf area that had been lost by those two leaves. Therefore $\sim 5\%$ plus $\sim 15\%$ = $\sim 20\%$ of the seedlings total leaf area had been presumably lost to herbivory.

- 4.3** *Pouteria altissima* : regression plot of average percent seedling leaf herbivory in plots at each distance for twenty conspecific adult trees. The regression equation is: $y = -0.3015x + 36.372$ (P = 0.105) **58**
- 4.4** *Newtonia buchananii*: regression plot of average percent seedling leaf herbivory in plots at each distance for twenty conspecific adult trees. The regression equation is:
 $y = 0.0165x + 11.195$ (P = 0.884). **59**
- 4.5** *Isolona pleurocarpa* regression plot of average percent seedling leaf herbivory in plots at each distance for twenty conspecific adult trees. The regression equation is:
 $y = 0.0383x + 9.8367$ (P = 0.755). **60**

Chapter 5

- 5.1** Building of nurseries: (a) Clearing / leveling a space for a nursery just inside from the forest edge. (b) building grass walls. (c) Filling plastic bags with soil. d) a completed nursery. **67**
- 5.2** Experimental design for seedling plantings: Seedlings were planted in rows of ten at 1m, 12.5m and 25m away from conspecific adult trees. **68**

- 5.3** *Deinbollia pinnata*: average proportion of seedlings surviving each month for each distance from conspecific adult trees. **72**
- 5.4** *Sterculia setigera*: average proportion of seedlings surviving each month for each distance from conspecific adult trees. **73**
- 5.5** *Entandrophragma angolense*: average proportion of seedlings surviving each month for each distance from conspecific adult trees. **73**
- 5.6** *Sterculia setigera*: Average planted seedling height at each month at each distance from conspecific adult trees. **75**
- 5.7** *Deinbollia pinnata*: Average planted seedling height at each month at each distance from conspecific adult trees. **75**
- 5.8** *Entandrophragma angolense*: Average planted seedling height at each month at each distance from conspecific adult trees. **76**
- 5.9** Regression plot: mean *Sterculia setigera* seedling leaf area lost to herbivory for each replicate against distance from conspecific adults at month three. The regression equation is:
 $y = -2.963x + 44.262$ ($R^2 = 0.0146$). **77**
- 5.10** Regression plot: mean *Deinbollia pinnata* seedling leaf area lost to herbivory for each replicate against distance from conspecific adults at month three. The regression equation is:
 $y = -4.3342x + 34.403$ ($R^2 = 0.0865$). **78**

- 5.11** Regression plot: mean *Entandrophragma angolense* seedling leaf area lost to herbivory for each replicate against distance from conspecific adults at month three. The regression equation is:
 $y = -0.3767x + 67.624$ ($R^2 = 0.0006$). **78**

Chapter 6

- 6.1** Method used for measuring clumping: Focal trees were between 15m-25m apart. Focal trees species identities were determined, the distance to their nearest neighbour was measured and its species identity determined and the distance to that neighbours' nearest neighbour was also measured and its species identity determined. **86**
- 6.2** Position of transects in the forest along which clumping of tree species was measured **87**

LIST OF TABLES

Chapter 1	Page
<p>1.1 Results of studies testing the Janzen-Connell model: illustrating variability of the aspects investigated and the variability of results found.</p>	12
Chapter 3	
<p>3.1 The number of seedlings measured in all plots at each distance for each species: <i>Pouteria altissima</i>, <i>Newtonia buchananii</i> and <i>Isolona pleurocarpa</i>.</p>	41
<p>3.2 Results of the regression analyses on the number of <i>Pouteria altissima</i> seedlings / m² in each height category versus distance from conspecific adult trees.</p>	41
<p>3.3 Results of the regression analyses on the number of <i>Newtonia buchananii</i> seedlings / m² in each height category versus distance from conspecific adult trees.</p>	42
<p>3.4 Results of the regression analyses on the number of <i>Isolona pleurocarpa</i> seedlings / m² in each height category versus distance conspecific adult trees.</p>	42
<p>3.5 Analysis of covariance results: predicting Density (or number of seedlings / m²) from: Species, Distance, (log)Height category, Species*Distance, Species*(log)Height category, Distance*(log)Height category, Species*Distance*(log)Height category. Significant values are in bold.</p>	45

- 3.6** Number of seedlings observed in each height category at each distance from all conspecific adult trees. (a) *Pouteria altissima*, (b) *Newtonia buchananii*, (c) *Isolona pleurocarpa*. **47**

Chapter 4

- 4.1** Regression results: *Pouteria altissima* average percent seedling leaf herbivory in plots versus distance: 0-5m; 5-10m; 10-15m; 15m-20m; 20-25m away from each of twenty conspecific adults. **57**
- 4.2** Regression results: *Newtonia buchananii* average percent seedling leaf herbivory in plots at each distance: 0-5m; 5-10m; 10-15m; 15m-20m; 20-25m away from each of twenty conspecific adults. **58**
- 4.3** Regression results: *Isolona pleurocarpa* average percent seedling leaf herbivory in plots versus distance: 0-5m; 5-10m; 10-15m; 15m-20m; 20-25m away from each of twenty conspecific adults. **59**

Chapter 5

- 5.1** For each species $N_1 =$ Sum of replicates at each of three distances (one replicate is the mean of a seedling row); For each Distance $N_2 =$ sum of replicates for all three species (one replicate is the mean of a seedling row). **72**
- 5.2** ANOVA result: To test whether or not species, distance and/or species*distance explains a significant portion of variation in **74**

proportions of seedlings surviving among replicates at each distance from conspecific adult trees, for all three species at month three.

- 5.3** ANOVA result: To test whether or not species, distance and/or species*distance explains a significant portion of variation in mean seedling heights among replicates at each distance from conspecific adult trees, for all three species at month three. **76**
- 5.4** ANOVA result: To test whether or not species, distance and/or species*distance explains a significant portion of variation in leaf herbivory among replicates at each distance from conspecific adult trees, for all three species at month three. **79**

Chapter 6

- 6.1** Expected number of conspecific nearest neighbours for each species or species' group, the observed number and Chi square test results for a significant difference between the two values. Bold Chi square values are greater than the critical value. **89**

ABSTRACT

A major question in ecology is ‘why are tropical forests so species diverse?’ One hypothesis to explain tropical species diversity is the Janzen-Connell hypothesis. This model assumes high levels of host-specific seed and seedling predation and / or pathogen attack when seedlings occur at high density near to the parent tree; seedlings are more likely to survive and reach maturity the further they are away from parents / conspecific adults. Theoretically this should lead to a random distribution of each species in the forest, which in turn will lead to high species diversity. Here I test the Janzen-Connell hypothesis for the first time in a submontane dry forest in Nigeria, West Africa.

Specifically I tested whether or not a) leaf herbivory decreases and b) seedling survival increases with distance from parent / conspecific adult trees. These two components were tested separately on naturally occurring seedlings and on experimentally planted seedlings. I also tested whether or not conspecific adult trees showed clumped distributions by testing if conspecific nearest neighbours were observed more often than would be expected by chance alone.

Naturally occurring seedlings of three species, *Pouteria altissima*, *Newtonia buchananii* and *Isolona pleurocarpa* showed significantly greater survival at distances away from parent / conspecific adult trees. Two out of a total of three species (*Entandrophragma angolense*, *Deinbollia pinnata* and *Sterculia pinnata*) of experimentally planted seedlings showed increased survival at distances away from conspecific adult trees, but this trend was non-significant. Leaf herbivory decreased with distance from parent / conspecific adult trees for four out of a total of six study species, but all relationships of leaf herbivory with distance for these six species were non-significant. Of two individual species, *Anthonotha noldeae* and *Carapa procera*, and two species groups tested for clumping, all had a greater number of conspecific nearest neighbours than would be expected to occur by chance alone, and this was significant for the two species groups. The decreased survival of seedlings under parent / conspecific adult trees is likely to maintain tree species diversity in West African submontane forests as predicted by the Janzen-Connell model. The role of host specific seedling herbivores in reducing recruitment under parent / conspecific adult trees requires further investigation. Although conspecific adults showed some

degree of clumping no conclusion was reached as to whether this was evidence for or against the Janzen-Connell model.

CHAPTER 1: PATTERNS IN BIODIVERSITY AND THE JANZEN-CONNELL HYPOTHESIS.

1.0 GENERAL INTRODUCTION

A major question in ecology is ‘why are tropical forests so species diverse?’ (Terborgh *et al.* 2002). Tropical forests are renowned for having hundreds of tree species recorded from within a single hectare (Condit *et al.* 2005; Leigh *et al.* 2004). One hypothesis which tries to explain tropical species diversity is the Janzen-Connell hypothesis. Developed independently by Janzen in 1970 and Connell in 1971, this hypothesis assumes high levels of host-specific seed predation when seeds occur in areas of high seed density near to the parent tree. Seedlings are more likely to survive and reach maturity at some distance away from parent / conspecific adult trees (Figure 1.1). Theoretically this should lead to a random distribution of each species in the forest, which in turn will lead to high species diversity.

The Janzen–Connell hypothesis has been tested over 70 times (*Pers. obs.*; Cintra 1997), but almost always in the Neotropics, such as Panama (Condit *et al.* 1992; Hubbell *et al.* 1990 *as cited in* Peters 2003; De Steven & Putz 1984; Augspurger 1983; Wright 1983 *as cited in* Clark & Clark 1984; Harms *et al.* 2000; Wills *et al.* 1997; Gilbert *et al.* 1994; Schupp 1992) or Costa Rica (Boucher 1981; Hubbell 1979; Silander 1978; Howe 1977; Vandemeer 1977; Janzen *et al.* 1976; Howe & Primack 1975; Janzen 1975, 1972, 1971, 1970; Wilson & Janzen 1972 *as cited in* Clark & Clark 1984), but also in Mexico (Burkey 1994) and Amazonian forests (Romo *et al.* 2004; Wyatt & Silman 2004; Terborgh *et al.* 2001; Cintra 1997). The Janzen –Connell hypothesis has been tested at a number of other locations in the tropics, such as in the lowland Asian forests of Malaysia (Okuda *et al.* 1997) and Borneo (Stoll & Newbury 2005; Webb & Peart 1999), French Guyana (Hammond & Brown 1998) and northern Australia (Connell 1971). While African forests are known to have less species than other tropical areas (Condit *et al.* 2005), they are still diverse relative to temperate forests. Yet no tests of the Janzen-

Connell hypothesis to my knowledge have been carried out in Africa, and certainly never in a dry African montane / submontane forest.

1.1 PATTERNS IN BIODIVERSITY.

Biodiversity can be viewed at several different levels of organisation ranging from genes to ecosystems (Gaston 2000). Although a number of different approaches to measuring biodiversity exist (Krebs 2001, Gaston 2000), most analyses of the patterns in biodiversity involve measuring diversity as the number of species observed, or estimated to occur, in a specified area (Condit *et al.* 2005; Gaston 2000).

Since the beginning of the 18th Century biologists have recognised that many different patterns of species diversity exist (Ricklefs 2004; Hawkins 2001). Of particular importance have been the patterns that relate species diversity to historical / evolutionary processes, area, latitude, habitat productivity and isolation on islands or peninsulas (Ricklefs 2004). These patterns have stimulated a large number of hypotheses which try and explain them (Ricklefs 2004, Hawkins 2001). However many of these hypotheses cannot be rejected with the available data (Ricklefs 2004), and faced with the likelihood that many different processes simultaneously influence patterns of diversity (Ricklefs 2004; Rohde 1992), biologists understandably hold divergent views on this issue.

While much research has been conducted in order to determine the significance and mechanisms behind many patterns in species diversity, latitudinal gradients are probably the most studied pattern of diversity described by ecologists (Hawkins 2001). Latitudinal gradients have been a feature of diversity for more than 100 million years (Rosenzweig 1995) and are one of the most universal features of nature (Rohde 1998).

Most terrestrial and freshwater groups are more speciose in tropical than temperate regions (Gaston 2000). For example (Krebs 2001) reported that 830 tree species were found in a 50-ha plot of tropical rain forest in Malaysia and a 6.6-ha area in Sarawak contained 711 species of trees. In comparison to these tropical areas, a deciduous forest in

Michigan contained 10 to 15 species on a plot of 2 hectares, and the whole of Europe north of the Alps has 50 tree species. Likewise there is typically more diversity at low altitudes than at high, and in forests than in deserts. However not all groups of organisms are distributed in this way (Gaston 2000), and a number of obscurities to this pattern exist, such as that declines in richness with latitude may be faster in the Northern than in the Southern Hemisphere, and that peaks in richness may not lie actually on the equator but some distance away from it (Gaston 2000).

The number of hypotheses trying to explain why tropical biomes rather than temperate biomes often have the highest species diversity is increasing rapidly, with over 30 hypotheses in the literature and new ones appearing almost annually (Hawkins 2001). Despite intense discussion scientists have not yet been able to agree on an explanation for latitudinal gradients in species diversity and they remain a puzzling phenomenon (Ricklefs 2004; Rohde 1992).

1.1 THE PREDATION HYPOTHESIS

Prior to c. 1960, most ideas about diversity were founded in history and geography (Ricklefs 2004). For example Willis (1922) suggested that a plant or animal species' age was a major determinant of its current global distribution, because older species had had a longer time to expand into habitats that were suitable to them. Later Fischer (1960) described the general belief at the time that gradients in diversity were related to gradients in environmental factors (e.g. temperature, humidity, salinity), which could be developed on a regional or local scale, on land or in water.

During the 1960s a long tradition of population biology that had begun in the 1920s was unified with the field of biogeography (MacArthur 1965, 1972 *as cited in* Ricklefs 2004). This unification saw the rise of new theories which maintained that species membership within ecological communities was limited by interactions among species such as competition, predation, and mutualism (Ricklefs 2004).

Robert Paine (1966), in his paper on food web complexity and species diversity formulated a hypothesis which stated that: “*species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species.*”

To test his hypothesis Paine (1966) compared the effect of removing the top predators from three different communities of rocky inter-tidal marine organisms. Removing the predators had the same effect on all three communities; with predator removal there was a disproportionate loss of species diversity (Paine 1966). This appeared to happen when the predators were effective in limiting the population sizes of particular prey species (Paine 1966). Once the predator was artificially removed the population sizes of these particular prey species increased dramatically, until they became the dominant species in the community (Paine 1966). Moreover as the particular prey species expanded in their population sizes it was found to cause the extinction of a number of other prey species through inter-specific competition (Paine 1966). However, even more species are lost after predator removal than is predicted due to inter-specific competition alone, which is probably because predator removal causes indirect effects to reverberate through the food web which are detrimental to one or more additional species in the community.

In other words, by holding the numbers of the aforementioned type of prey species' in check, predators keep space open in which a number of other species can establish themselves.

Early observations revealed that there was a disproportionate increase in the number of predators accompanying regional increases in animal diversity (Hiatt & Strasburg 1960; Grice & Hart 1962; Bakus 1964 *as cited in* Paine 1966), These observations lead Paine (1966) to extend his hypothesis and propose that species diversity was highest in the tropics because of the disproportionately higher number of predators that are present there than elsewhere.

Paine's (1966) predation hypothesis was later applied by Barbehenn in 1969 to interactions of tropical mammals with their predators and parasites and by Lowe-McConnell in 1969 to tropical fishes. McArthur (1969) generalized the system for vertebrates that prey on other animals in tropical communities.

1.3 TROPICAL FORESTS AND THE JANZEN-CONNELL HYPOTHESIS.

Studies during the 1950's and 1960's revealed that wet lowland tropical forests characteristically have many tree species, with low densities of adults of each species spread out in a regular pattern in the forest. This characteristic structure is quite different to that of temperate zone forests of similar aerial extent, topographic diversity and edaphic complexity (Janzen 1970).

These observations led Daniel H. Janzen (1970) to extend Paine's (1960) predation hypothesis to the plant community. Janzen (1970) formulated a model where the activity of host specific seed and seedling predators and pathogens was used to explain the high diversity and characteristic tree species' distributions of lowland tropical forests. Janzen distinguished between two different types of predator that he believed were responsible. The first type he termed "distance-responsive" predators, which are commonly parasites on adult trees but predators on their seedlings. This is because seedlings cannot withstand the loss of leaves and shoot tips to the same degree that their parent trees can (Janzen 1970). Janzen termed the second group of predators "density-responsive" predators. He defined the probability of a juvenile plant being eaten by a density-responsive predator as being primarily a function of the ecological distance between that juvenile and other juvenile plants of the same species (Janzen 1970). Regardless of the mode of seed dispersal, the amount of any species' seeds landing in an area declines monotonically with increasing distance from parent trees (Figure 1.1) (Janzen 1970). Thus, the densities of seeds and young seedlings of any given species are highest in the immediate vicinity of their respective parent trees (Janzen 1970).

Therefore, the activities of both distance responsive and density responsive host specific predators are centered on areas that surround the parent trees of their host species.

The activities of both these types of predators cause seeds and seedlings that are in the immediate vicinity of their parent tree to have the lowest chance of surviving and becoming mature adult trees (Janzen 1970). Hypothetically this frees up the space surrounding parent trees from their own seedlings, which is then available for colonization by non-conspecific seedlings (Janzen 1970). This would explain why most adults of a given lowland tropical tree species appear to be more regularly distributed than if the probability of a new adult appearing at a point in the forest were proportional to the number of seeds arriving at that point (Janzen 1970). Also, as in Paine's (1966) predation hypothesis, it would prevent any one species from becoming common enough as to outcompete one, or a number of other species, and thereby maintains the high tree species diversity of these forests (Janzen 1970).

Although Janzen distinguishes between the two different types of host specific predators, he does explain that many predators on seeds and seedlings can act in both a distance- or density-responsive manner, depending (among other factors) on season, availability of alternate foods, and relative density of juvenile plants (Janzen 1970). Despite this, he found it useful to make this distinction because in his model he expects the two predator types to interact differently with variable seed crop size and the mode of seed dispersal of their host. Janzen's model consists of three different curves (see Figure 1.1):

The "seed shadow" (seeds per unit area) curve (I), is a monotonically decreasing function of distance from parent tree.

The per capita chance of seed survival to maturity (P) is a monotonically increasing function of distance from the parent tree.

The product of the I and P curves yields the "population recruitment curve" (PRC), which describes the density of offspring which survive to maturity at different distances from the parent tree (see Figure 1.1).

Janzen's model graphically describes how the shape of PRC curve changes with:

- (i) Average seed crop size
- (ii) Different modes of seed dispersal
- (iii) The nature of seed / seedling predators

Taking these factors into account Janzen predicted that collectively, all the adults of a tree species in the forest will generate a probability recruitment "surface". The surface is lowest around parent trees and conspecific adult trees in close proximity to each other. These will share their predators, and recruitment will be low in the area between them,

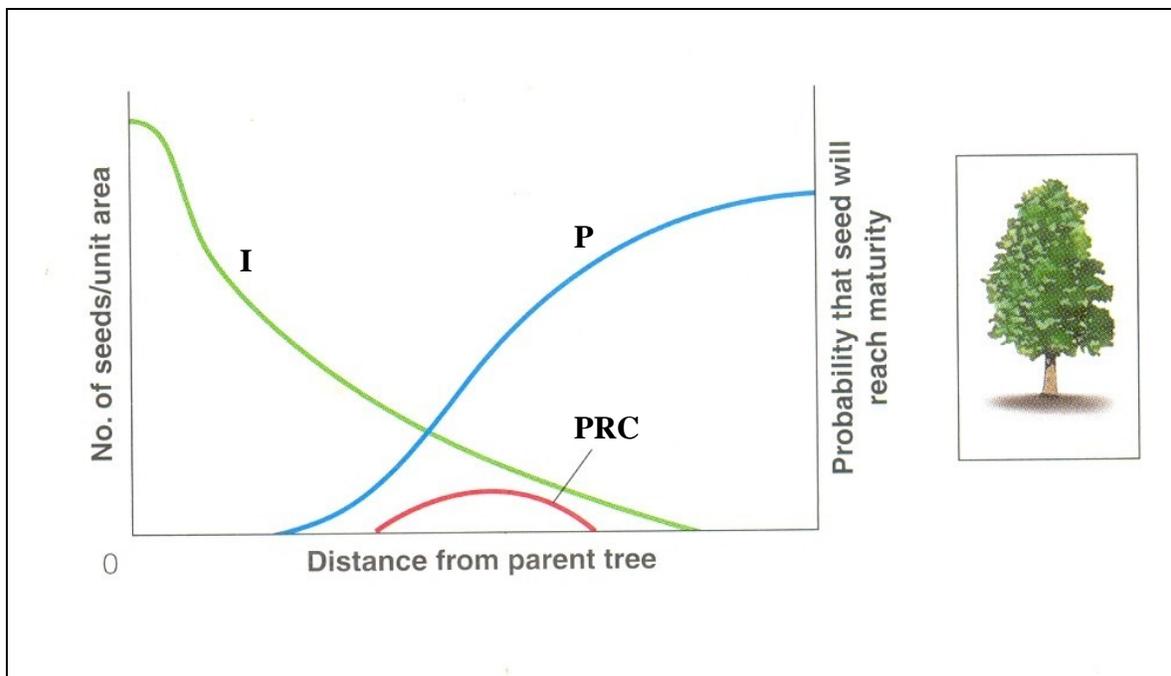


Figure 1.1 Graphical representation of the Janzen-Connell model adapted from Krebs (2001). The amount of seeds dispersed per unit area decreases monotonically with distance from parent tree (curve (I)). The probability of seedling survival increases monotonically with distance from parent tree (curve (P)). The product of these two factors determines a recruitment curve that peaks at the distance from the parent at which a new adult is likely to appear (curve (PRC)).

but at greater distances where their seed shadows overlap recruitment will be high. The PRC curves calculated for individual parent trees is an intersection of the high crater rims in the “surface” that surround adult trees where high seed density and probability of seed survival are simultaneously optimized. Janzen explains a number of instances in which the shape of this surface will be disturbed (Janzen 1970). Importantly, many tropical tree species fruit at intervals of two or more years, and adults will often synchronize their reproductive efforts (Janzen 1976). These “mast seeding” events produce such high densities of seeds that the seed predators are satiated, also by seeds being unavailable in the intervening years populations of obligatorily host specific predators will be so low by the time the mast seeding trees fruit that the predator populations often may not be able to grow rapidly enough to consume all the seeds (Janzen 1970, 1976). Thus, seeds will escape predation and may become established in the vicinity of their parents (Janzen 1970, 1976). Another important situation where seeds may escape predation is during situations when environmental or other conditions adversely affect the host specific seed / seedling predators (Janzen 1970). Janzen further describes a number of other factors which would make it difficult to detect the seed / seedling distributions as predicted by the model, when conducting research in modern day forests (Janzen 1970)

Shortly after Janzen (1970) published his model Joseph Connell (1971) independently published a paper in which he put forward a very similar hypothesis, in that species distribution was governed by predators. However despite the similarities, Connell (1971) argued that the distance / density dependant effects of seed predators, as described by Janzen (1970), were not important in maintaining the high tree species diversity of tropical rain forests and that the mortality which is proposed to maintain this diversity occurs mainly after germination during the seedling and sapling stages (Connell 1971). Connell based his argument on the findings of research from two rain forests in northern Australia which he undertook with J. G. Tracey and L. J. Webb (Connell 1971). They placed seeds under conspecific and non conspecific adult trees at a density of 100 seeds

per m², and at a low density comparison at 1 seed per meter along a transect line through the forest (Connell 1970). They found that after one year almost every seed was killed, and therefore concluded that most seeds are killed most of the time regardless of their position or density (Connell 1971). Based on previous studies by himself, and independently by a number of other scientists on the interactions between predators and their prey Connell concluded that seeds will only escape predation when, for some reason, their predator populations are reduced (Connell 1971). Connell believed that seedlings which do manage to establish themselves in the immediate vicinity of their parent trees will be adversely affected by the heavy shade of their parent trees, their growth will be suppressed by the shade and they will eventually succumb to the attack insects and other enemies which come from the parent tree itself or the soil below it (Connell 1971). By causing high mortality of seedlings under their host adult trees Connell believed that the host specific seedling herbivores maintained tree species diversity in the same manner as described by Janzen (1970). In his paper Connell focused on describing the conditions which may reduce or improve the effectiveness of host specific seed / seedling predators in maintaining tropical tree species diversity (Connell 1971). The results of Connell's studies and those of other workers too (Landenberger (1969); Paine (1966); DeBach *et al.* (1955); Lord & MacPhee (1953); Michelbacher & Leighly (1940) *as cited in* Connell (1971)), indicated that fluctuations in the physical environment appear to reduce the degree of host specificity of predators and their abilities in reducing the numbers of their prey (Connell 1971). Results of these studies showed that prey populations were less vulnerable to, and better able to recover from, extreme fluctuations in weather than their predators (Connell 1971). This meant that extreme fluctuations in weather would allow seedlings to escape predation under parent / conspecific adult trees and be able to reach an age where they can tolerate the attack of herbivorous insects and therefore gain a greatly increased chance for survival (Connell 1971). The problem with this argument was that the seed / seedling predators would then also be released from their predators. Therefore they would probably also increase in numbers, which meant extreme fluctuations in weather theoretically would have little overall effect on seedling's chances of escaping predation (Connell 1971). There was

however sufficient evidence to suggest that species nearer the ‘top’ of food webs tend to be less specialized in their choice of food (Paine 1963, 1966; Brues 1946 *as cited in* Connell 1971). Other research showed that insects, which are low trophic level predators, are generally responsible for attacking seeds and seedlings (Janzen 1970; Connell 1971). Assuming that these low trophic level, specialized, predators are better at reducing the numbers of their prey than generalists, Connell was able to validate his hypothesis (Connell 1971). Connell further theorized that irregular or unpredictable fluctuations in the physical environment may cause such unpredictable variations in the supply of some critical resource, such as the number of a species of prey, that predators cannot afford to become specialized on their prey (Connell 1970). As conditions are generally more stable in the tropics than in temperate climates Connell proposed that predators should be more specialized in the tropics and better able to keep their prey populations in check because they are not subjected to as many extreme fluctuations in weather (Connell 1971). Therefore in agreement with Janzen (1970) Connell proposed that host specific seed and seedling predators are largely responsible for maintaining the high tree species diversity found in tropical rain forests (Connell 1971).

1.4 RESEARCH FINDINGS SINCE THE JANZEN-CONNELL HYPOTHESIS.

Over the past 35 years a vast array of studies have been conducted by a large number of different authors whom have taken numerous different approaches to testing the complex set of assumptions, predictions and hypotheses generated by the Janzen-Connell model (Schupp 1992; Connell 1971; Janzen 1970), but results have been highly variable (Adler & Muller-Landau 2005; Romo *et al.* 2004; Wyatt & Silman 2004; Hyatt *et al.* 2003; Wright 2002; Hammond & Brown 1996; Burkey 1994; Terborgh 1993; Schupp 1992; Clark & Clark 1984) (see Table 1.1).

A meta-analysis on the results of a large number of these studies was conducted by (Hyatt *et al.* 2003). They found no general support for the Janzen-Connell model among

these studies and concluded that further testing of the Janzen-Connell model was unnecessary (Hyatt *et al.* 2003). However the high variation and non-significant effects they found would be expected by realizing that part of the variability in these results may be due to authors not having carefully adhered to the predictions and assumptions of the Janzen-Connell model (Hammond & Brown 1996; Clark & Clark 1984).

Table 1.1 Results of studies testing the Janzen-Connell model, illustrating variability of the aspects investigated and the variability of results found				
Author (s)	Date range	Number of references	Aspect	Proportion of studies which support the Janzen-Connell model.
Romo <i>et al.</i> (2004)	1992- 2002	17 29 independent test cases, since some authors analyzed several plant species seperately.	Density-dependant seed predation by rodents.	7, (possibly 8), of 29 studies supported the Janzen-Connell model.
Hammond & Brown (1996)	1971- 1996	46 independently studied tree species.	Comparison between insect and vertebrate predators for supporting distance/ density predictions of the model.	15/19 insect support. 2/27 vertebrate support. 17/46 of the studies supported Janzen-Connell model.
Burkey (1994)	1972- 1992	19 papers.	list of papers that theoretically or empirically support or do not support the Janzen-Connell hypothesis.	1/2 theoretically support. 11/17 empirically support.
Clark & Clark (1984)	1970- 1984	24 studies.	Number of studies of tropical woody plants consistant or inconsistant with: Density dependant mortality; Distance dependant mortality; Minimum critical distance.	Density dependant mortality - 7-8 out of 24 support. Distance dependant mortality - 8-15 out of 24 support. Minimum critical distance - 4-7 out of 24 support.

Many studies have been restricted to very few adults for a brief period of time and at single stages in the life cycle of trees (Harms *et al.* 2000; Clark & Clark 1984). This is likely to cause variability in results because a lack of Janzen-Connell spacing at one stage in the life cycle could be followed by pronounced spacing through mortality at a later stage in the life cycle (Harms *et al.* 2000; Clark & Clark 1984). In addition, studies carried out over a short time would not detect which cohorts have previously escaped predation through mast seeding events (Janzen 1970, 1976) or when escape happened after environmental conditions had adversely affected their predators (Connell 1971; Janzen 1970).

Studies have focused on a large variety of different seed / seedling predators but in general, many insects and some pathogens, but very few mammals and other vertebrates preferentially attack seeds or seedlings near conspecific adults (Leigh *et al.* 2004, Hammond & Brown 1996)

A lack of attention has been paid to the important role that light availability might play in determining the outcome of seed / seedling attack (Hammond & Brown 1996). An increase in light availability can ‘buffer’ the effects of attack by invertebrates leading to establishment where normally under low light conditions there would be mortality (Hammond & Brown 1996; Augspurger 1984).

A large portion of tests conducted on the Janzen-Connell model had been conducted prior to 1984 (Cintra 1997), which were summarized by Clark & Clark (1984) (Table 1.1), but the importance of light availability as a source of variability in the results was only realized after these studies had been conducted (Augspurger 1984). Also realized after these tests were conducted were the effects of testing the model over short time spans (Harms *et al.* 2000; Clark & Clark 1984), and more recently the different results from vertebrate versus insect seed and seedling predators (Hammond & Brown 1996). In addition, allelopathy (Wright 2002), higher frequency of destructive litterfall (Molofsky & Augspurger 1992) and local depletion of critical nutrients around the adult trees’ root zone, or particularly effective shading by the adult crown, could produce apparent

distance- or density- dependant progeny mortality, because due to those factors mortality is higher under adult crowns and low away from them (Clark & Clark 1984).

These examples are not an exhaustive list of the developments that have been made in discovering the sources of variation in results of tests of the Janzen-Connell model, but this variation, and thus the conclusion of the meta-analysis by Hyatt (2003), is blinded by the fact that various sources of variation in these test results have come to light over time. It is obvious that due to time limitations and practicalities it is not possible to account for all these sources of variation when conducting tests of the Janzen-Connell model. It is therefore important to take these factors into account when interpreting the results of such tests.

It has recently been discovered that the structure of tropical lowland forests as described by Janzen (1970) appears to be an incorrect description, data from intensively studied forests indicate that species distributions are better described by random or clumped models than uniform ones (Hyatt *et al.* 2003).

However, this pattern may not be contradictory to the Janzen-Connell hypothesis because true tests of the Janzen-Connell hypothesis do not rely on static analyses of the spatial distribution of entire species or even juveniles with respect to distance from conspecific adults, but rather look at the changes in the degree of clumping over time, compared to the initial distribution of seeds and seedlings (Gilbert 2002).

The phenomenon of enhanced propagule survival with distance from the parent may be important for the population biology of particular species, but it is not a general phenomenon across communities, life history stages or life forms (Hyatt *et al.* 2003). Negative effects on growth and survival are particularly likely to reinforce one another over longer time intervals, and the eventual reduction in recruitment near conspecific adults may be much greater than is now appreciated (Wright 2002).

Most tests of the model have been conducted in tropical forests (Gilbert 2002), but a few have been conducted in temperate regions (Lambers *et al.* 2002; Packer & Clay 2000).

There is now strong evidence that Janzen-Connell effects may play a part in structuring temperate forests as well (Lambers *et al.* 2002; Packer & Clay 2000). It has been suggested that further research in a variety of forests at different latitudinal / altitudinal locations may reveal that Janzen-Connell effects are important for the structuring of a number of different forest types (Gilbert 2002).

1.5 TESTING THE JANZEN-CONNELL MODEL IN WEST AFRICA.

This study aims to test whether the Janzen–Connell model applies in an Afro-Montane forest in the Taraba State, Nigeria (Figure 2.1). As of yet no tests of the Janzen-Connell model have been conducted in an Afro-Montane forest. Therefore this study aims to contribute knowledge to the generality of the Janzen-Connell hypothesis across different forest types.

Studies by Chapman & Chapman (1995) in East African forests showed that up to 60 percent of tree species studied suffered reduced recruitment in the vicinity of their parent trees. Further studies by Chapman (1996), showed the importance of primate seed dispersers, and that hunting and destruction of their habitat may have serious consequences for tree species recruitment. Chapman (1996) also found high variation in the amount of seeds dispersed for different tree species and pointed out that it was unknown how this may affect forest structure. These two studies were the closest I could find in Africa to the testing of the Janzen-Connell hypothesis.

1.6 OBJECTIVES OF THIS STUDY

The objective of the research was to examine whether the Janzen-Connell model applies in an Afro-montane forest in Nigeria. The following 3 hypotheses that are expected to be true according to the Janzen- Connell hypothesis were tested:

- 1) Seedling survival increases with distance from conspecific adult trees.**

- 2) Seedling leaf herbivory decreases with distance from conspecific adult trees.**

These two hypotheses were tested on:

- (i) Naturally occurring seedlings: (Chapter 3 – seedling survival) and (Chapter 4 – seedling leaf area lost to herbivory).
- (ii) Experimentally planted seedlings (Chapter 5).

- 3) There is little clumping of tree species, there should be low densities of adults of each tree species and they should be spread out in a regular pattern in the forest.**

Hypothesis 3 is tested in Chapter 6.

CHAPTER 2: THE STUDY SITE AND STUDY SPECIES.

2.0 THE STUDY SITE: NGEL NYAKI.

My study site, Ngel Nyaki Forest Reserve, is an approximately 7.2km² stand of submontane dry forest on the Mambilla plateau, on the Nigerian Cameroon border (Figure 2.1), approximately 45 minutes walk north-west of Yelwa village (Figure 2.2). The forest lies on a steep southwest facing slope of an ancient volcano, and is between 1400-1600masl.

Geology and climate

The part of Mambilla plateau where Ngel Nyaki is located is volcanic, and is described by (Chapman & Chapman 2001) as a dissected lava upland. The volcanic soils of Ngel Nyaki have a pH of 6 – 6.5, they have a high clay content and base exchange capacity, also, they have a relatively high nutrient status although they are strongly leached, and they are quite able to retain moisture (Chapman & Chapman 2001). Annual burning and overgrazing of the surrounding grassland reduces vegetative cover and further increases leaching of the soils and the frequency of gullyng and landslips (Chapman & Chapman 2001).

The region experiences distinct wet and dry seasons. The dry season runs from November to March with the first storms arriving in early April. Mean annual rainfall exceeds 1780mm with little to no rain falling in the dry season (Chapman & Chapman 2001).

Evidence suggests that the Mambilla plateau once had an extensive forest cover (Chapman & Chapman 2001), which by the 1980's had been reduced to overgrazed tussock grassland with scattered fragments of forest (Dowsett-Lemaire 1989). Today Ngel Nyaki is the only forest of more than 2ha² that remains on the plateau (*pers. comm.* with Hazel Chapman), with almost all the streamside fragments being destroyed for firewood and farming. Ngel Nyaki survives because it was designated as a forest reserve in the 1969, and was well protected from poaching, burning and grazing until the 1980's (*pers. comm.* with Hazel Chapman). Since then, because of a lack of

patrolling as a consequence of salaries not being paid, there have been attempts at farming within the reserve, and cattle grazing is a major problem. Hunting pressure has increased dramatically since the 1970s (Chapman *et al.* 2004), although at Ngel Nyaki this is now much more under control because of the presence of researchers.

More extensive areas of montane forest similar in species composition to Ngel Nyaki, occur approximately 60km east of the study site in the Gotel Mountains (Figure 2.2). These forests are offered some protection because they are in Gashaka-Gumti National Park and because they are extremely remote (Dowsett-Lemaire 1989; Chapman & Chapman 2001).

Physiognomy

The forest vegetation at Ngel Nyaki has four distinct layers *sensu* Richards (1952): A (emergent species to 40 m in height); B (trees to 30 m); C (trees to 13 m); D (understory shrubs and seedlings) (Chapman & Chapman 2001). There are three principle emergent species in Ngel Nyaki forest: *Pouteria altissima* (Sapotaceae), *Entandrophragma angolense* (Meliaceae) and *Newtonia buchananii* (Leguminosae-Mimosoidae) (Dowsett-Lemaire 1989). All three emergent species were included as study species in this project. A small proportion of tree species make up the B storey, but the vast majority of tree species comprise the C storey (8-13 m tall). The three remaining study species used in this project, *Isolona pleurocarpa* (Annonaceae), *Deinbollia pinnata* (Sapindaceae) and *Sterculia setigera* (Sterculiaceae), belong to the tree species that make up the B and C layers. There is no clear division between the third tree story and the shrub layer which includes tree seedlings, shrubs and very small trees (Chapman & Chapman 2001). The ground layer consists of smaller tree seedlings, herbs, ferns, bryophytes and forest grasses. There are many steep cliffs, ridges and valleys along the south-west facing slope on which the forest lies. The vegetation varies in density and composition. It is very dense in some areas, but can be relatively sparse in others. In the densest areas vines and lianes make the forest practically impenetrable.

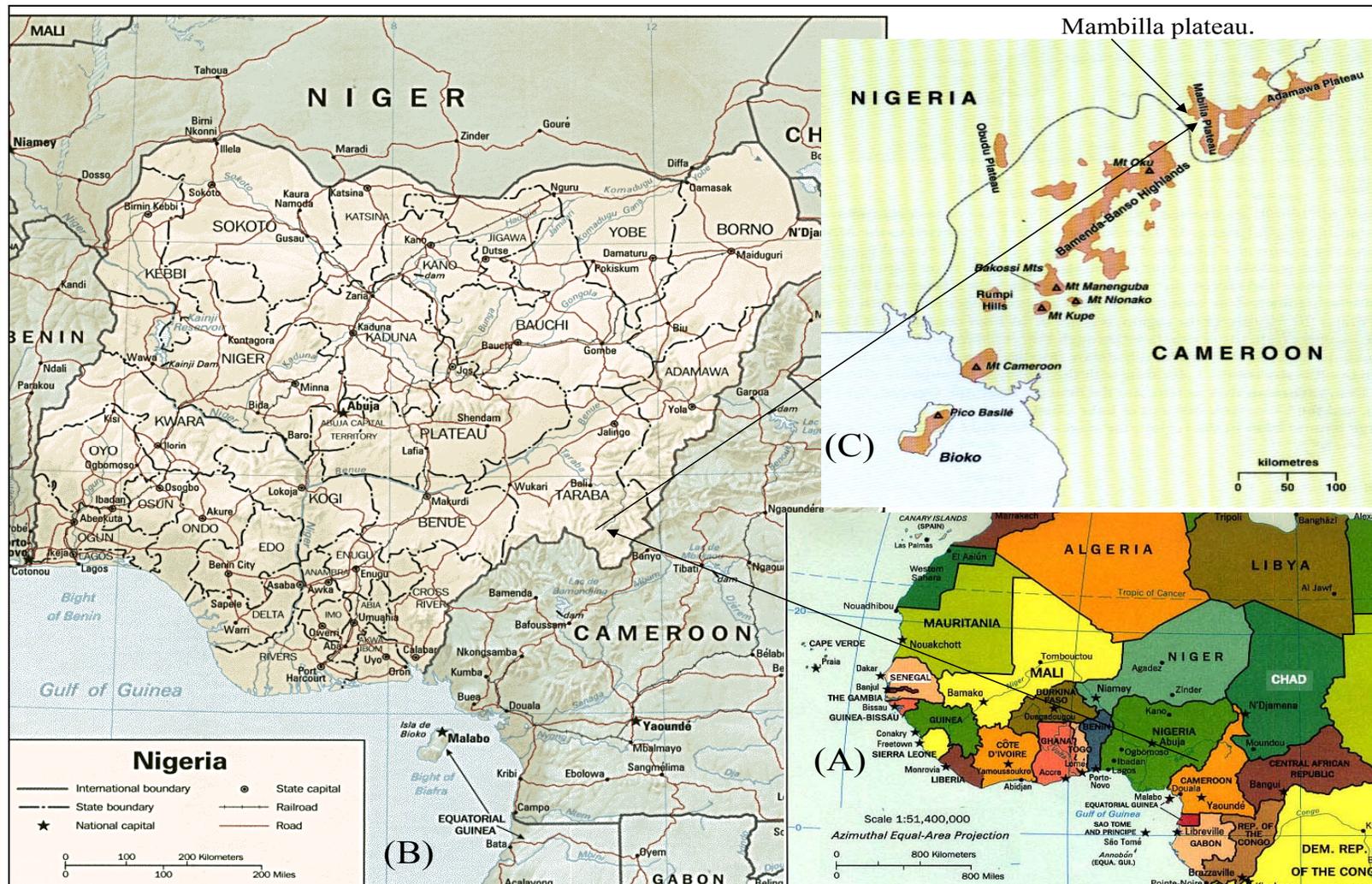


Figure 2.1 West Africa Maps: (A) Location of Nigeria in West Africa (adapted from: www.africa-expedition.com/rout_nigeria_fr.html), (B) Location of the Mambilla plateau in Nigeria (adapted from: <http://hausamissions.org/Images/WestAfricaMap2.jpg>), (C) Location of the Mambilla plateau in the Cameroon Highlands (adapted from Borrow & Demey 2001).

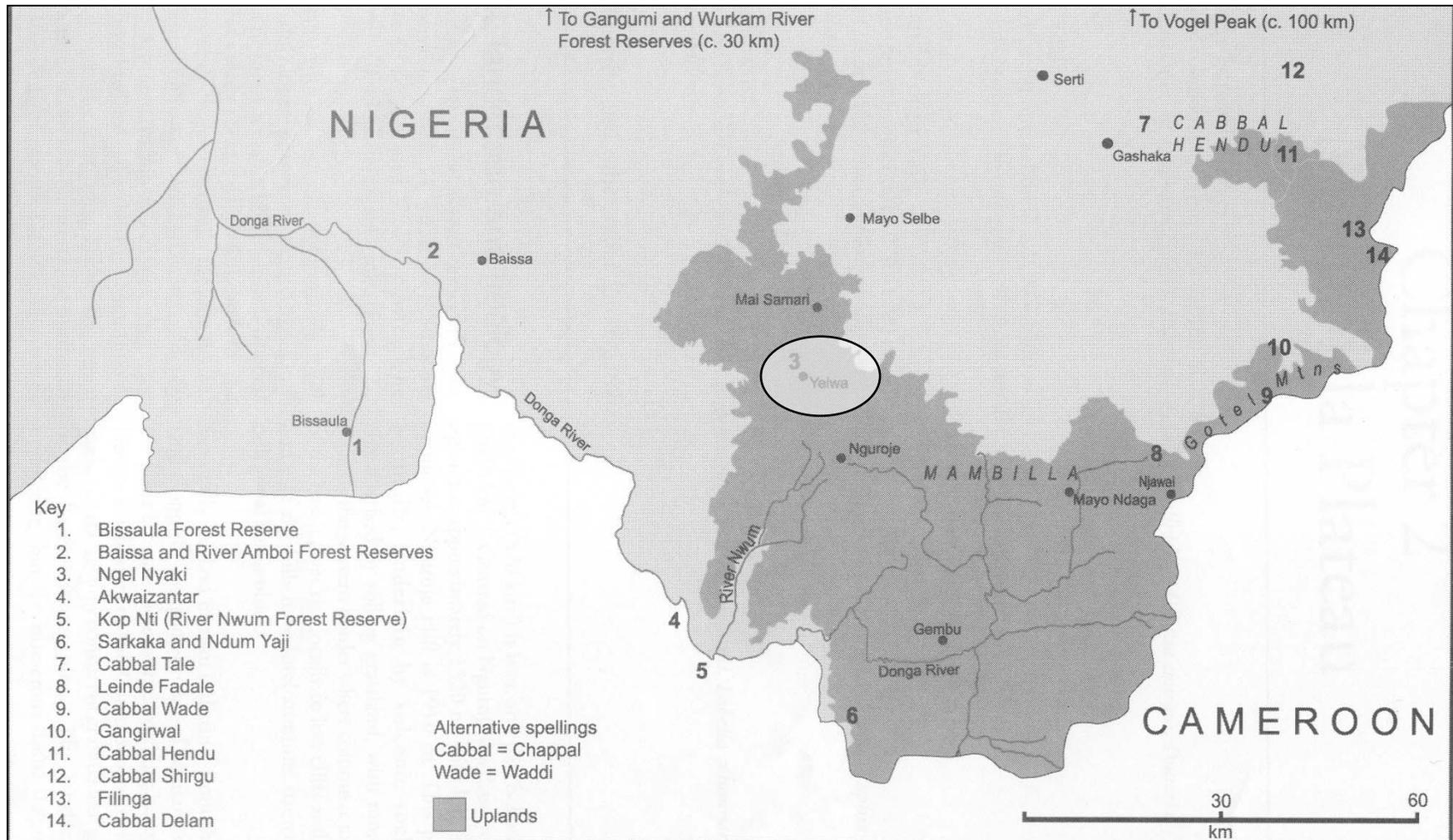


Figure 2.2 The Mambilla plateau and the location of Ngel Nyaki (3). Ngel Nyaki is situated north-west of Yelwa village (center).

Although tree seedlings and shrubs are to a large extent abundant in the understory, areas which experience a lot of disturbance from ground water, slips, and in places that have a heavy leaf litter layer, seedlings can be very sparse.

Herbivores and frugivores

The Janzen-Connell hypothesis predicts that dispersal away from parent / conspecific adult trees increases the probability that a seed will become a mature tree. A diverse assemblage of mammals is present in Ngel Nyaki, many of which are likely to be important seed or seedling herbivores or seed dispersers. These include several species of monkey such as the Putty nosed monkey (*Cercopithecus nictitans*, cf. subspecies *martini*), Mona monkey (*Cercopithecus mona*), Tantelose monkey (*Cercopithecus aethiops*) and Colobus monkeys (*Colobus guereza*). Other important primates present in the forest included chimpanzees (*Pan troglodytes* subsp. *vellerosus*) and baboons (*Papio anubis*). Aside from primates many other small mammals were also present including duikers, pigs, porcupines, rodents and bats. At least three species of fruit bat were present in Ngel Nyaki (*pers. obs*), and fruit bats are known to be important seed dispersers (Romo *et al.* 2004). Also, there are species of antelope, such as bushbuck (Sessions & Chapman 2003) and occasionally buffalo present in the forest (Chapman *et al.* 2004; Sessions & Chapman 2003). The forest harbors many frugivorous birds, the larger gaped ones (capable of dispersing large seed) included Hornbills (*Tockus alboterminatus*), Tauracos (*Turacus persa*, *T. leucolophus* and *Musophaga violacea*) and Pigeons (*Columba sjostedti*). Herbivorous insects were also abundant in the forest, many species of butterflies were seen, where caterpillars show high host specificity to seedlings (Novotny *et al.* 2004) and are very important seedling herbivores in Ngel Nyaki (*pers. com* with field assistants). Also a great diversity of beetles were seen (*pers. obs.*), and beetles are seed predators which often show high host specificity (Janzen 1980). Ngel Nyaki is home to a small but thriving population of the Red data Listed chimpanzee (*Pan troglodytes* subsp. *vellerosus*), the putty nosed monkey (*Cercopithecus nictitans*, cf. subspecies *martini*) (Chapman & Chapman 2001) and it is classified as an Important Bird Area (Chapman *et al.* 2004). Ngel Nyaki is the most diverse upland forest in the Taraba

State mountains (Dowsett-Lamaire 1989), although it lies outside of the National Park (Sessions & Chapman 2003).

2.1 NGEL NYAKI IN AN INTERNATIONAL CONTEXT

Ngel Nyaki Forest Reserve is of international interest because of its location and species composition. Ngel Nyaki and associated montane forests in the neighboring Gotele Mountains in Taraba State are north east outliers of the Cameroon Highlands ecoregion (Chapman *et al.* 2004) (Figure 2.1), and are part of Afro-montane Archipelago (*sensu* White 1983) (Figure 2.3). Many Afro-montane endemic tree species are at their western limits here, meaning they may be genetically distinct or even separate subspecies from eastern populations (Sessions & Chapman 2003). Four IUCN Red Data List tree species, *Entandrophragma angolense*, *Lovoa trichiliodes*, *Millettia conraui*, and *Pouteria altissima* are present in Ngel Nyaki, and it is likely more are yet to be discovered. There is no evidence to suggest any tree (Chapman *et al.* 2004) or mammal (Sessions & Chapman 2001) species has become extinct over the past 30 years, but in general Eastern Nigeria's montane forests are severely threatened (Chapman *et al.* 2004).

Ngel Nyaki is important in terms of its role in the 'Afromontane archipelago'. The idea of an Afromontane archipelago was proposed by White (1983, 1981), and refers to the mountains of Africa as being a series of islands because their flora and fauna show remarkable continuity throughout much of Africa, and appear to be distinctively different to that of lowland African areas (White 1983). Although there is some debate concerning whether or not the Afromontane flora should be classified as a single phytochoria (vegetation zone based on floristic distinctiveness) (Linder *et al.* 2005; Lovett 1998, 1993; Fris 1994; Hamilton 1975 *as cited in* Chapman 2006 *in prep*) there is no doubt that African mountains are home to many montane endemics (Thomas & Achoundong 1994; White 1983, 1978; Wickens 1977, 1976 *as cited in* Chapman 2006 *in prep*). Many of the tree species at Ngel Nyaki have their nearest neighbours in East Africa (Sessions & Chapman 2003; Chapman & Chapman 2001). There are several competing hypotheses as to how the continuity of the Afro-montane flora has arisen, but

no clear consensus has been reached (Brühl 1997; Meadows & Linder 1993; White 1983, 1981, 1978; Livingstone 1975; Moreau 1966, 1963 *as cited in* Chapman 2006 *in prep*). This is likely to be because the Afromontane regions' history goes back to the Cretaceous, and the entire archipelago occurs on a single landmass which has been geographically isolated since the break up of Gondwanaland, and relatively stable since the Precambrian (White 1981). Therefore the Afromontane archipelago is of greater interest to the student of island biogeography than any other archipelago in the world (White 1983). Very little is understood of the ecology and ecological processes of forests in the Afro-montane archipelago (Chapman 2006 *in prep*). Despite this Afromontane forests are one of the rarest and most threatened habitats in Africa, and this is especially true of West Africa (Chapman 2006 *in prep*).

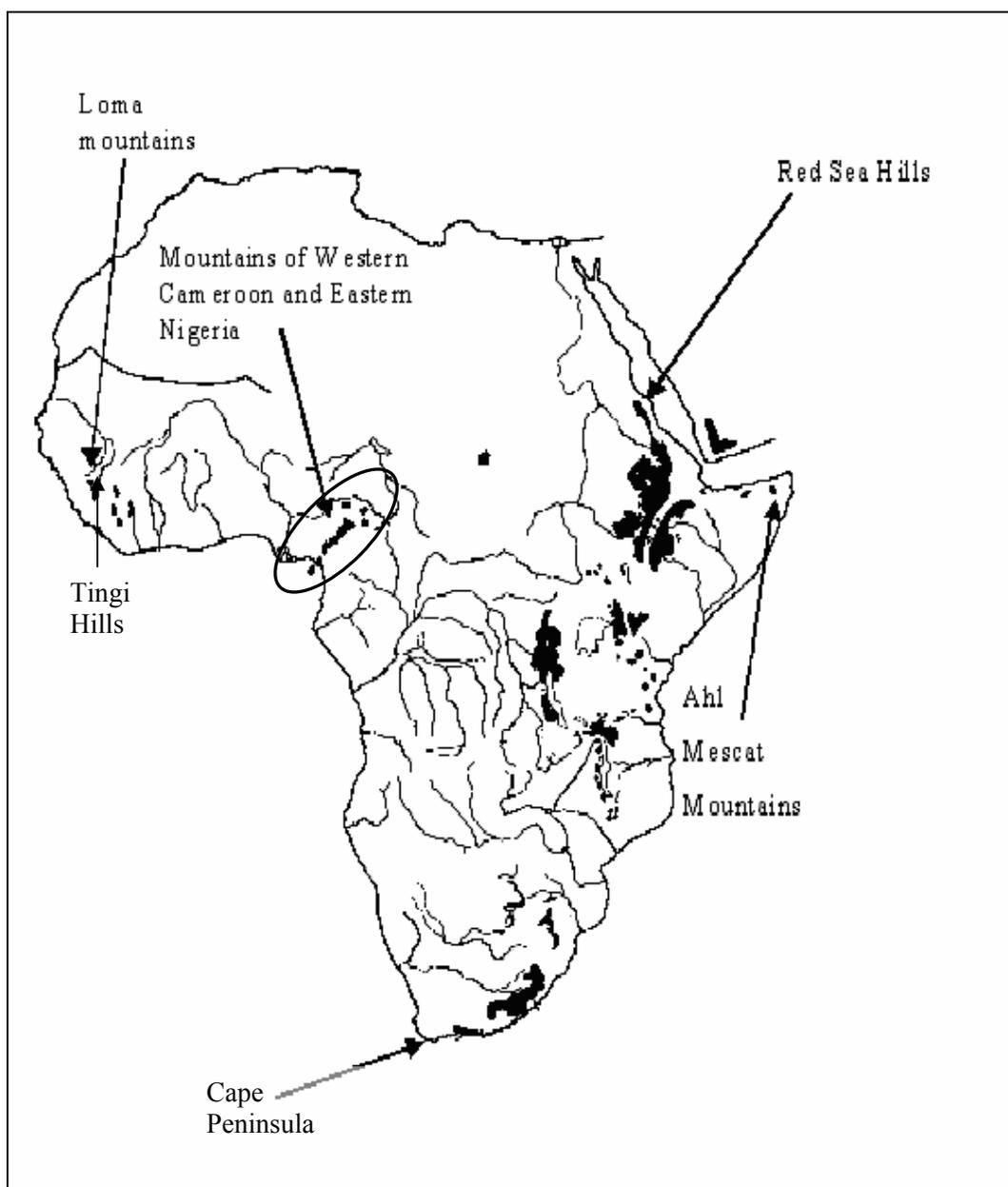


Figure 2.3 The Afro-montane archipelago (shown as solid black areas). Adapted from White (1983).

2.2 SPECIES USED FOR MEASURING SURVIVAL AND LEAF HERBIVORY OF NATURALLY OCCURRING SEEDLINGS AT INCREASING DISTANCE FROM CONSPECIFIC ADULT TREES.

The following three tree species were chosen for measuring the survival and leaf herbivory of naturally occurring seedlings at increasing distance from conspecific adult trees: *Pouteria altissima* (Figure 2.4), *Newtonia buchananii* (Figure 2.6) and *Isolona pleurocarpa* (Figure 2.8).

2.2.1 *Pouteria altissima*.



Figure 2.4 (left) - A clump of *Pouteria altissima* trees growing at the edge of the forest (photo by Arne Matthesius), (right) View of the trunk and root buttresses of *P. altissima* (photo from Chapman & Chapman (2001)).

Pouteria altissima (Sapotaceae) was chosen as a study species for these objectives because it is a principle emergent species (Figure 2.4) which is present in every tree stratum and has high densities of seedlings which are morphologically distinct and thus easy to identify (see Figure 2.5).

P. altissima reaches a maximum height of 46m, with a diameter above the buttresses of 1.8m. Leaves are elliptic and 5-16cm long and 3-7cm broad (see Figure 2.5). It loses its leaves for differing periods. Its fruits are obovoid-globulose olive-shaped berries which have a single large, ovoid, seed (1.3cm) (Hutchinson & Dalziel 1963). These seeds are reliant on frugivorous birds and primates for aiding their dispersal (Chapman & Chapman 2001). *P. altissima* has been assigned the category of: LR/cd on the IUCN Red Data List for endangered vascular plants (Chapman & Chapman 2001). This category means that *P. altissima* has a lower risk (LR) of extinction based on (c) a decline in the area of occupancy and / or quality of habitat, and / or (d) actual or potential levels of exploitation (IUCN, 2000 as cited in Chapman & Chapman 2001).



Figure 2.5 *Pouteria altissima* seedling (photo by Arne Matthesius).

2.2.2 *Newtonia buchananii*.



Figure 2.6 *Newtonia buchananii* at the forest edge (photo by Arne Matthesius).

Newtonia buchananii (Leguminosae-Mimosoidae) was chosen as a study species for these objectives because it is a principle emergent species (Figure 2.6), it is widely distributed throughout the forest and its seedlings are morphologically distinct and thus easy to identify (Figure 2.7). *N. buchananii* reaches a height of 38m, but is typically about 31m tall and is buttressed with narrow plank buttresses to a height of 3m (Chapman & Chapman 2001). It has large, bipinnate compound leaves (20-30cm) (see Figure 2.7). Its seeds are borne in long, narrow (15-35cm long by 18-32mm broad), pendulous, dehiscent pods which split open to expose 6-8 seeds which are well adapted to wind dispersal (Keay 1989). The seeds are elliptic, very flat and about 25mm long each with a papery elongated surrounding wing 5-7.5cm long by 12-25mm broad (Keay 1989). *N. buchananii* fruits prolifically during the rains (Chapman & Chapman 2001).



Figure 2.7 *Newtonia buchananii* seedling (photo by Arne Matthesius) (left). Field assistant Usmanu Abubakar and a *N. buchananii* sapling (photo by Hazel Chapman) (right).

2.2.3 *Isolona pleurocarpa*



Figure 2.8. *Isolona pleurocarpa* adult (left). *I. pleurocarpa* seedling (right). (Photos by Arne Matthesius).

Isolona pleurocarpa (Annonaceae) (Figure 2.8) was chosen as a study species for these objectives because it is a common species in the forest and its seedlings are morphologically distinct and thus easy to identify (Figure 2.8). *I. Pleurocarpa* has oblong-oblanceolate leaves, 8-15cm long, 2-4.5cm broad (Hutchinson & Dalziel 1954) (see Figure 2.8). The fruits are 8-10cm long and 7-8cm broad, they have a knobbly surface (see Figure 2.9) and contain numerous glossy, more or less ellipsoid seeds (Keay 1989).



Figure 2.9. *Isolona pleurocarpa* seed pod (photo by Hazel Chapman).

2.3 SPECIES USED FOR MEASURING SURVIVAL AND LEAF HERBIVORY OF EXPERIMENTALLY PLANTED SEEDLINGS AT INCREASING DISTANCE FROM CONSPECIFIC ADULT TREES.

Seedlings of three tree species were raised in nurseries and then planted at various distances from conspecific adult trees in the forest. The aim of this was to measure the effect of distance from conspecific adult trees on the survival, growth and leaf herbivory of experimentally planted seedlings (see Chapter 5 for more details).

The following three tree species were chosen for the experimental planting of seedlings: *Entandrophragma angolense* (Figure 2.10), *Deinbollia pinnata* (Figure 2.12) and *Sterculia setigera* (Figure 2.14). These three species were chosen due to the availability of their seeds at the beginning of the study period (end of February 2005), because they are relatively common in Ngel Nyaki, and because they represented a range of growth forms.

2.3.1 *Entandrophragma angolense*



Figure 2.10 *Entandrophragma angolense* (photos by Arne Matthesius).

Entandrophragma angolense (Meliaceae) reaches 48m in height, with a long straight bole, buttresses are broad but low (Keay 1989) (Figure 2.10).

Leaves have 7- 10 pairs of oblong elliptic leaflets opposite or sub-opposite up to 12.5cm long and 5cm broad. Periods of leaf loss are variable (Chapman & Chapman 2001). Seeds are well adapted to wind dispersal and have a long membranous wing attached at one end (Keay 1989). They are borne in pendulous woody capsules that have five valves which split open to expose 5-6 seeds on each face of the column (Keay 1989) (Figure 2.11). *E. angolense* has a sporadic distribution within Ngel Nyaki forest (Chapman & Chapman 2001). Chapman & Chapman (2001 p27,51) hypothesized this may be due that its seeds have a relatively high mass which causes most of them to land beneath, or near parent trees. These seeds suffer heavy predation pressure, but occasional seeds travel considerable distances and manage to establish (Chapman & Chapman 2001). *E.*

angolense has been assigned the category of: VU A1cd on the IUCN Red Data List for endangered vascular plants (Chapman & Chapman 2001). This category means that *E. angolense* is vulnerable (VU) to extinction in the medium term future, as defined by (A), a population reduction in the form of (1), an observed, estimated, inferred or suspected reduction of at least 20 % over the last 10 years or three generations, whichever is longer, based on (c) a decline in the area of occupancy and / or quality of habitat, and / or (d) actual or potential levels of exploitation (IUCN, 2000 *as cited in* Chapman & Chapman 2001).



Figure 2.11. *Entandrophragma angolense* seed pod: (left) apex with seeds still attached and inside pod, (right) Apex separated from pod (photos by Arne Matthesius).

2.3.2 *Deinbollia pinnata*



Figure 2.12 *Deinbollia pinnata* (photo by Arne Matthesius).

Deinbollia pinnata (Sapindaceae) (Figure 2.12) reaches a height of 11m (Hutchinson & Dalziel 1958). It has compound leaves that are up to 112cm long (Hutchinson & Dalziel 1958). It has tomentose, orange, subglobose drupe-like fruits, which are between 1.3 – 1.5cm in diameter (Hutchinson & Dalziel 1958). *D. pinnata* seedlings are shown in Figure 2.13.



Figure 2.13 *Deinbollia pinnata* seedling (photo by Arne Matthesius) (left). *D. pinnata* seedling making a new leaf after having all its leaves and a portion of its stem lost to herbivory (Photo by Hazel Chapman) (right).

2.3.3 *Sterculia setigera*

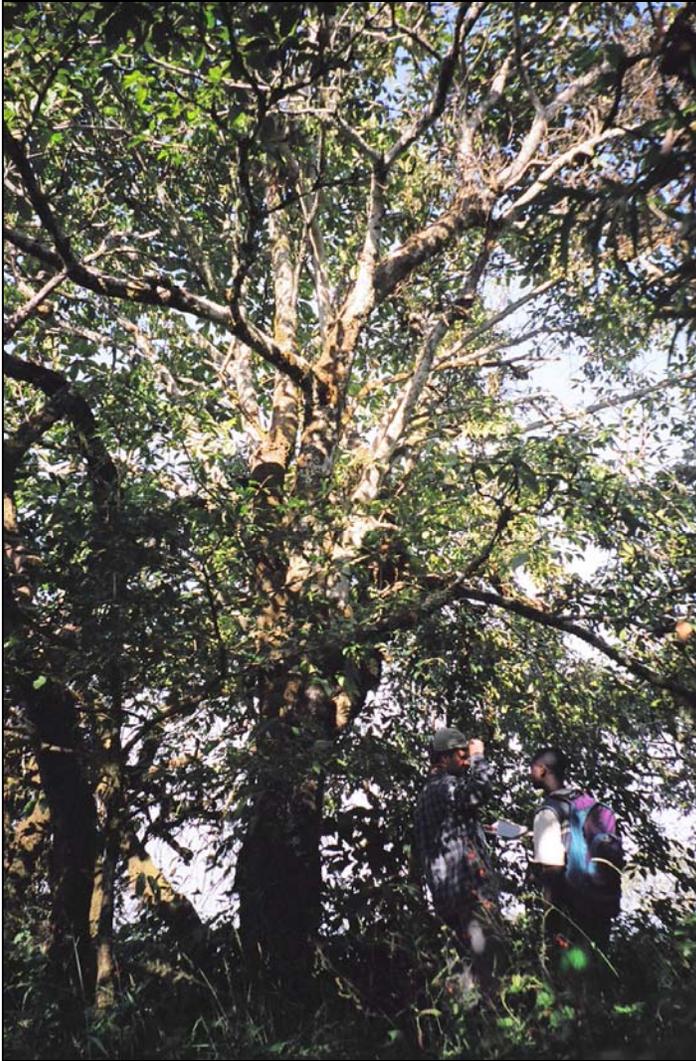


Figure 2.14: *Sterculia setigera* (photo by Gerd Matthesius).

Sterculia setigera (Sterculiaceae) (Figure 2.14) is a borderline montane forest species and savanna tree species. It reaches a height of approximately 16m and has a thick lower bole with small sharp buttresses (von Maydell 1990). It has a large crown and has alternate, palmate leaves (von Maydell 1990). Fruit is a bright red dehiscent capsule which opens to reveal subglobose greyish-black seeds (1-1.5cm).

CHAPTER 3: TESTING THE HYPOTHESIS THAT SEEDLING SURVIVAL INCREASES WITH INCREASING DISTANCE AWAY FROM CONSPECIFIC ADULT TREES.

3.0 INTRODUCTION.

Despite the evolution of complex seed dispersal mechanisms (Howe *et al.* 1985) the amount of seed dispersed declines rapidly with distance from parent trees (Romo *et al.* 2004; Terborgh *et al.* 2002; Janzen 1970). Host specific seed / seedling predators behave as either distance or density dependant predators (Janzen 1970). Distance dependant seed / seedling predators predate on the seeds and seedlings that are in the immediate vicinity of the parent trees on which they live (Janzen 1970; Connell 1971) and density dependant predators predate on those seeds / seedlings as well because seeds, and seedlings initially (Wright 2002; Hubbell 1980), are in their greatest densities near their parent trees (Janzen 1970). Therefore, according to the Janzen-Connell hypothesis, the probability of seedling survival increases monotonically (Figure 1.1) with distance from parent trees (Janzen 1970). In addition, conspecific adult trees share their host specific predators so seedling survival is lowest near conspecific adult trees regardless of whether they are parental or not (Janzen 1970).

Many studies report seedling survival increasing with distance from conspecific adult trees (Clark & Clark 1984; DeSteven & Putz 1984; Wills *et al.* 1997; Barot *et al.* 1999; Barone 2000; Grau 2000; Packer & Clay 2000 *as cited in* Wyatt & Silman 2004).

This chapter involves testing the hypothesis that seedling survival increases with distance from conspecific adult trees.

3.1 METHODS

Seedling survival at increasing distances from conspecific adult trees was measured for twenty adult trees of each of the following three tree species: *Pouteria altissima*, *Newtonia buchananii* and *Isolona pleurocarpa* (see above section 2.3 for details about each species). These three species were chosen for this investigation because they are common tree species in Ngel Nyaki forest, represent a range of dispersal mechanisms (*N. buchananii* is wind dispersed), and because their seedlings are morphologically distinctive and easy to identify. Care was taken to ensure that the conspecific adult trees used in this investigation were not closer than 50m to each other in order to avoid the overlapping of their seed shadows and the sharing of seedling predators between them as predicted by the Janzen-Connell model (Janzen 1970). Seedling height was used as a best estimator of seedling survival (Webb & Peart 1999) because it was a quick and easy method for measuring large amounts of seedlings. Seedling height estimates a seedlings size, therefore how long it has been growing and thus its survival through time.

Seedling heights were measured at five distance intervals away from conspecific adult trees: 0-5m; 5-10m; 10-15m; 15m-20m and 20-25m. The heights of all conspecific seedlings were measured in 5m by 5m plots at intervals: 0-5m; 5-10m and 10-15m. At 15-20m plots were 5m by 10m, and at 20-25m intervals, plots were 5m by 15m (Figure 3.1). Area of plots at 15-20m and 20-25m away from conspecific adults were larger in order to obtain a better representation of seedling height distributions at these greater distances where conspecific seedling densities are lower.

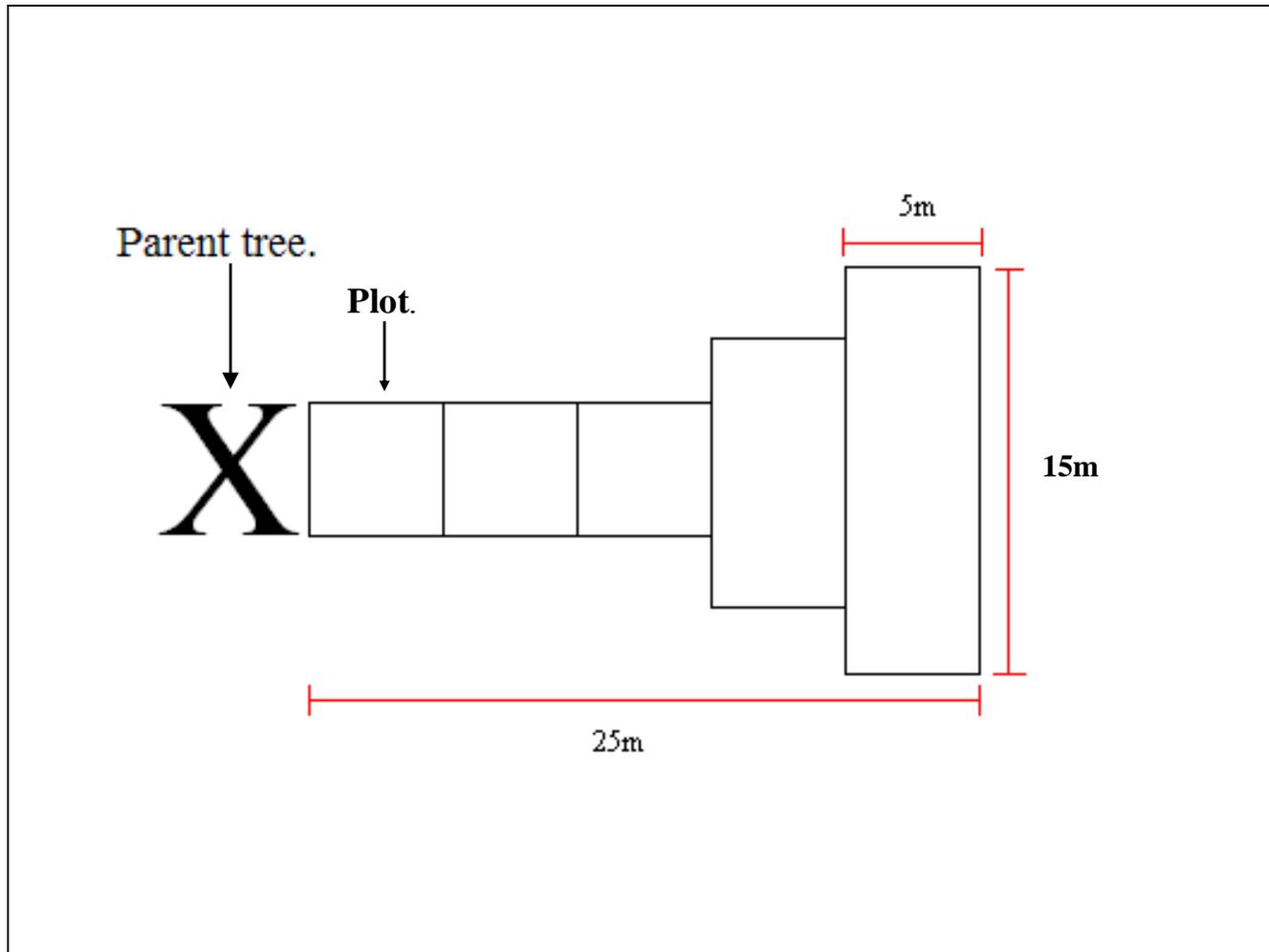


Figure 3.1: Layout of plots for measuring seedling heights. At 0-5m, 5-10m and 10-15m plots were 5mx5m, at 15-20m they were 5mx10m and at 20-25m they were 5mx15m.

3.2 DATA ANALYSIS METHODS

The number of seedlings in each of the following height categories: 0-10cm, 11-20cm, 21-40cm, 41-70cm, 71-120cm, 121-200cm and above 200cm, that were present in plots at each distance from the 20 parent / conspecific adult trees for each the 3 species were tabulated. The number of seedlings / m² in each height category at each distance was calculated for each parent / conspecific adult tree measured. Numbers of seedlings were converted to number / m² because the area sampled doubled at 15-20m, and tripled at 20-25m away from parent / conspecific adult trees (Figure 3.1). Consequently there were twenty numbers of seedlings / m² for each height category for each distance away from parent / conspecific adult trees for each species. As there were many zero values, the numbers of seedlings / m² for each height category for each distance under five adult trees were averaged to give four values for each distance for each species. Regression analyses were used to determine if there was a significant increase in the number of seedlings in the larger height categories at greater distances from conspecific adult trees. Using the statistical features in Microsoft Excel, for each species the mean numbers of seedlings / m² / five trees were regressed against the five distance intervals for each height category (Appendix: Figure 1-3). The majority of these regression analyses were non-significant (Table 3.2-3.4), but the slopes revealed a pattern (Figure 3.2-3.4). Due to the fact that the data revealed a pattern and that most results of the regression analyses were non-significant, the raw data was re-analysed by analysis of covariance (ANCOVA). As Microsoft Excel does not run ANCOVAs I used the R statistics program (v. 2.1.1; R Development Core Team 2005) to do this. The ANCOVA would reveal whether or not the pattern revealed by the regression analyses was significant. Specifically, the ANCOVA tested whether the interaction between seedling height categories and distance from parent / conspecific adult trees significantly explains a portion of the variance in number of seedlings / m².

For the ANCOVA all three species were entered at once to predict density from one categorical variable (log (height category)), one variate (distance), species as a factorial variable and all their interaction terms. Height categories were log transformed because they

increased in the range of heights they covered as height increased, and this reduced the variation in their range sizes.

3.3 RESULTS

A total of 4031 seedlings were measured over all plots for *Pouteria altissima*, 4037 for *Newtonia buchananii* and 383 for *Isolona pleurocarpa* (Table 3.1).

Table 3.1 The number of seedlings measured in all plots at each distance for each species: *Pouteria altissima*, *Newtonia buchananii* and *Isolona pleurocarpa*.

Distance	<i>Pouteria altissima</i>	<i>Newtonia buchananii</i>	<i>Isolona pleurocarpa</i>
2.5m	986	626	47
7.5m	998	629	53
12.5m	526	567	58
17.5m	870	1179	116
22.5m	651	1036	109
Total	4031	4037	383

The regression analyses on the four means of abundance of seedlings / m² in each height category against distance, for each of the three species, were largely non-significant (Table 3.2-3.4). Despite this the analyses showed that for all species the regression slopes of seedling density (number of seedlings / m²) versus distance changed from being negative for seedlings in the smaller height categories to being positive for seedlings in the larger height categories (Figure 3.2 – 3.4).

Table 3.2 Results of the regression analyses on the number of *Pouteria altissima* seedlings / m² in each height category versus distance from conspecific adult trees.

Height category	F	df	P	slope	intercept
0-10cm	1.013	18, 1	0.328	-0.000023	0.001
11-20cm	0.766	18, 1	0.393	-0.000093	0.005
21-40cm	3.206	18, 1	0.090	-0.00035	0.014
41-70cm	1.943	18, 1	0.180	-0.0011	0.026
71-120cm	3.794	18, 1	0.067	0.000157	0.001
121-200cm	0.036	18, 1	0.852	1.00E-05	0.001
above 200cm	1.832	18, 1	0.193	0.000068	0.001

Table 3.3 Results of the regression analyses on the number of *Newtonia buchananii* seedlings / m² in each height category versus distance from conspecific adult trees.

Height category	F	df	P	slope	intercept
0-10cm	0.835	18, 1	0.373	-0.00514	0.318
11-20cm	0.224	18, 1	0.642	-0.00011	0.005
21-40cm	0.121	18, 1	0.732	-1.50E-05	0.001
41-70cm	0.000	18, 1	1.000	2.17E-20	0.001
71-120cm	3.796	18, 1	0.067	0.00005	0.000
121-200cm	0.993	18, 1	0.332	6.30E-05	0.001
above 200cm	2.086	18, 1	0.166	0.000096	0.001

Table 3.4 Results of the regression analyses on the number of *Isolona pleurocarpa* seedlings / m² in each height category versus distance from conspecific adult trees.

Height category	F	df	P	slope	intercept
0-10cm	2.296	18, 1	0.147	-0.0022	0.042
11-20cm	4.756	18, 1	0.043	-0.0081	0.233
21-40cm	4.998	18, 1	0.038	-0.0073	0.222
41-70cm	0.241	18, 1	0.630	8.16E-05	0.004
71-120cm	0.033	18, 1	0.858	-0.00001	0.002
121-200cm	0.374	18, 1	0.548	3.16E-05	0.001
above 200cm	0.000	18, 1	1.000	0	0.000

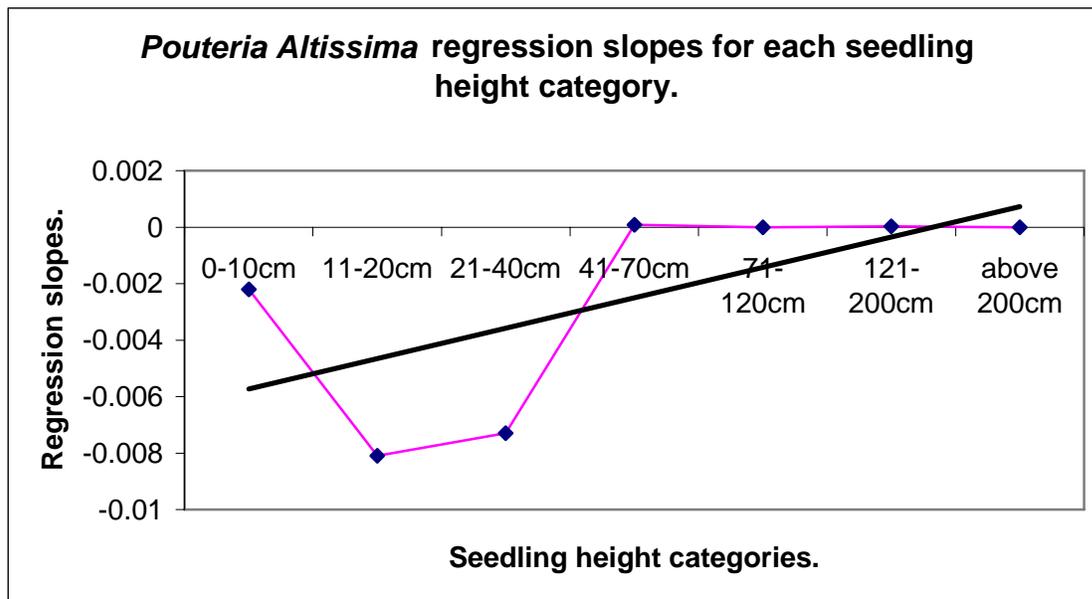


Figure 3.2 *Pouteria altissima*: regression slopes of seedling abundance versus distance, for each height category, changed from being negative for smaller height categories to being positive for the larger height categories.

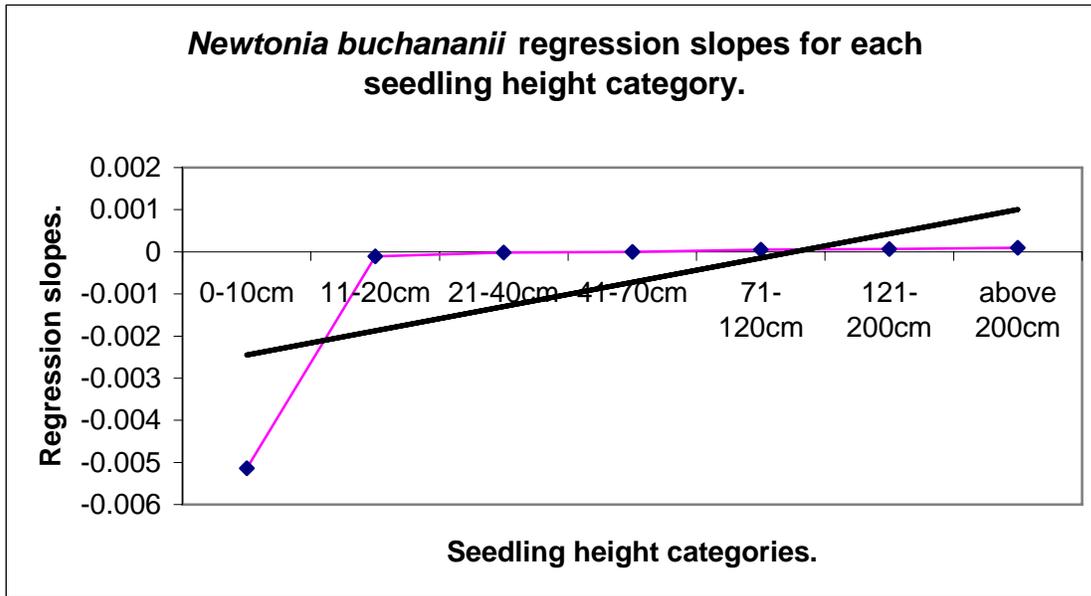


Figure 3.3 *Newtonia buchananii*: regression slopes of seedling abundance versus distance, for each height category, changed from being negative for smaller height categories to being positive for the larger height categories.

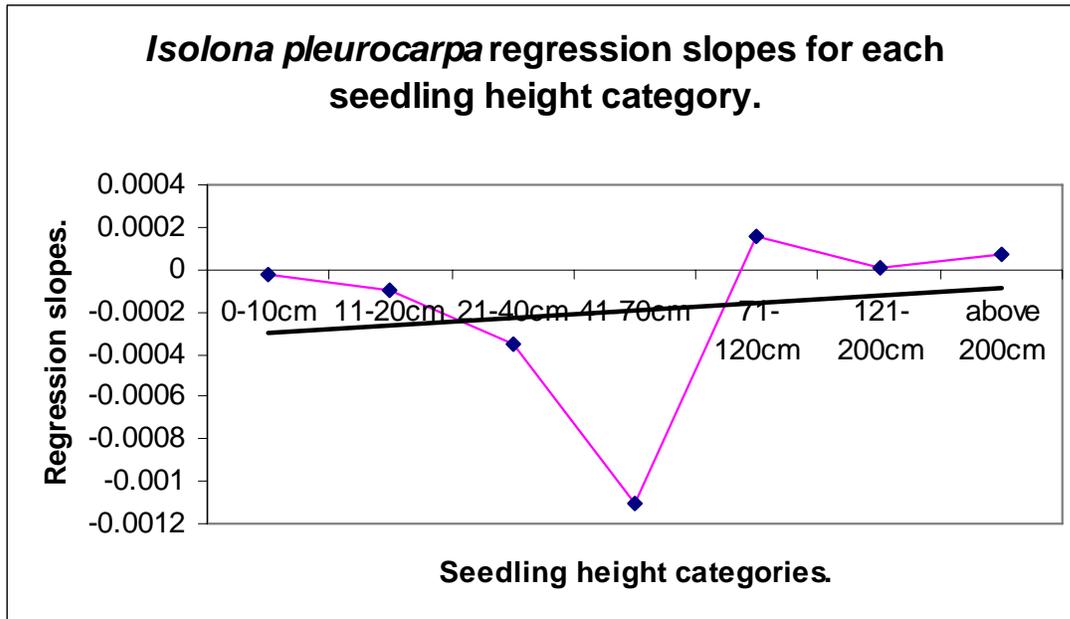


Figure 3.4 *Isolona pleurocarpa*: regression slopes of seedling abundance versus distance, for each height category, changed from being negative for smaller height categories to being positive for the larger height categories.

Further analysis of the data by analysis of covariance (ANCOVA) yielded a significant result for the interaction term: distance* log (height category) ($P = 0.0261$)(Table 3.5).

This means that the increase in abundance of large seedlings and the decrease in abundance of small seedlings at distances away from parent / conspecific adult trees (Figure 3.2-3.4) is a significant trend across all three species. Species, distance and log (height category) each significantly explained a portion of the variance in seedling density (Table 3.5). This means that the three species differed in the abundance of their seedlings; seedling densities differed at distances away from parent / conspecific adult trees; and that seedling densities were different between height categories among all three species.

Table 3.5. Analysis of covariance results: predicting Density (or number of seedlings / m²) from: Species, Distance, (log)Height category, Species*Distance, Species*(log)Height category, Distance* (log)Height category, Species*Distance*(log)Height category. Significant values are in bold.

	Df	Deviance	Resid. Df	Resid. Dev	F Value	Pr (F)
NULL			418	46.05248		
As.factor (species)	2	1.798957	416	44.25352	11.2133	0.000182
Distance	1	0.444976	415	43.80855	5.54727	0.0189833
Log(height category)	1	5.852409	414	37.95614	72.95872	0
As.factor (species) : distance	2	0.320933	412	37.6352	2.00045	0.1366025
As.factor(species) : log(height category)	2	4.38114	410	33.25406	27.30861	0
Distance : log (height category)	1	0.400135	409	32.85393	4.98826	0.0260626
As.factor (species) : distance : log(height category)	2	0.20628	407	32.64765	1.28579	0.2775527

3.4 DISCUSSION

The analysis of covariance yielded a significant result for the interaction term: distance* log (height category) $P = 0.0261$ (Table 3.5), which shows that the slope of the regression changes from being negative to being positive as seedlings get taller (Figure 3.1 - 3.3), and therefore that, over all three species, *Pouteria altissima*, *Newtonia buchananii* and *Isolona pleurocarpa*, larger seedlings are more commonly found further away from conspecific adult trees and smaller seedlings are more abundant near conspecific adult trees (Appendix: Figure 1-3). This pattern of size distribution is consistent with the seedling recruitment pattern predicted by the Janzen-Connell model. The fact that the vast majority of seedlings measured were below 30cm tall and found near to the conspecific adults indicates that the vast majority of seeds land and are able to germinate under parent trees. This is illustrated in Table 3.6 where numbers of small seedlings appear to occur in similar numbers at all distances from parent / conspecific adult trees, but at 20 m and 25m away the area sampled was twice and three times larger respectively. Therefore, smaller seedlings were in greater abundance near to parent trees. The high abundance of small seedlings close to parent trees in contrast to the lower number of larger seedlings (Table 3.6) implies that the high densities of seedlings near conspecific adults suffer high mortality over time. The obvious corollary is that despite fewer seeds reaching the furthest distances, larger seedlings are more abundant there, which together suggest a strong relationship of survival increasing with distance from parent trees.

Table 3.6 Number of seedlings observed in each height category at each distance from all conspecific adult trees.

(a) *Pouteria altissima*, (b) *Newtonia buchananii*, (c) *Isolona pleurocarpa*

(a) height (cm)	0-10	(11-20)	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110
2.5m	113	443	388	34	0	1	2	2	0	1	1
7.5m	18	498	441	19	3	11	2	1	1	2	0
12.5m	3	231	252	20	4	7	1	0	0	0	0
17.5m	24	403	406	19	7	5	3	1	1	0	0
22.5m	9	256	286	39	8	14	13	4	5	3	3
(b) height (cm)	0-10	(11-20)	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110
2.5m	614	5	3	1	0	1	0	0	0	0	0
7.5m	600	15	2	1	0	2	0	0	0	0	0
12.5m	543	10	0	0	0	0	0	0	0	0	0
17.5m	1136	12	2	1	0	0	4	0	1	0	1
22.5m	963	17	9	3	1	1	2	3	1	0	1
(c) height (cm)	0-10	(11-20)	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	101-110
2.5m	1	9	15	9	1	3	2	0	1	0	0
7.5m	1	5	13	13	3	8	4	0	0	0	1
12.5m	1	9	10	9	1	9	3	0	3	1	0
17.5m	0	13	14	24	7	15	9	2	6	2	2
22.5m	1	10	13	16	10	9	9	6	7	3	3

(a) height (cm)	111-120	121-130	131-140	141-150	151-160	161-170	171-180	181-190	191-200	above 200
2.5m	0	1	0	0	0	0	0	0	0	0
7.5m	0	0	0	2	0	0	0	0	0	0
12.5m	2	1	1	1	1	0	0	0	0	2
17.5m	0	0	0	0	1	0	0	0	0	0
22.5m	1	4	0	1	0	0	2	2	1	0
(b) height (cm)	111-120	121-130	131-140	141-150	151-160	161-170	171-180	181-190	191-200	above 200
2.5m	0	1	0	0	0	0	0	0	0	1
7.5m	0	0	0	1	0	0	0	0	0	8
12.5m	1	0	1	5	0	1	0	1	0	5
17.5m	0	3	1	1	1	2	0	2	1	11
22.5m	2	2	0	1	0	0	1	1	3	25
(c) height (cm)	111-120	121-130	131-140	141-150	151-160	161-170	171-180	181-190	191-200	above 200
2.5m	0	1	0	1	1	0	0	0	1	2
7.5m	0	0	0	0	1	0	0	0	0	4
12.5m	5	0	0	0	1	0	0	0	0	6
17.5m	2	0	0	2	2	0	0	0	0	16
22.5m	0	4	0	3	0	0	1	1	3	10

The significant ANCOVA results suggest that this is a consistent pattern across the three species studied here, but the non-significant regression results indicate that there is considerable variation in this recruitment pattern.

There are a number of factors which may explain why seedlings become established and survive well near to the parent tree. For instance, the growth and survival of a parent tree / conspecific adult in an area may indicate that the area is a suitable microhabitat for its

seedlings as well (Wright 2002, Fenner 1985). The advantages of high initial seed / seedling densities, which can overwhelm seed / seedling predators (Harms *et al.* 2000; Janzen 1976), and favourable microhabitat may allow for the survival of a small proportion of the initially abundant seedlings present under parent / conspecific trees. If seedlings escape the attack of host specific pests initially, they may be able to tolerate later attacks (Connell 1971). Therefore over time similar numbers of larger seedlings could accumulate near to, and at distances away from, parent / conspecific adult trees. The non-significant linear relationships between abundance of large seedlings and distance may then have come about despite that host specific pests are substantially reducing the number of recruits near to parent trees.

The negative effects of host specific seed / seedling predators on the abundance, growth and survival of seedlings are particularly likely to reinforce one another over longer time intervals, so that the eventual reduction in recruitment near adults is much greater than is evident from a study such as this one, which has been undertaken in one point in time (Wright 2002). The ANCOVA result (Table 3.1) may thus be evidence of the Janzen-Connell model operating in Ngel Nyaki.

Although it is possible that the significant result found in this study is an indication that host specific seed / seedling predators are causing seedling mortality to be highest under parent / conspecific adult trees, there are a number of other factors which may cause seedling survival to be lowest under parent / conspecific adult trees.

Plants release a variety of primary and secondary metabolites from their roots and decaying leaf litter which may harm their neighbours (Taiz & Zeiger 1998) and these compounds, when secreted by adult trees or conspecific seedlings, may cause seedling survival to be lowest for seedlings near parent / conspecific trees and /or where conspecific seedling densities are highest (Wright 2002; Janzen 1970; Connell 1971). For instance (Webb, Tracy & Haydock 1967 *as cited in* Janzen 1971) found that the roots of an Australian rain forest tree, *Grevillea robusta*, release a compound that kills their own seedlings, leading to wide spacing of adults. In addition, Molofsky & Augspurger (1992) found that leaf litter layers negatively affected the growth and survival of the majority of their study species' seedlings, although they did not determine whether this was due to chemicals released from the leaves. Nevertheless, species whose seedlings are negatively affected by their parents' leaf litter or heavy leaf litter layers in

general, may suffer high mortality under their parent trees. A litter effect may have contributed to seedling survival being lowest under parent trees of *Pouteria altissima* in this study. *P. altissima* seedlings were often absent from areas with heavy leaf litter (*pers. obs.*), and while no attempt was made to measure whether leaf litter was characteristically high under *Pouteria altissima* adults than away from them, this species does periodically shed all of its large leaves (Figure 2.5) (Chapman & Chapman 2001). Therefore it is possible that when leaf litter is dense under adult *P. altissima* trees that its seedlings' growth and survival are negatively affected.

Intra-specific competition may also negatively affect the survival of conspecific seedlings under parent trees, because of direct competition with their parent trees (Janzen 1970) or because the density of young seedling highest there (Wright 2002; Duncan 1991). This is because the most intense competition, particularly for light, water and nutrients, occurs when zones of resource depletion of near neighbours overlap (Wright 2002; Duncan 1991). Conspecific seedlings compete for the same resources (Connell 1971); therefore the high young seedling densities under *N. buchananii* and *P. altissima* parent / adult trees (Table 3.6) may suffer higher mortality than at distances away from parent / conspecific adult trees because of intense interspecific competition.

Chance events may also have caused variability in the relationship between survival and distance from parent trees. Such events include lightning strikes, wind throws and falling debris. Falling debris may cause significant mortality. For example, falling debris killed 33 % of the liana saplings that died over a two year period on Barro Colorado Island, Panama (Aide 1987), and buried 19 % of artificial seedlings over one year at the La Selva Biological Station in Costa Rica (Clark & Clark 1989). Lightning strikes, strong winds and land slides which are all common in Ngel Nyaki, can cause branches to break and trees to fall, which open up light gaps in the canopy.

Carol Augspurger (1984) investigated whether seedling survival differed for seedlings growing in light gaps versus closed canopy areas in a deciduous lowland forest in Panama. She found that seedling survival was highest in light gaps for all nine of her study species. Augspurger (1984) also found that relative to any other cause of mortality (e.g., drought, poor root establishment, herbivory, branch falls, erosion, and mammal digging) pathogens were

responsible for the highest proportion of deaths within six of her nine study species. Additionally Augspurger (1984) discovered that pathogen-related mortality was greatly reduced in light gaps for all of her study species' seedlings. A number of authors have shown that conditions of high radiation, high temperature and low humidity that are present in tropical light gaps adversely affect the pathogens that cause damping off of seedlings (Augspurger 1984). Additionally, due to the elevated light levels, seedlings in gaps may be more efficient in compensating for or replacing leaves and other tissues lost due to invertebrate attack (Hammond & Brown 1996). Thus when light gaps appear in the canopy of a parent / conspecific adult tree conspecific seedlings growing in those gaps may escape the attack of host specific insects and pathogens, or they may be better able to tolerate these attacks through their initial stages and become established seedlings or saplings near parent / conspecific adult trees. Additionally, local depletion of critical nutrients by the parent / conspecific adult tree or particularly effective shading by the adult crown may cause seedling survival to be lowest under parent / conspecific adult trees (Clark & Clark 1984). It has also been suggested by a number of authors that tree fall gaps can potentially create environmental heterogeneity and thus may obscure density/ distance dependant mortality patterns (Augspurger & Kitajima 1992; Cintra 1994; Clark and Clark 1984, 1987; Kiltie 1981 *as cited in* Cintra 1997).

The occurrence of mast seeding events may be unpredictable for seed predators, so that their populations cannot expand fast enough to consume the vast amount of seeds available to them at such times (Packer & Clay 2000; Janzen 1970). As a result seedlings may become established near to parent / conspecific adult trees (Janzen 1970, 1976; Packer & Clay 2000) and reach an age where they can tolerate the attack of host specific pests in future years (Connell 1971). Extreme fluctuations in weather (Connell 1971), or lack of seeds in the years between masting events (Janzen 1970), may decimate host specific predator populations so that seedlings are able to become established under conspecific adult trees at those points in time.

Further variation in the pattern of increased seedling survival with distance from parent / conspecific adult trees can be caused by micro-topography. Micro-topography can cause drainage, moisture, and possibly nutrients to vary from ridges to slopes and nearby streams

over just tens of meters, and many tropical forest plants have been shown to be non-randomly distributed with respect to such micro-topographic gradients (Wright 2002).

Considering all the reasons mentioned above of how seedlings may become established under parent / conspecific adult trees, the significant ANCOVA result may be a strong indication of high seedling mortality under parent / conspecific adult trees. The causes of seedling mortality were not determined in this investigation, but the possibility remains that it is due to host specific seed / seedling predators as was proposed by Janzen (1970) and Connell (1971).

CHAPTER 4: TESTING THE HYPOTHESIS THAT SEEDLING LEAF AREA LOST TO HERBIVORY DECREASES WITH INCREASING DISTANCE AWAY FROM CONSPECIFIC ADULT TREES.

4.0 INTRODUCTION

Janzen (1970) stated that distance dependant predators are typically herbivores who are parasites on adult trees, but predators on seedlings. This he believed was because seedlings are less able to withstand the loss of leaves and shoot tips than are adult trees (Janzen 1970). Connell (1971) found that there was much more grazing on seedlings planted under adults of the same species than on those under other species, and concluded that this was due to a large number of host specific herbivores in tropical forests.

There are literally thousands of species of herbivores in tropical forests that attack leaves in different ways (Janzen 1983). They eat holes and notches in leaves, bite off shoot apices, suck phloem and xylem fluid from stems and leaves, roll leaves, mine in leaves, scrape epidermis off leaf surfaces, cut and carry off leaves to eat elsewhere and web up young shoots (Janzen 1983).

Several studies have shown high levels of host specificity in herbivorous insects and other pests that consume either leaf or seed tissue of tropical plants (Augspurger 1984; Howe 1990; Gilbert *et al.* 1994; Janzen 1980; Barone 1998; Clark & Clark 1987 *as cited in* Harms *et al.* 2000). Results of studies by both Janzen (1970) and Connell (1971), suggested that most herbivory on seedlings was by herbivorous insects. More recently it has been shown that approximately 70 % of herbivory in several tropical forests is due to insects (Givnish 1999). Barone (1998) studied 46 species of folivorous insects on Barro Colorado island, Panama, and found many to be host specific; 26 % were specialized to a single plant species, 22 % were limited to feeding on a single genus, 37 % were able to feed on several genera within a single family and the remaining 15 % were generalists. Barone (1998) also found that specialist herbivores did far more damage to young leaves than did generalists, which gives strong

support to the Janzen-Connell model. On the other hand results of studies by Novotny and co-workers (2002) in a forest in Papua New Guinea show low host specificity of herbivorous insects. They compared the degree of faunal overlap between herbivore communities feeding on closely and distantly related plants. They found that even between phylogenetically distant hosts, herbivore communities typically shared a third of their species. Nevertheless, Janzen (1970) and Connell (1971) both believed that host specific herbivores were a major cause of seedling mortality close to parent / conspecific adult trees. In addition, Janzen (1970) states that many herbivores may only behave as host specific on a given species at certain points in time in their life cycles, or when their host is abundant. Also, pathogens and other groups of tropical forest herbivores are host specific and generalist herbivores may be host specific at certain times, for example when a food source is abundant (Harms *et al.* 2000; Givnish 1999; Janzen 1971).

This chapter investigates whether leaf herbivory is more intense near to parent / conspecific adult trees in Ngel Nyaki. If it is, this would suggest that herbivores in West African montane forests are host specific and behave in a distance / density dependant fashion as predicted by the Janzen-Connell model.

4.1 METHODS

Seedling leaf herbivory was measured at increasing distances from twenty adult trees of each of the following three tree species: *Pouteria altissima*, *Newtonia buchananii* and *Isolona pleurocarpa* (see above section 2.3 for details about them). These species were chosen for this investigation because they are common tree species in Ngel Nyaki forest, and because their seedlings are distinctive and therefore easy to identify. Care was taken to ensure that the conspecific adult trees used in this investigation were not closer than 50m to each other in order to avoid the overlapping of their seed shadows, and the sharing of seedling herbivores between them as predicted by the Janzen-Connell model (Janzen 1970). Seedling leaf herbivory was measured in one 5m by 5m plot at each of five distance intervals away from conspecific adult

trees: 0-5m; 5-10m; 10-15m; 15m-20m and 20-25m (see Figure 4.1). Leaf herbivory was measured for a maximum of twenty seedlings in each plot.

Leaf herbivory was measured by visually estimating the percent of the total leaf area of a seedling that is missing (Stotz *et al.* 2000). Remains of petioles indicating whole leaves lost were included in this estimate (Figure 4.2). Leaf herbivory estimates were made by my two field assistants while I recorded the estimates, but I constantly checked to see if I agreed with the estimates they made throughout the recording period.

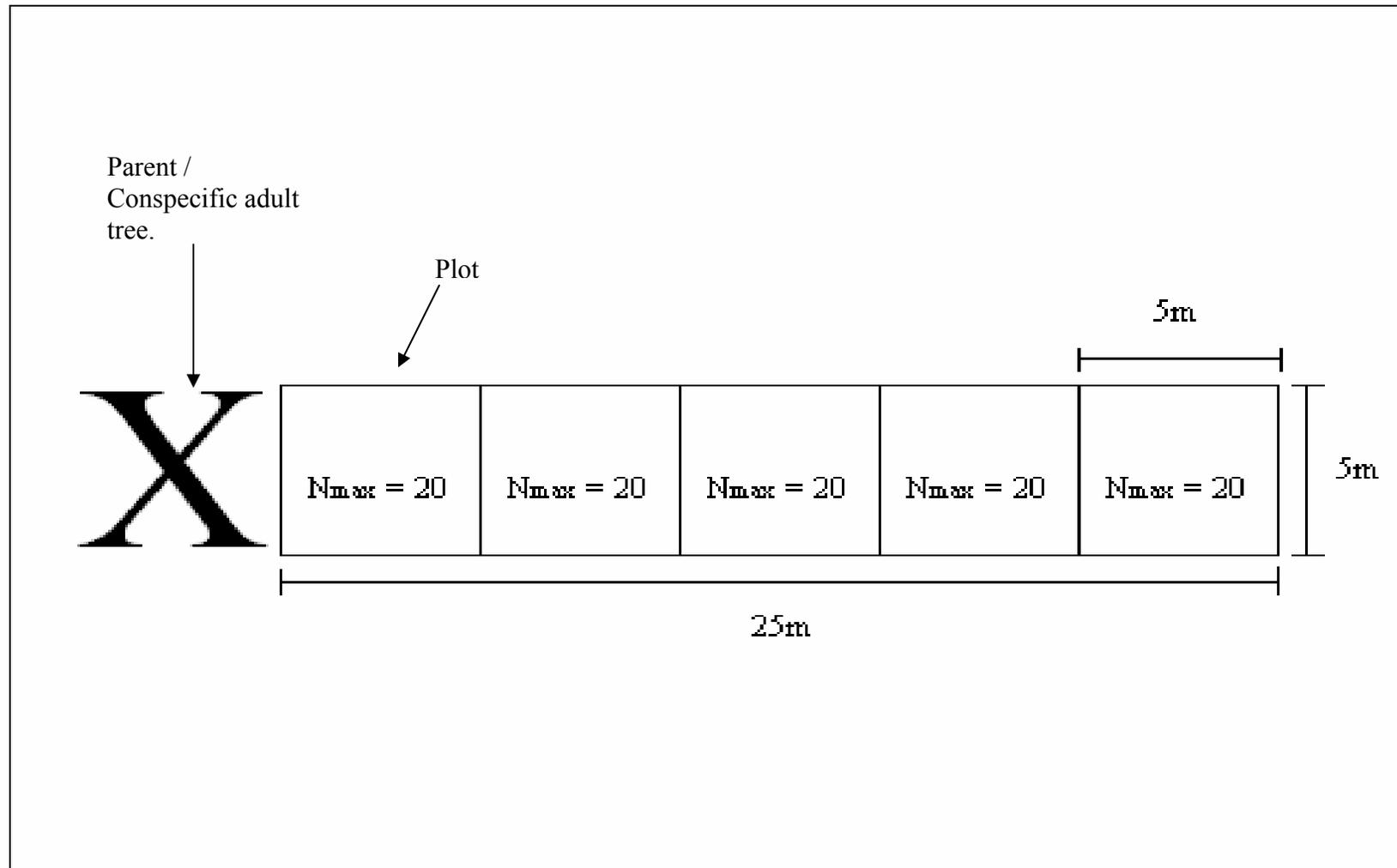


Figure 4.1 Layout of plots for seedling leaf herbivory measurements. Herbivory was measured for a maximum of twenty seedlings in each 5m x 5m plot. There was one 5m x 5m plot at each distance interval: 0-5m, 5-10m, 10-15m, 15-20m and 20-25m.

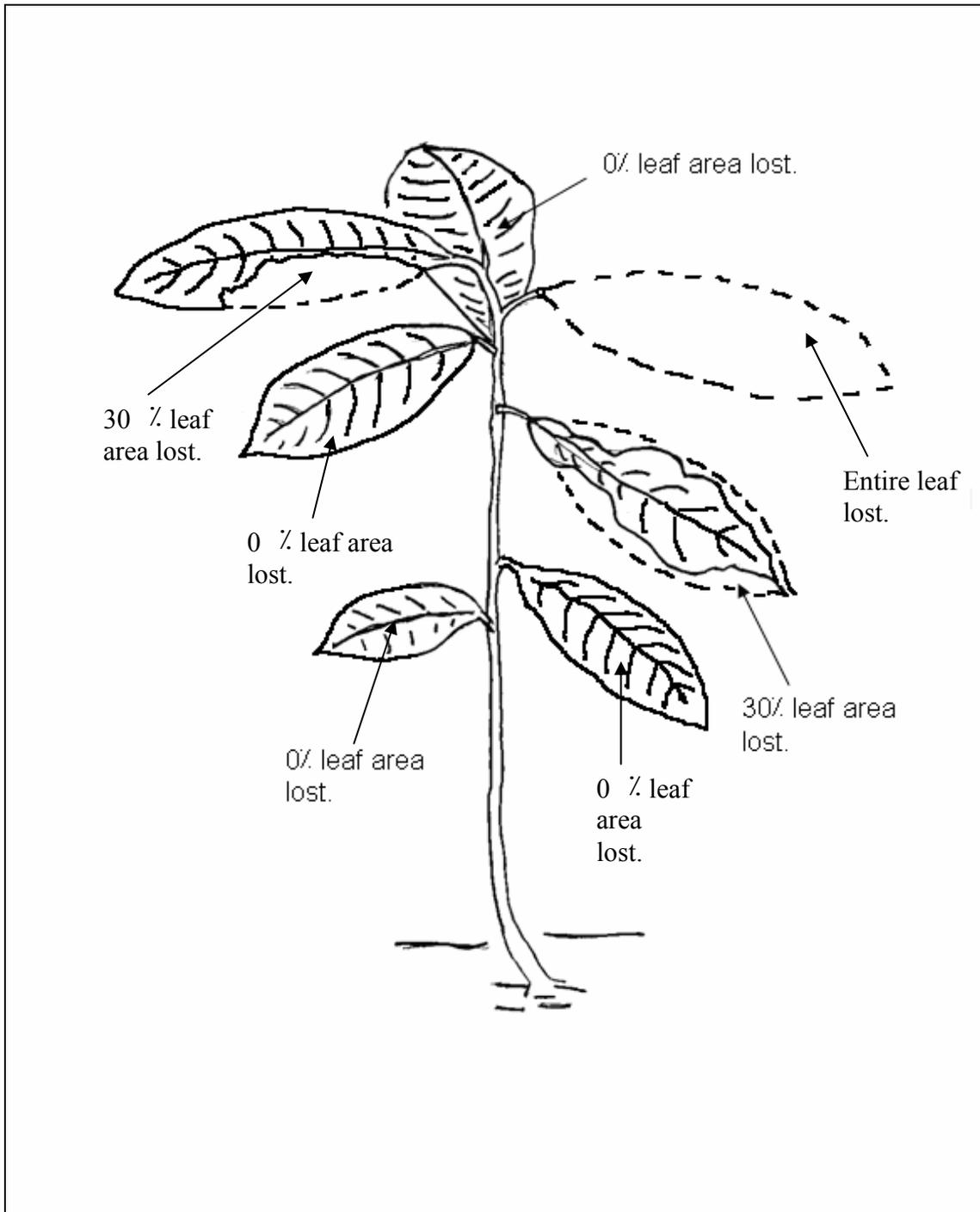


Figure 4.2: Diagram depicting method for visually estimating total seedling leaf area lost to herbivory: Calculations were made roughly without the use of a calculator. As 1 entire leaf was lost (only the petiole remains) out of seven original leaves, approximately 15.0 % of total leaf area was lost through the loss of that leaf. Additionally, two leaves out of the seven original leaves suffered 30 % leaf area loss. Therefore, approximately 5 % of the total leaf area had been lost through the leaf area that had been lost by those two leaves. Therefore $\sim 5\%$ plus $\sim 15\%$ = $\sim 20\%$ of the seedlings total leaf area had been presumably lost to herbivory.

4.2 DATA ANALYSIS METHODS

The averages of estimated percent leaf herbivory of all seedlings at each distance (0-5m; 5-10m; 10-15m; 15-20m and 20-25m) from 20 conspecific adult trees for each species were calculated. This gave twenty values for each distance away from conspecific adults for each of the three species. Linear regressions were run on the herbivory averages at each distance for each species separately. I used Microsoft Excel for doing the regression analyses.

4.3 RESULTS

Regressions of average percent leaf area lost to herbivory versus distance (0-5m; 5-10m; 10-15m; 15-20m and 20-25m) from each parent tree were non-significant for all three species, *Pouteria altissima*, *Newtonia buchananii* and *Isolona pleurocarpa* (Table 4.1 - 4.3). Degrees of freedom (n-1) in the analyses (Table 4.1 – 4.3) varied between species because some plots contained no seedlings. Average percent leaf area lost to herbivory showed no consistent trend with increasing distance from parent trees among the three study species (Figure 4.3 – 4.5). Leaf area lost to herbivory showed a negative, but non-significant, relationship with distance from parent / conspecific adult trees for *Pouteria altissima* (Figure 4.2). *Newtonia buchananii* seedlings showed close to no change (slightly positive) in leaf area lost to herbivory with increasing distance from parent / conspecific adult trees (Figure 4.3). *Isolona pleurocarpa* showed a slightly positive, but non-significant, relationship in the degree of seedling leaf area lost to herbivory with increasing distance from parent / conspecific adult trees.

Table 4.1 Regression results: *Pouteria altissima* average percent seedling leaf herbivory in plots versus distance: 0-5m; 5-10m; 10-15m; 15m-20m; 20-25m away from each of twenty conspecific adults.

Model	df	Sum of Squares	Mean Square	F value	Sig.
Regression	1	454.411	454.411	2.67	0.105
Residual	98	16679.44	170.198		

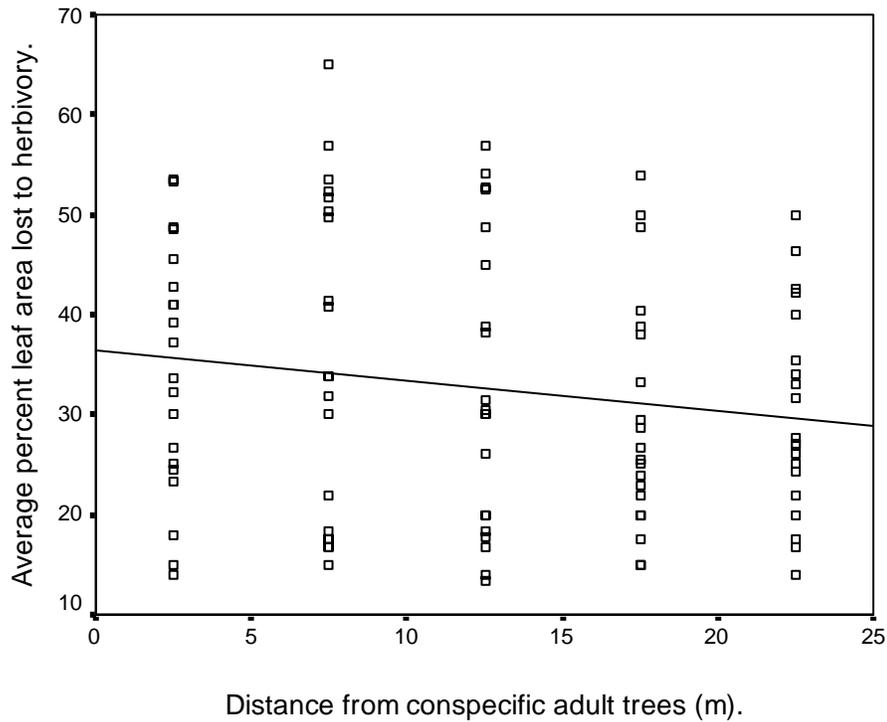


Figure 4.3 *Pouteria altissima* : regression plot of average percent seedling leaf herbivory in plots at each distance for twenty conspecific adult trees. The regression equation is: $y = -0.3015x + 36.372$ ($P = 0.105$)

Table 4.2 Regression results: *Newtonia buchananii* average percent seedling leaf herbivory in plots versus distance: 0-5m; 5-10m; 10-15m; 15m-20m; 20-25m away from each of twenty conspecific adults.

Model	df	Sum of Squares	Mean Square	F value	Sig.
Regression	1	1.072	1.072	0.021	0.884
Residual	82	4107.867	50.096		

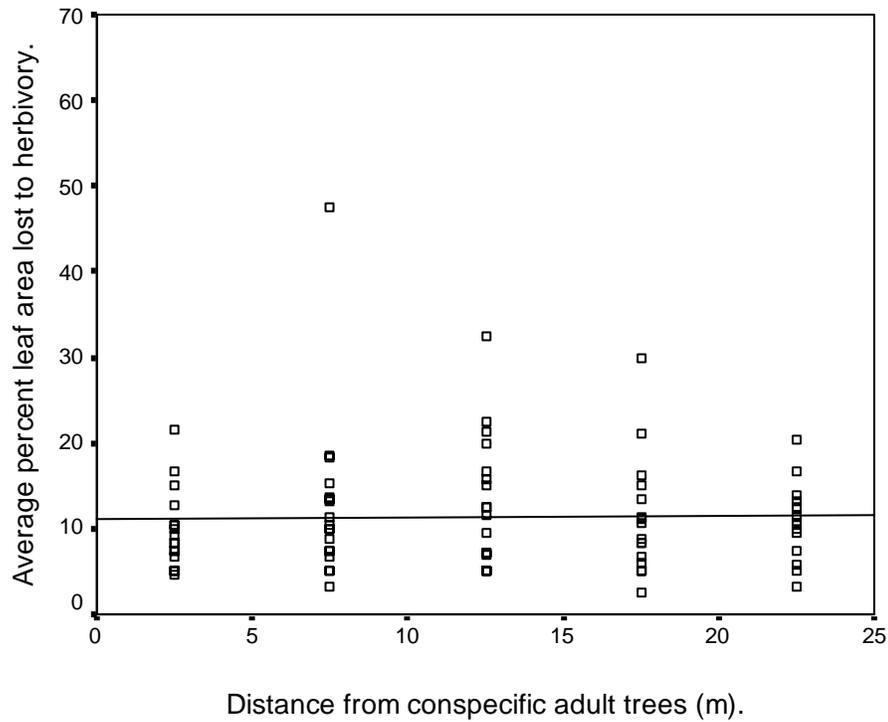


Figure 4.4 *Newtonia buchananii*: regression plot of average percent seedling leaf herbivory in plots at each distance for twenty conspecific adult trees. The regression equation is: $y = 0.0165x + 11.195$ ($P = 0.884$).

Table 4.3 Regression results: *Isolona pleurocarpa* average percent seedling leaf herbivory in plots versus distance: 0-5m; 5-10m; 10-15m; 15-20m; 20-25m away from each of twenty conspecific adults.

Model	df	Sum of Squares	Mean Square	F value	Sig.
Regression	1	5.62	5.62	0.098	0.755
Residual	78	4457.2	57.144		

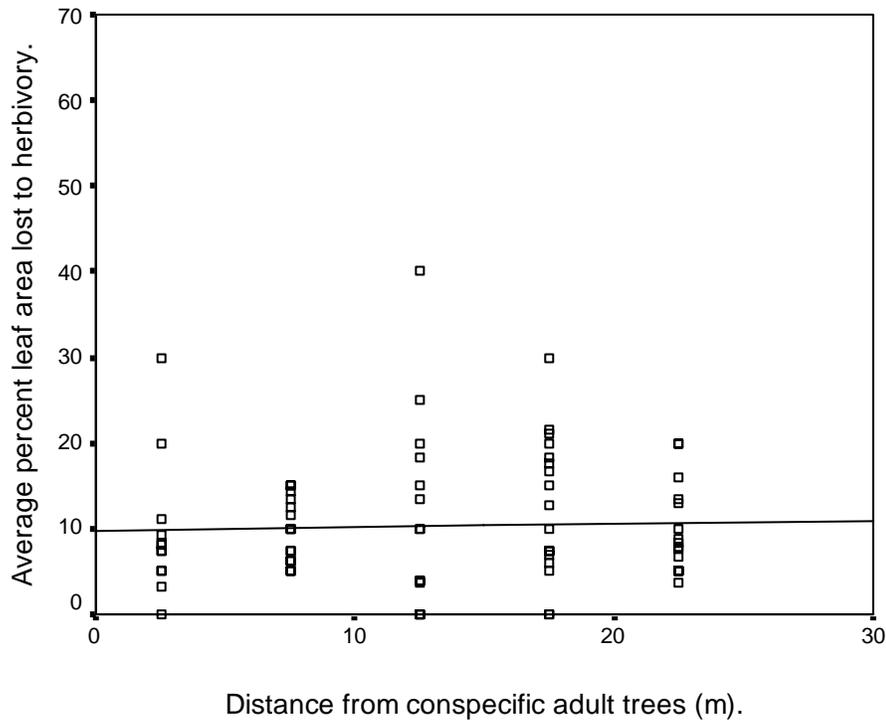


Figure 4.5 *Isolona pleurocarpa* regression plot of average percent seedling leaf herbivory in plots at each distance for twenty conspecific adult trees. The regression equation is: $y = 0.0383x + 9.8367$ ($P = 0.755$).

4.4 DISCUSSION

Although non-significant, each species showed a different trend in leaf area lost to herbivory versus distance from conspecific adult trees (Figure 4.2 – 4.4).

The difference in trends shown among the three study species may be attributable to their differing leaf types (Figure 2.5, 2.7 and 2.8) and leaf chemistry. The lower amount of leaf herbivory on *Newtonia buchananii* and *Isolona pleurocarpa* seedlings compared to *Pouteria altissima* seedlings (Figure 4.2 - 4.4) may be due to higher levels of tannins and phenols in their leaves (Givnish 1999). *N. buchananii* showed the least change in herbivory with distance (Table 4.4). This may be because *N. buchananii* has large compound leaves composed of many small thick, tough leaflets (Figure 2.7), where thick,

tough leaves with thick cell walls are likely to be effective against a broad spectrum of herbivores and some pathogens (Givnish 1999). The non-significant relationship, and barely any change in leaf area lost to herbivory with distance for *I. pleurocarpa* seedlings may be because of their sparse distribution during the study period (Table 3.2). Their sparse distribution would make it difficult for many density dependant predators to move between seedlings and therefore survive (Janzen 1970). Therefore, herbivory may have been mainly by generalist herbivores, which are unlikely to preferentially feed on *I. pleurocarpa* seedlings near to parent / conspecific adult trees (Janzen 1970).

Another possible reason for the non-significant results is that adverse environmental conditions, or low food abundance in the past season had caused there to be a lack of host specific herbivores (Connell 1971). This is likely in a seasonal dry forest such as Ngel Nyaki where the dry season would be adverse to desiccation intolerant herbivores such as insects, fungi and nematodes (Givnish 1999).

If the tree species studied were usually attacked by specialist herbivores, but they were low in numbers or absent, then generalist herbivores, which are less likely to focus their feeding near to parent / conspecific adult trees (Janzen 1971), may have caused herbivory levels not to change with distance from parent trees (Howe *et al.* 1985). Mammalian herbivores such as porcupines, rodents, pigs and duikers are present in Ngel Nyaki (*pers. obs*) and are likely always to be generalists (Leigh *et al.* 2004). These generalist herbivores may cause highest damage to seedlings away from parent trees and work against patterns of high mortality under parent / conspecific adult trees caused by host specific herbivores (Howe *et al.* 1985).

The measurements of herbivory made in this study may not have revealed the true rates of herbivory on seedlings near to as opposed to away from parent / conspecific adult trees. This is because most (approximately 70 %) of tissue loss to herbivores occurs when a leaf is young and has a soft texture, thin cell walls, low concentrations of tannins and phenols and high nutritional quality (Givnish 1999; Coley & Barone 1996). Herbivores prefer, and usually will only eat the edges of mature leaves (Clark & Clark 1985). Thus, the estimates of total leaf area lost to herbivory made at one point in time as used in this

study does not reveal the amount of tissue lost in new leaves, where a higher new leaf turn-over rate may have occurred on seedlings close to parent / conspecific adult trees. The greater amount of new leaves lost by seedlings closer to parent / conspecific adult trees would stunt their growth (Clark & Clark 1985), and this is consistent with the result of greater seedling survival (measured as height) away from parent / conspecific adult trees found in Chapter 3. I was unaware of the fact that herbivory was much greater on new leaves than on old leaves prior to making the measurements for this investigation therefore it was not taken into account.

Also related to suppressing growth, and not measured in this study, is the amount of apical meristem damage (Clark & Clark 1985). Results of studies on seedlings in a forest in Costa Rica by Clark & Clark (1985) revealed that meristem damage suppressed seedling growth and that meristem damage was higher for seedlings closer to parent / conspecific adult trees and for seedlings in higher densities. Meristem damage was not measured in this study because it was thought that measuring leaf herbivory would be sufficient to reveal any patterns in herbivory with distance from parent / conspecific adult trees.

A number of studies in seasonal forests have reported that trees produce a flush of new leaves at the end of the dry season before the peak in herbivorous insect biomass at the start of the rainy season (Givnish 1999) but the authors did not say whether seedlings behave in this way as well. It is also possible that the seedlings produce an ephemeral super abundance of edible tissue, which temporarily overwhelms their herbivores (Clark & Clark 1991), which could obscure patterns in herbivory with distance from parent / conspecific adult trees.

Despite all the possibilities as to how density / distance dependant effects by herbivores may have remained undetected by this study (Harms *et al.* 2000; Givnish 1999; Coley & Barone 1996; Clark & Clark 1991; 1985; Janzen 1971) (despite in fact occurring), it is also possible that the majority of herbivores in Ngel Nyaki are not host specific. This is

consistent with Novtny *et al.*'s (2002) findings that herbivorous insects show low host specificity.

Ngel Nyaki's seasonal climate may not favor a great diversity of host specific invertebrates because of its long dry season (mid-October-mid April) and the fact that many invertebrates are desiccation intolerant (Leigh *et al.* 2004; Givnish 1999).

The non-significant results found in this study may be because herbivory is not as important a factor in Ngel Nyaki for causing seedling survival to be lowest near to parent trees as Janzen (1970) and Connell (1971) suggested it was for non-seasonal tropical lowland forests. In support of this argument, Coley and Barone (1996) reported that the daily rates of herbivory on young leaves in tropical wet forests (mean=0.70 %/per day) are more than four times higher than those in tropical dry forests (mean=0.15 % per day). Despite this, it is more likely that herbivory is important in Ngel Nyaki, because as Coley and Barone (1996) report, herbivory on young leaves and mature leaves combined is higher in tropical dry forests (14.2 %/yr) than in tropical wet forests (11.1 %/yr). In addition the results in Chapter 3 suggest that seedling survival is lowest near to parent trees. Also, for the reasons given in this chapter, although undetected, herbivory may be an important cause of mortality creating this pattern. Measurements of leaf herbivory that keep track of all leaves lost over time may reveal that herbivory is highest near to parent / conspecific adult trees in Ngel Nyaki.

CHAPTER 5: TESTING WHETHER OR NOT SURVIVAL INCREASES AND HERBIVORY DECREASES WITH DISTANCE AWAY FROM CONSPECIFIC ADULT TREES FOR EXPERIMENTALLY PLANTED SEEDLINGS.

5.0 INTRODUCTION

The aim of this chapter is to test the hypothesis (1) that seedling survival increases at distances away from conspecific adult trees and (2) that seedling herbivory decreases with distance away from conspecific adult trees. Here I use experimentally planted seedlings to measure the effect of increased distance from conspecific adult trees on seedling survival and leaf herbivory.

The Janzen-Connell hypothesis predicts that seedling survival will be lowest under parent / conspecific adult trees because each tree species in a tropical forest has host specific herbivores. These herbivores, typically insects, usually live and feed in the canopies of adult trees and also descend to feed on conspecific seedlings underneath the parent / conspecific adult. These host specific herbivores do not leave the immediate vicinity of their host adult tree, after feeding on the conspecific seedlings directly beneath the host tree they return to its canopy (Janzen 1970; Connell 1971). While adult trees can tolerate the herbivory of their host specific herbivores the conspecific seedlings beneath them eventually die because they cannot withstand the loss of leaves and shoot tips to the same degree that the adult trees can (Janzen 1970). Other more mobile host specific herbivores respond to the density of seedlings (Janzen 1970). They focus their attack on high densities of seedlings where young seedling densities are highest under parent trees because this is where the majority of its seeds land (Janzen 1970). Therefore the Janzen-Connell model hypothesizes that seedling herbivory will be greatest for seedlings under parent / conspecific adult trees and thus seedling survival will be lowest there as well.

Although the same predictions of the Janzen-Connell model are investigated in this chapter as were investigated in Chapters 3 and 4, the approach is different. In Chapter 3 seedling height was used to estimate a seedlings age and thus its survival through time. Change in seedling

survival at increasing distance was inferred from the relative abundance of large seedlings at each distance (0-5m, 5-10m, 10-15m, 15-20m and 20-25m) away from parent / conspecific adult trees. In Chapter 4 seedling leaf herbivory was measured by visually estimating the percent of the total leaf area of a seedling that is missing. Remains of petioles indicating whole leaves lost were included in this estimate (Figure 4.2). Leaf herbivory was measured the same way in this chapter although it was measured over three months instead of at one point in time, and measurements were made on even - aged planted seedlings instead of a variety of ages of naturally occurring seedlings. Instead of inferring survival from seedling height as in Chapter 3, seedling height in this chapter was measured over three months on the planted seedlings to measure whether or not they managed to increase in height over time despite herbivory.

5.1 METHODS

Seed collection for the experimental plantings took place from the end of February to the end of March in the dry season of 2005. Unfortunately, ripe seeds were not abundant at the time of collection. My two field assistants and I searched the forest for ripe seeds. We came across a few species with ripe or nearly ripe seed. Of these species, common species in the forest with an abundance of available seeds were chosen. These were *Newtonia buchananii*, *Isolona pleurocarpa*, *Entandrophragma angolense*, *Sterculia setigera*, *Deinbollia pinnata* and *Polyscias fulva*. We collected between 50 – 300 seeds from each of them. It was possible to collect the seeds of all of these species except *P. fulva*, *D. pinnata* and *I. pleurocarpa* from the forest floor. The field assistants had to climb the trees to collect *P. fulva*, *D. pinnata* and *I. pleurocarpa* fruits as they were not quite ripe. We peeled the fruits of *D. pinnata* and *I. pleurocarpa* to expose their seeds, and dried them, and the small fruits of *P. fulva* for a week on black plastic sheeting in the sun. Three seeds of each species were planted in each of four plastic planting bags (Figure 5.1 (c)) in order to test how many of, and how quickly each species seeds germinated. Many of the *D. pinnata*, *E. angolense* and *S. setigera* seeds germinated within 2 to 3 weeks, *N. buchananii*, *P. fulva* and *I. pleurocarpa* seeds did not germinate at all. In order to have enough replicates for the experimental design (see below) we collected more seeds of *D. pinnata*, *E. angolense* and *S. setigera* until we had a minimum of 600 seeds for each species.

The seeds were germinated, and seedlings raised in two nurseries. The nurseries were constructed on the forest edge just under the canopy (see Figure 5.1). This was done in order to shelter the seedlings from possible destruction of the nurseries by cattle grazing, and to avoid direct sunlight which would cause rapid evaporation of water from the soil in planting bags. The nurseries, being under the forest canopy also kept the seedlings in an environment of higher moisture and less day / night temperature fluctuation than they would have experienced in the grassland. Night time temperatures in the dry season are cooler than in the wet season when many seedlings germinate (*pers. comm* field assistants) and thus cool temperatures may adversely affect seedling germination and growth. After the majority of seeds had germinated plastic sheeting was used to make roofs for the nurseries (not shown in Figure 5.1) in order to accelerate seedling growth by trapping heat and moisture in them. Once the seedlings had reached an average height of about 15cm they were planted in the forest. They were planted in rows of ten at 1m, 12.5m, and 25m away from conspecific adult trees (Figure 5.2). Seedlings were planted in this fashion under a total of 18 conspecific adult trees for *Sterculia setigera*, 19 conspecific adult trees for *Deinbollia pinnata* and 20 conspecific adult trees for *Entandrophragma angolense*. The number of replicates varied among the species due to differing amounts of seedlings being successfully raised (Table 5.1). Care was taken to ensure that the conspecific adult trees under which the seedlings were planted were not closer than 50m to each other in order to avoid the sharing of predators among them as expected by the Janzen-Connell model (Janzen 1970). Coloured tape was tied to stakes at the end of each seedling row, and to the stems of seedlings in order to aid relocation of the seedlings over time. All the seedlings had been planted by mid-June in the wet season of 2005. After planting seedling heights were measured, and leaf herbivory was estimated once a month for three months. Seedling height over time, or growth, was used to estimate plant performance following the method of Howe (1990). Seedling leaf herbivory was measured by visually estimating the percentage of a seedlings total leaf area (when the leaf areas of all leaves are combined) that was missing (Stotz *et al.* 2000). This estimate included leaves which were entirely missing as evident from cut off petioles (Figure 4.2). Seedlings were measured in the same order they were planted in to keep time intervals between measurements as similar as possible.



Figure 5.1 Building of nurseries: (a) Clearing / leveling a space for a nursery just inside from the forest edge. (b) building grass walls. (c) Filling plastic bags with soil. (d) a completed nursery .

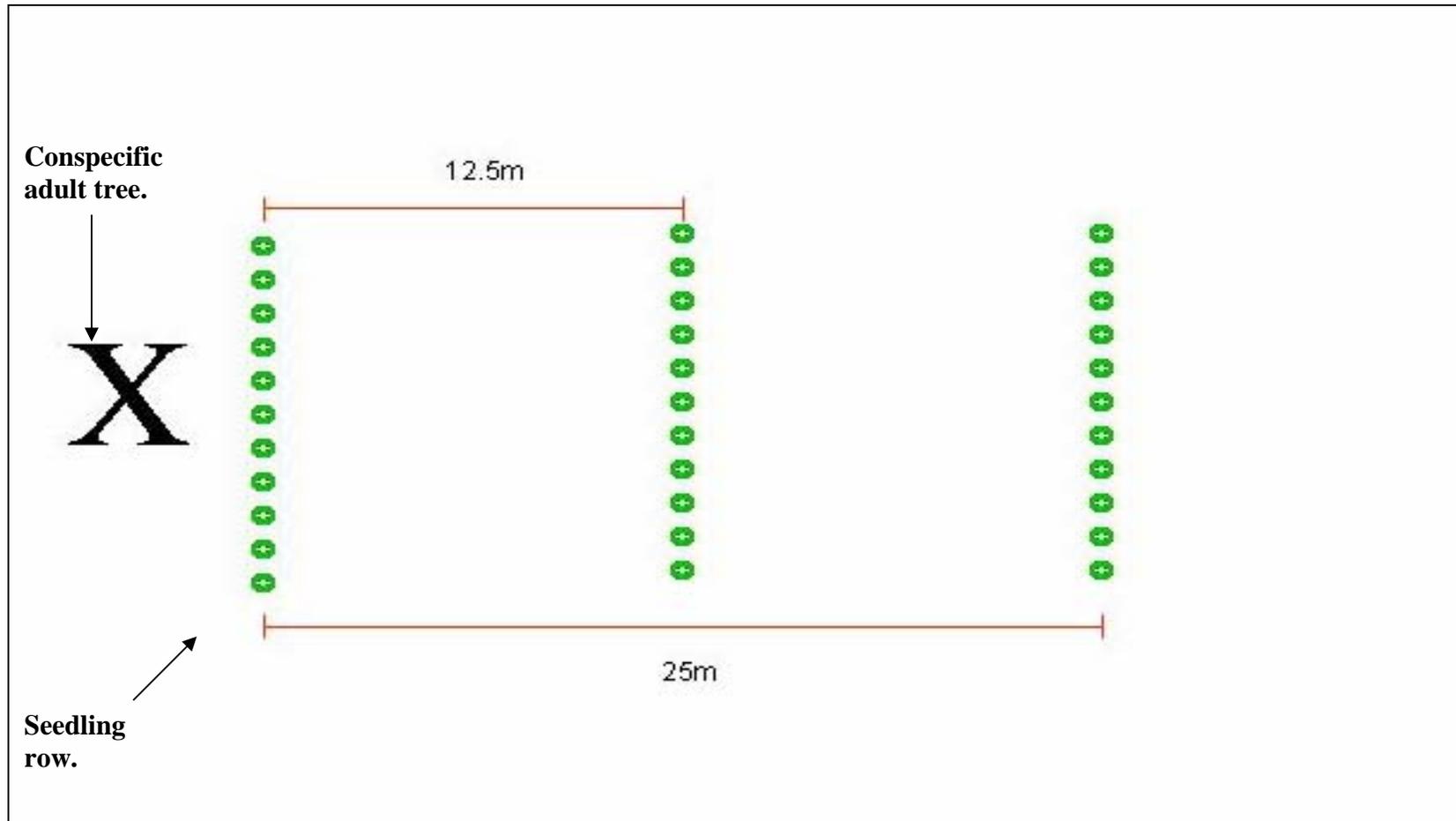


Figure 5.2 Experimental design for seedling plantings: Seedlings were planted in rows of ten at 1m, 12.5m and 25m away from conspecific adult trees.

5.2 DATA ANALYSIS METHODS

5.2.1 SEEDLING SURVIVAL

The seedling survival data was composed of two data sets. The first data set was survival recorded as presence / absence of seedlings over time. It was analysed by tallying the proportion out of ten seedlings in a row that survived at 1m, 12.5m and 25m from each conspecific adult tree at each month for each species. The mean of proportions of seedlings surviving at each month, at each distance, was calculated for each species. Then the means of the proportions of seedlings surviving at each month was graphed on a logarithmic scale for each distance for each of the three species (Figure 5.3 – 5.5). Survival was graphed on a logarithmic scale because the proportion of seedlings surviving decreased over time, so it shows decreases as the difference in the proportion of seedlings surviving in one month relative to the proportion surviving in the previous month.

The proportions of seedlings surviving at each distance for each replicate were then analysed by analysis of variance (ANOVA) using Microsoft Excel. All three species were entered at once, with the proportions of their seedlings surviving at each distance for each replicate at month three. Only the data from month three was analysed because it was the last measurement made in time. By month three seedlings had been exposed to mortality factors for the longest time period so any differences between distances in seedling mortality were expected to be greatest then. Also because survival was measured at each distance, and also over three months, the analyses would become unnecessarily complicated involving a repeated measures analysis of variance on the effect of distance and time on survival. The ANOVA was used to detect whether a significant proportion of the variance in the mean leaf area lost to herbivory could be explained by species, distance or the interaction term species*distance. The ANOVA result would reveal whether distance or species had an effect on survivorship and the interaction term species*distance would reveal whether the three species seedlings responded in the same way to increased distance from conspecific adult trees.

5.2.2 SEEDLING GROWTH

The second seedling survival data set was composed of seedling heights, where seedling height over time, or growth, was used to estimate plant performance (Howe 1990). The seedling height data was analysed by calculating the mean height of seedlings in a row at 1m, 12.5m, and 25m away from conspecific adult trees for each replicate for each month. Then the mean of mean seedling heights for all replicates at each month was graphically presented for each distance for each species (Figure 5.7 - 5.9). The mean height replicates at each distance at month three were then analysed by analysis of variance (ANOVA) using Microsoft Excel. Only data from month three was analysed because the differences between distances in seedling heights were assumed to be most pronounced at month three, and it avoided unnecessary complicated analyses (see above section 5.2.1). All three species were entered at once with their mean heights for each replicate at each distance at month three. The ANOVA was used to detect whether a significant proportion of the variance in mean heights could be explained by species, distance or the interaction term species*distance. The ANOVA result would reveal whether distance or species had an effect on seedling height and the interaction term species*distance would reveal whether the three species seedlings responded in the same way to increased distance from conspecific adult trees.

5.2.3 LEAF HERBIVORY

The seedling leaf herbivory data was analysed by calculating firstly, the mean percent leaf area lost to herbivory for seedlings in each row, for each distance, at month three for each species. This gave 18, 19, 20 mean values at each distance (1m, 12.5m and 25m) for *Sterculia setigera*, *Deinbollia pinnata* and *Entandrophragma angolense* respectively (Table 5.1). Only data from month three was analysed because the differences between distances in seedling leaf area lost to herbivory were assumed to be most pronounced at month three and it avoided unnecessary complicated analyses (see above section 5.2.1). Also, 100 % leaf area was often lost in one month but the following month seedlings had made new leaves so that herbivory was back to 0 % (Figure 2.13) which made analyses

over the three months difficult. Regressions plots on these mean herbivory data for each distance away from conspecific adult trees describe the change in the means of percent leaf area lost to herbivory with distance from conspecific adult trees for each species (Figure 5.9 – 5.11).

Change in the degree of seedling leaf herbivory with distance was analysed by analysis of variance (ANOVA) using Microsoft Excel. All three species were entered at once with the mean leaf area lost to herbivory for each replicate, at each distance, at month three. The ANOVA was used to detect whether a significant proportion of the variance in mean leaf area lost to herbivory could be explained by species, distance or the interaction term species*distance. The ANOVA result would reveal whether distance or species had an effect on leaf area lost to herbivory and the interaction term species*distance would reveal whether the three species seedlings responded in the same way to increased distance from conspecific adult trees.

5.3 RESULTS

5.3.1 SEEDLING SURVIVAL

The mean of average proportions of seedlings surviving decreased over the three months for all three species, but the amount by which survival decreased over the months differed among the distances away from conspecific adult trees and among species (Figure 5.3 – 5.5). Decrease in survival over time was lowest for *Deinbollia pinnata* (Figure 5.3), intermediate for *Sterculia setigera* (Figure 5.4) and greatest for *Entandrophragma angolense* seedlings (Figure 5.5). The amount by which survival decreased over the three months became greater with increasing distance away from conspecific adult trees for *S. setigera* (Figure 5.4) seedlings. The decrease in survival over time for *D. pinnata* (Figure 5.3) and *E. angolense* (Figure 5.5) seedlings was greatest at 0.5m, intermediate at 25m and lowest at 12m away from conspecific adult trees.

The analysis of variance for a significant difference in seedling survival rate between each distance from conspecific adult trees for all three species combined, at month three was not significant (p-value = 0.597) (Table 5.2). The p-value for the interaction term species*distance was 0.873 (Table 5.2) so the species did not significantly differ in their response regarding the effect of distance on seedling survival.

Table 5.1 For each species N_1 = Sum of replicates at each of three distances (one replicate is the mean of a seedling row); For each Distance N_2 = Sum of replicates for all three species (one replicate is the mean of a seedling row).

Between-Subjects factors	
Species	N_1
<i>Sterculia setigera</i>	54
<i>Deinbollia pinnata</i>	57
<i>Entandrophragma angolense</i>	60
Distance	N_2
0-1m	57
12.5m	57
25m	57

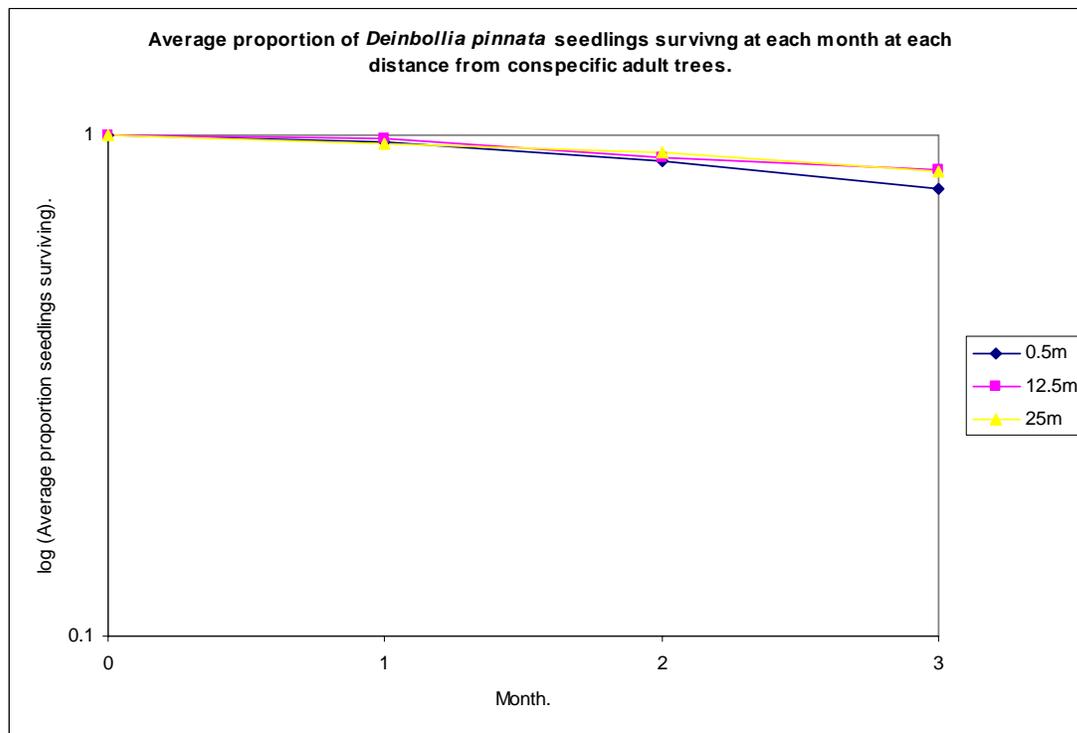


Figure 5.3 *Deinbollia pinnata*: average proportion of seedlings surviving each month for each distance from conspecific adult trees.

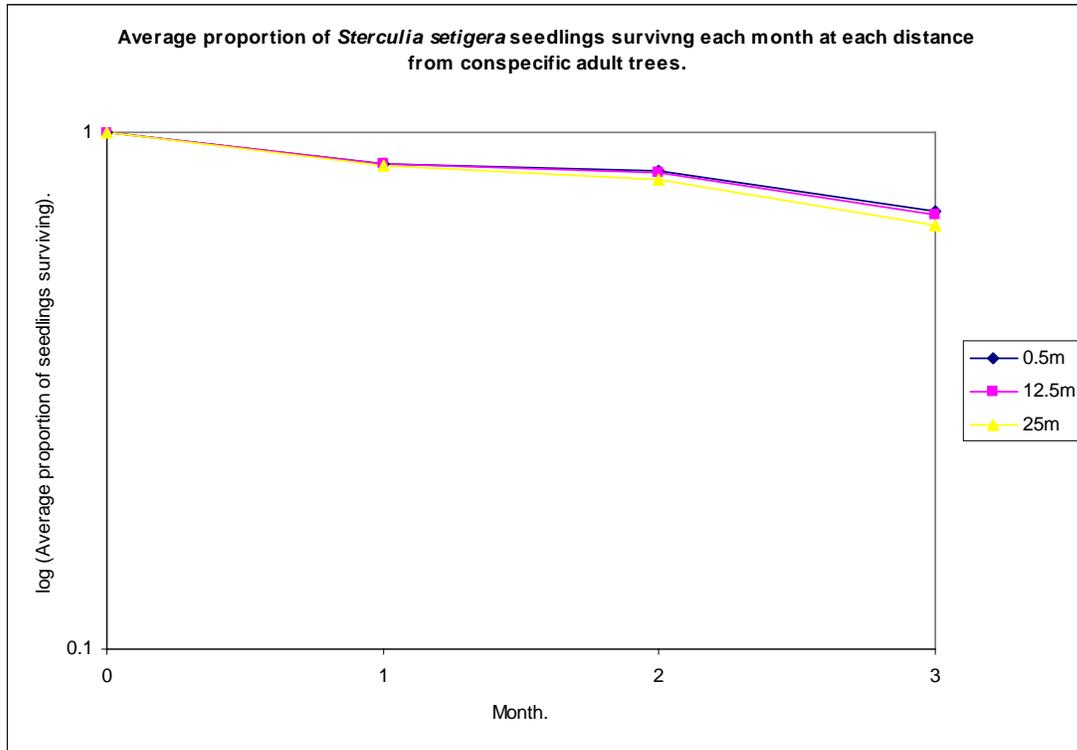


Figure 5.4 *Sterculia setigera*: average proportion of seedlings surviving each month for each distance from conspecific adult trees.

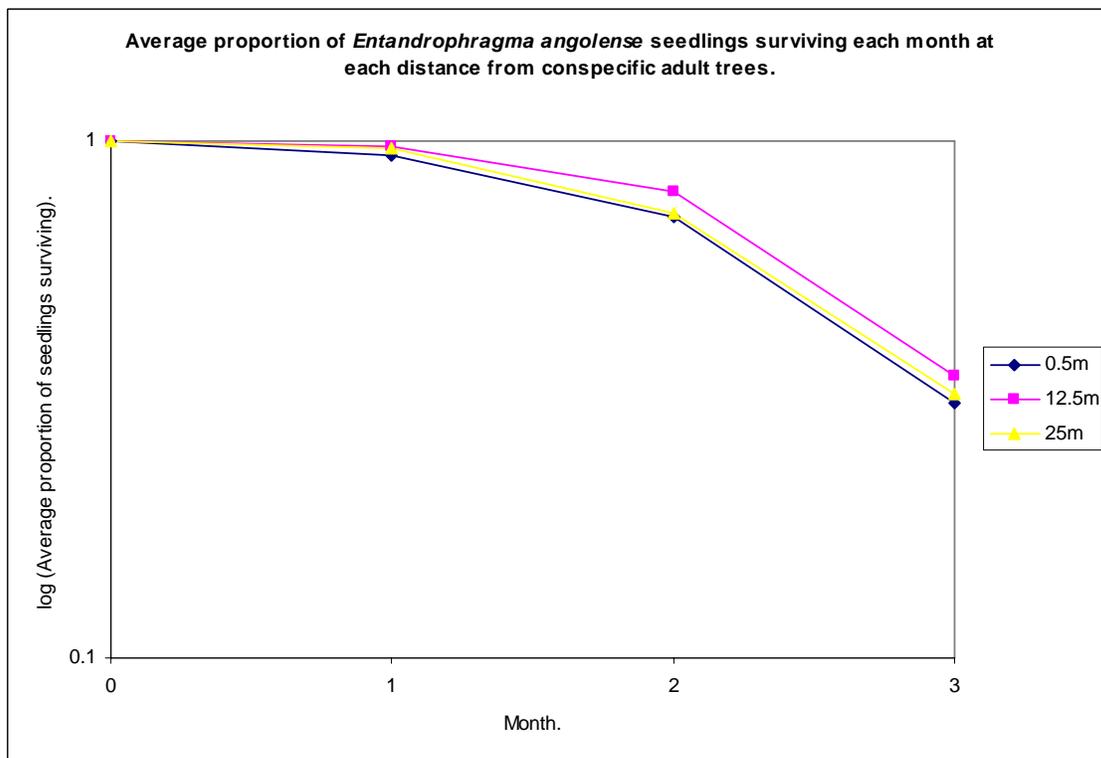


Figure 5.5 *Entandrophragma angolense*: average proportion of seedlings surviving each month for each distance from conspecific adult trees.

Table 5.2 ANOVA result: To test whether or not species, distance and/or species*distance explains a significant portion of variation in proportions of seedlings surviving among replicates at each distance from conspecific adult trees, for all three species at month three.

Test of Between-Subjects Effects					
Dependant Variable: Average proportion of seedlings surviving					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected model	7.976a	8	0.997	16.345	0.000
Intercept	64.527	1	64.527	1057.901	0.000
DISTANCE	0.06319	2	0.0316	0.518	0.597
SPECIES	7.786	2	3.893	63.827	0.000
DISTANCE * SPECIES	0.07504	4	0.01876	0.308	0.873
Error	9.881	162	0.061		
Total	81.23	171			
Corrected Total	17.857	170			

a. R Squared = 0.447 (Adjusted R Squared = 0.419)

5.3.2 SEEDLING GROWTH

The mean of average seedling heights at each distance over time showed varying trends among the three study species. The mean of average seedling height decreased slightly at all distances for *Sterculia setigera* (Figure 5.6), it increased over time at all distances for *Deinbollia pinnata* (Figure 5.7) and decreased dramatically at all distances for *Entandrophragma angolense* (Figure 5.8). Means of average seedling height at each distance over the three months for *S. setigera* were highest at 12.5m, intermediate at 0.5m and lowest at 25m from conspecific adult trees (Figure 5.6). Means of average seedling height at each distance over the three months for *D. pinnata* were highest at 25m, intermediate at 12.5m and lowest at 0.5m from conspecific adult trees (Figure 5.7). Means of average seedling height at each distance over the three months for *E. angolense* were highest at 12.5m, intermediate at 25m and lowest at 0.5m from conspecific adult trees (Figure 5.8).

The differences between the distances in mean seedling heights at month three for all species combined were non-significant (p-value = 0.511) (Table 5.4). The p-value for the interaction term species*distance was 0.769 (Table 5.4) so the species did not significantly differ in their response regarding the effect of distance on seedling height.

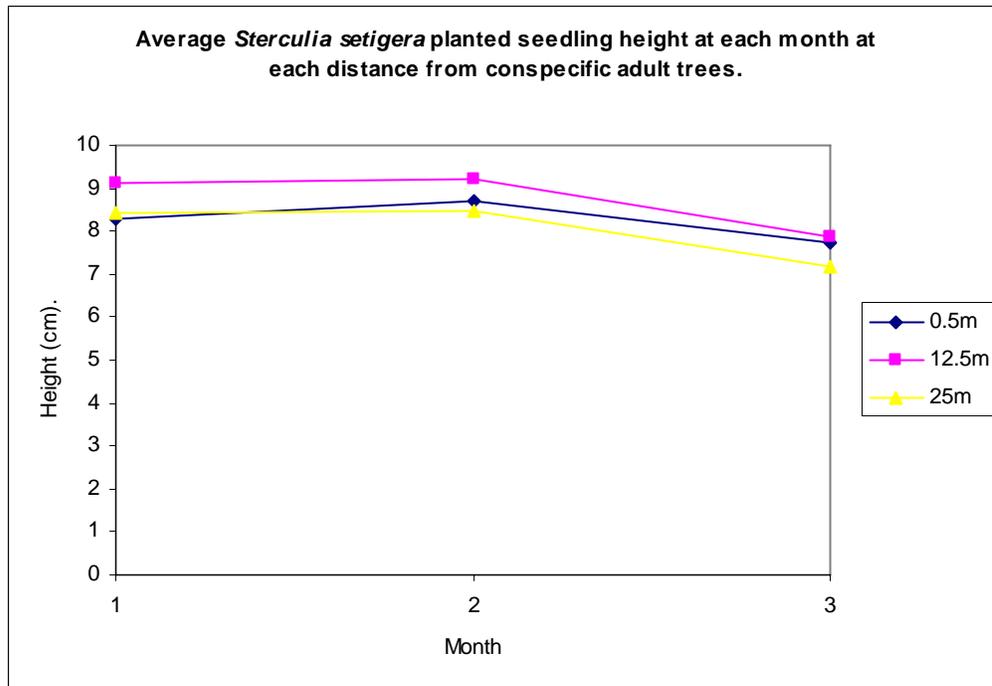


Figure 5.6 *Sterculia setigera*: Average planted seedling height at each month at each distance from conspecific adult trees.

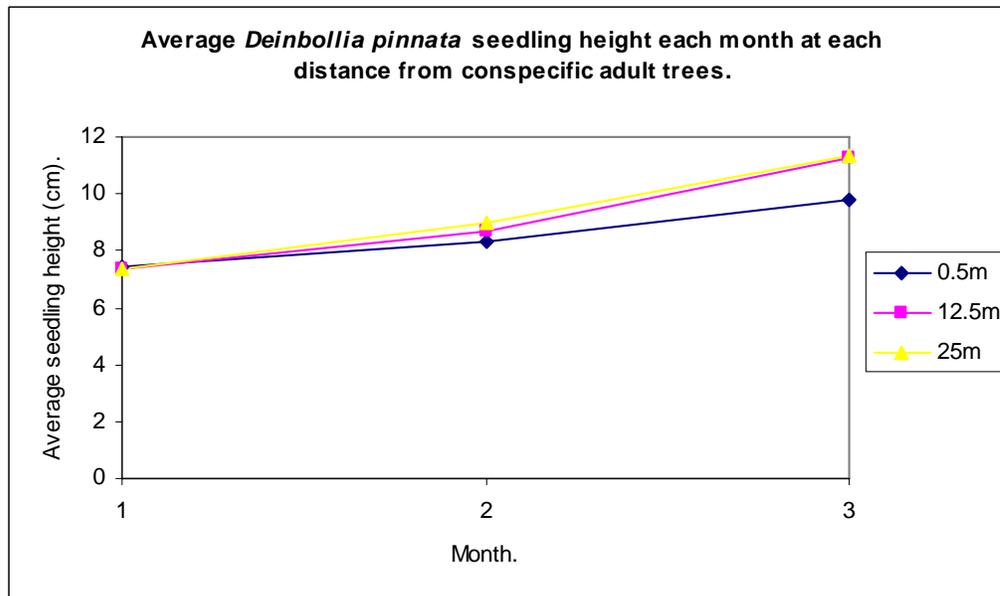


Figure 5.7 *Deinbollia pinnata*: Average planted seedling height at each month at each distance from conspecific adult trees.

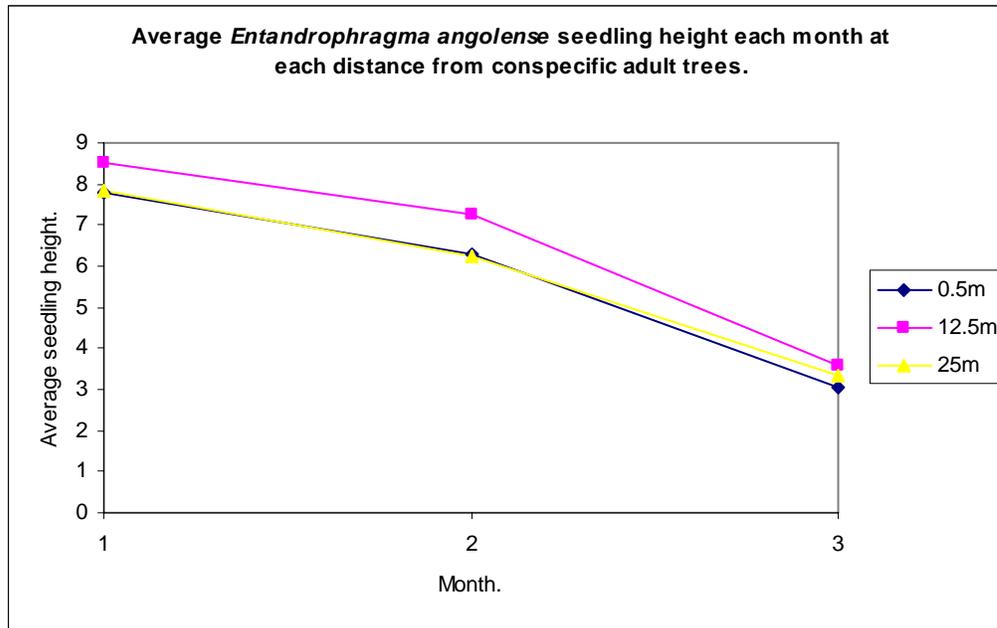


Figure 5.8 *Entandrophragma angolense*: Average planted seedling height at each month at each distance from conspecific adult trees.

Table 5.3 ANOVA result: To test whether or not species, distance and/or species*distance explains a significant portion of variation in mean seedling heights among replicates at each distance from conspecific adult trees, for all three species at month three.

Test of Between-Subjects Effects					
Dependant Variable: Heights					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected model	1680.332a	8	210.014	18.071	0.000
Intercept	8934.432	1	8934.432	768.656	0.000
SPECIES	1643.106	2	821.553	70.681	0.000
DISTANCE	15.691	2	7.845	0.675	0.511
SPECIES * DISTANCE	21.15	4	5.288	0.455	0.769
Error	1882.998	162	11.623		
Total	12330.32	171			
Corrected Total	3563.33	170			

a. R Squared = 0.472 (Adjusted R Squared = 0.445)

5.3.3 LEAF HERBIVORY

The regression plots of the mean seedling leaf area lost to herbivory against distance from conspecific adult trees at month three show that mean leaf area lost to herbivory decreased with distance for all three species (Figure 5.9 – 5.11). Although the slope is negative the decrease in herbivory for *Entandrophragma angolense* seedlings is negligible (Figure 5.11). The analysis of variance revealed that distance did not explain a significant proportion of the variation in leaf herbivory (p-value = 0.173) (Table 5.6).

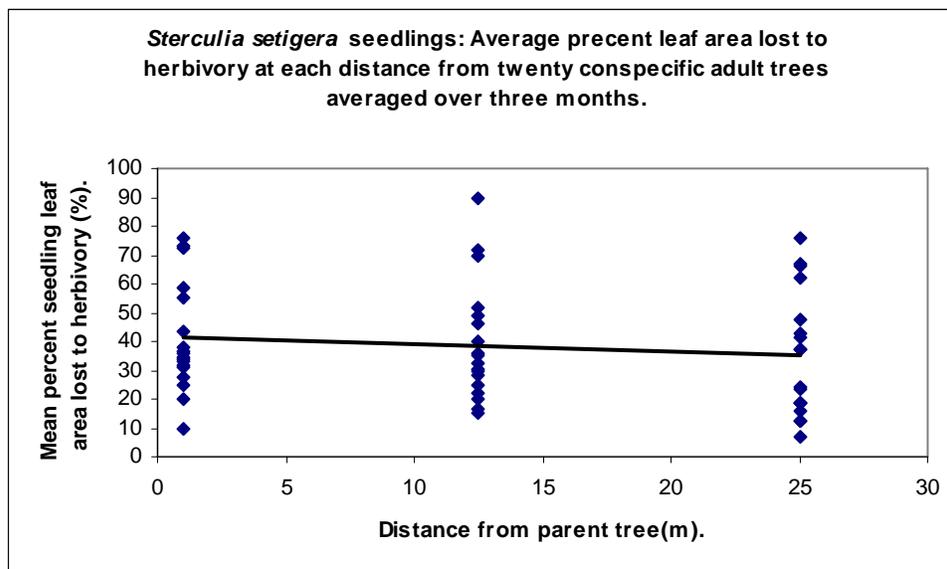


Figure 5.9 Regression plot: mean *Sterculia setigera* seedling leaf area lost to herbivory for each replicate against distance from conspecific adults at month three. The regression equation is: $y = -2.963x + 44.262$ ($R^2 = 0.0146$).

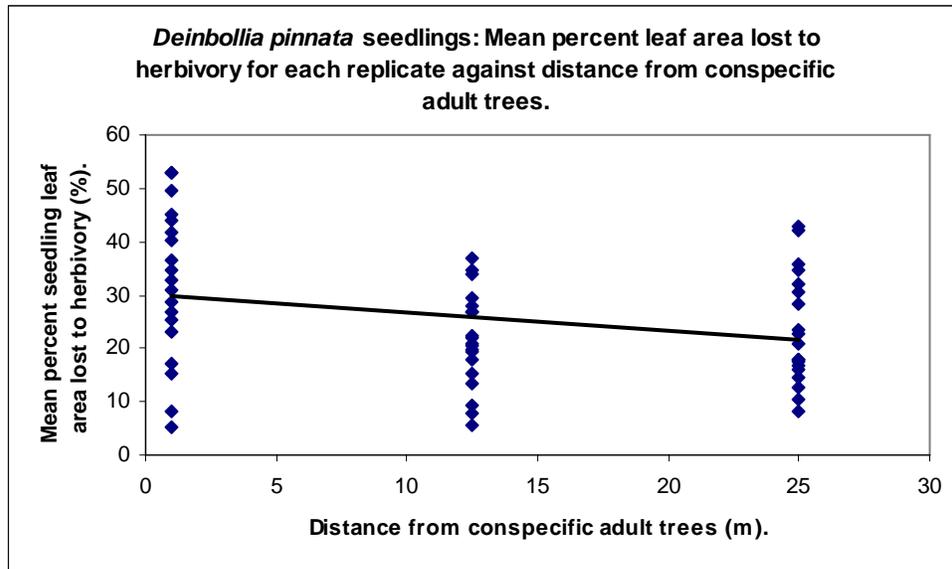


Figure 5.10 Regression plot: mean *Deinbollia pinnata* seedling leaf area lost to herbivory for each replicate against distance from conspecific adults at month three. The regression equation is: $y = -4.3342x + 34.403$ ($R^2 = 0.0865$).

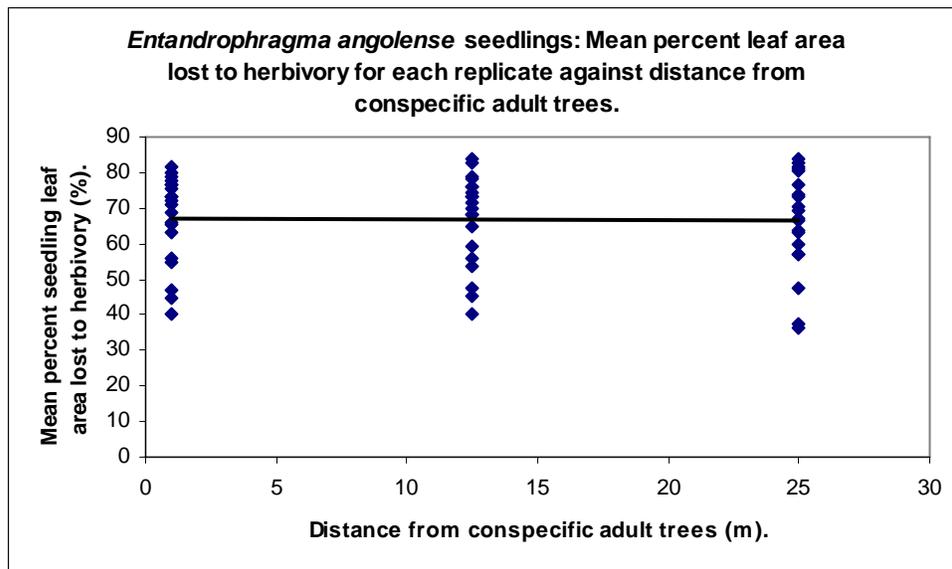


Figure 5.11 Regression plot: mean *Entandrophragma angolense* seedling leaf area lost to herbivory for each replicate against distance from conspecific adults at month three. The regression equation is: $y = -0.3767x + 67.624$ ($R^2 = 0.0006$).

Table 5.4 ANOVA result: To test whether or not species, distance and/or species*distance explains a significant portion of variation in leaf herbivory among replicates at each distance from conspecific adult trees, for all three species at month three.

Test of Between-Subjects Effects					
Dependant Variable: Average percent leaf herbivory.					
Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected model	53683.708a	8	6710.463	28.552	0.000
Intercept	325168.344	1	325168.344	1383.525	0.000
SPECIES	52130.45	2	26065.225	110.902	0.000
DISTANCE	832.458	2	416.229	1.771	0.173
SPECIES * DISTANCE	742.691	4	185.673	0.79	0.533
Error	38074.688	162	235.029		
Total	425044.539	171			
Corrected Total	91758.396	170			

a. R Squared = 0.585 (Adjusted R Squared = 0.565)

5.4 DISCUSSION

The mean proportions of seedlings surviving decreased over the three months for all three species *Deinbollia pinnata*, *Sterculia setigera* and *Entandrophragma angolense* (Figure 5.3 – 5.5), but differences in proportions of seedlings surviving among the distances from conspecific adult trees (1m, 12.5m and 25m) at month three were not significant (Table 5.2). Despite the differences between distances being non-significant, for *D. pinnata* and *E. angolense*, the means of the proportions of seedlings surviving was lowest at the closest distance (1m) to conspecific adult trees (Figure 5.3 and 5.5). Consequently, although differences among distances were non-significant, the results indicate that seedling survival may be lowest near to conspecific adult trees. Strength is given to this suggestion by the fact that the results in Chapter 3 support the hypothesis that seedling survival increases with distance from parent / conspecific adult trees, for at least some species, in Ngel Nyaki forest.

The means of average seedling height for each replicate decreased over time for *S. setigera* (Figure 5.6) and dramatically so for *E. angolense* (Figure 5.8). There was no significant difference between the distances for mean seedling heights at month three for all three species (Table 5.4). This may be an indication that there is significant pressure on *S. setigera* and *E. angolense* seedlings from generalist herbivores, who do not usually concentrate their browsing near to parent trees (Hammond & Brown 1998; Howe *et al.* 1985). For instance, while measuring *S. setigera* seedlings it was discovered that

seedlings under three conspecific adult trees lay on a chimpanzee route to a stream. Almost all of these seedlings were completely eaten at all distances, and it is most likely that the chimpanzees had eaten them (*pers. comm* field assistants).

Additionally, seedling height may not have been significantly different between distances (1m, 12.5m and 25m) from conspecific adult trees because of other causes of damage which are not necessarily distance dependant such as by leaf litter (Augspurger 1992), or falling debris (Aide 1987). Otherwise damage could have been caused by host specific distance or density dependant herbivores that were able to locate seedlings at all distances at which the seedlings were planted (Hammond & Brown 1998; Augspurger 1984; Janzen 1970). For *D. pinnata* the mean average seedling height for replicates increased over the three month period and seedling leaf herbivory was lowest for this species (Figure 5.10), which may indicate that *D. pinnata* leaves are well defended against herbivores (Coley & Barone 1996). Plants that have chemically defended leaves often have specialist herbivores (Coley and Barone 1996) which are expected to cause seedling survival to be lowest near to parent / conspecific adult trees (Connell 1971; Janzen 1970). The idea that *D. pinnata* has specialist herbivores is further supported by the fact that although differences in herbivory between distances at month three were non-significant, leaf herbivory declined with distance (Figure 5.10). Although the average heights of seedlings for all three species were not significantly different among the three distances from conspecific adult trees at month three (Table 5.3), *D. pinnata* seedling height increments were lowest at the closest distance (0.5m) to conspecific adult trees (Figure 5.7). This may be an indication that for *D. pinnata* seedlings performance was lowest for seedlings near to conspecific adult trees, which is in accordance with the survival data for *D. pinnata* (Figure 5.4). The small but non-significant decline in *D. pinnata* seedling survival and increase in herbivory at the closest distances to parent / conspecific adult trees may become more exaggerated over time (Wright 2002). For example, in a study on *Dipteryx panamensis* seedlings Clark & Clark (1985) found that a small (8 %) increase in leaf loss caused an 85 % increase in annual seedling mortality.

Although seedling leaf area lost to herbivory was not significantly different among the distances among the three species at month three (Table 5.6), there was a decline in

herbivory with distance for all three species (Figure 5.0 – 5.11). Although the decreases with distance were not significant, the consistent pattern across species may be an indication that seedling leaf herbivory is greater near to conspecific adult trees. Again, a small increase in the rate of herbivory near to conspecific adult trees could have a larger effect over time (Wright 2002; Clark & Clark 1985). In addition, higher rates of herbivory on seedlings growing under conspecific adults may make those seedlings more vulnerable to mortality from other causes such as falling branches or secondary pathogen infection (Coley & Barone 1996).

While collecting seeds for experimental planting of *S. setigera* seedlings, a great abundance of juvenile beetles of the same species were observed inside unopened seed pods. Larger beetles were abundant in open pods and also on the ground surrounding the adult trees. It was assumed that the small beetles inside the seed pods and the larger beetles in open pods and on the ground were the same species because these were the only beetles present and the juveniles and adults were morphologically very similar except for that the smaller ones were bright red, the same colour as the seed pods. As many seeds had been attacked it is likely that these beetles are specialists on *S. setigera* seeds and use them to lay their eggs in. According to Janzen's (1970) model, pre-dispersal seed predation reduces seed crop size, decreasing the amount of seeds reaching the furthest distances to which they are dispersed, and therefore reducing the number of seedlings that survive to maturity. This would decrease the probability that *S. setigera* could form monospecific stands (Janzen 1970) and therefore according to the Janzen-Connell model it would contribute to maintaining tree species diversity in Ngel Nyaki (Janzen 1970; Connell 1971; Paine 1966).

E. angolense seedling survival (Figure 5.5) and seedling height (Figure 5.8) showed by far the greatest decline over the three month period of the experiment, and the level of leaf herbivory on *E. angolense* seedlings was highest among the three study species (Figure 5.11). As *E. angolense* seeds are wind dispersed, but heavy and do not disperse far (Chapman & Chapman 2001), they lie in a relatively large radial area around parent trees (*pers obs*). Chapman & Chapman (2001) hypothesized that the sparse, wide

distribution of *E. angolense* adults was because almost all seeds around adults are eaten most of the time and that only seeds dispersed considerable distances may be able to become established seedlings and reach adulthood. Consistent with this suggestion, it is possible that predators on *E. angolense* seedlings prey on seedlings in a large radial area around parent trees as they are normally distributed in this manner, and that very few survive. Therefore as seedlings were only planted up to 25m away in this experiment they were too close to detect a distance effect on increased survivorship, but recruitment is likely to still be consistent with the Janzen-Connell hypothesis.

In summary, seedling survival, performance and leaf herbivory were not significantly different between the distances from conspecific adult trees. Despite this, consistent with the Janzen-Connell hypothesis *Dienbollia pinnata* and *Entandrophragma angolense* seedlings had the lowest survival (Figure 5.3 and 5.5) and performance (Figure 5.7 and 5.8) at the closest distance (1m) from conspecific adult trees. Also consistent with the Janzen-Connell hypothesis is that although herbivory was not significant between distances at month 3 (Figure 5.4), all three species' seedling herbivory decreased with distance from conspecific adult trees. *E. angolense* seedlings showed only a slight decrease in herbivory with distance from conspecific adult trees (Figure 5.11). This may be because its host specific seedling predators forage over a larger distance around conspecific adults than the distance at which seedlings were planted. *Sterculia setigera* seedling recruitment may be reduced by the activity of host specific beetles which hatch from its seeds. According to the Janzen-Connell hypothesis this would decrease the chances of *S. setigera* forming monospecific stands which would contribute to the maintenance of tree species diversity in Ngel Nyaki (Connell 1970; Janzen 1970).

CHAPTER 6: TESTING WHETHER OR NOT TREE SPECIES IN NGEL NYAKI SHOW CLUMPED DISTRIBUTIONS.

6.0 INTRODUCTION

Janzen (1970) observed that the adults of most tree species in lowland tropical forests grow at low densities, and that they are more regularly distributed than normal, i.e. they have a more random distribution than if the probability of a new adult arriving at a point in the forest were proportional to the number of seeds arriving at that point.

Janzen (1970), and a number of other authors (Black *et al.* 1950; Richards 1952; Poore 1968; Ashton 1969 *as cited in* Janzen 1970), observed that tree species in temperate zone forests grew in higher densities with more clumped distributions than tree species in wet lowland tropical forests of similar areal extent, topographic diversity, and edaphic complexity.

Independently Janzen (1970) and Connell (1971) proposed that the activities of host specific predators were responsible for the difference in tree species distributions found in tropical forests compared to in temperate zone forests. They proposed that host specific predators cause seed / seedling survival to be lowest under parent / conspecific adult trees which opens up space surrounding parent / conspecific adult trees for the establishment on non-conspecifics. Janzen (1970) and Connell (1971) both hypothesized that the high tree species diversity and the species distribution in tropical lowland forests was maintained by the activities of a high abundance and diversity of host specific predators which prevent clumping of adult conspecific trees in wet lowland tropical forests. Based on work by Paine (1966), Janzen (1970) and Connell (1971) believed that if tree species were not prevented from becoming clumped they would form monospecific stands and out-compete other species, which would reduce tree species diversity in wet tropical lowland forests.

The aim of this chapter is to test whether the adult trees of tree species in Ngel Nyaki show clumped distributions or not.

6.1 METHODS

Clumping was measured by identifying a focal tree, measuring the distance to, and species identity of its nearest neighbour, and the distance to, and species identity of that neighbour's nearest neighbour. All trees measured were at least 8cm DBH, as it was assumed this would be large enough to ensure all trees measured were adults.

This method was based on papers by Batchelor (1973, 1975) where he uses nearest neighbour triplets as described above to estimate the density and dispersion of populations of animals or trees. While doing the data analysis for this investigation it turned out that Batchelor's (1973, 1975) formulae were unnecessarily complicated for testing clumping with the data I had collected, therefore a simpler data analysis method was adopted (see section 6.2).

200 triplets in total were measured. Focal trees were between 15m and 25m apart (Figure 6.1). Between thirty and fifty focal trees were measured down the length of each of five transects which ran from the top of the slope on which Ngel Nyaki is situated, downhill through the forest until coming out of the downhill forest edge. The five transects were evenly spaced through the forest from the south-west to the north east side of the forest (Figure 6.2) to ensure a good coverage of the forest (Figure 6.2). The degree of clumping was tested by checking for significant differences between the calculated expected and observed numbers of conspecific nearest neighbours for individual species or species groups using the Chi-square test (for more detail see section 6.2).

6.2 DATA ANALYSIS METHODS

Each of the 200 triplets of adult trees measured consisted of two sets of nearest neighbours. This gave 400 data points for whether a species had the same species or a different species as a nearest neighbour. The number of times a given species was observed out of the 400 was divided by 400, and then the quotient was multiplied by the number of times it was observed. This gave the number of conspecific nearest neighbours expected to occur by chance alone given the number of times that species was observed out of 400. Chi square tests require an expected value of at least 5 to ensure the power of the test (Dytham 1999). As most species were rare, all but the two most commonly observed species (*Anthonotha noldeae* and *Carapa*

procera) had to be combined in order to get the acceptable expected value of 5. The expected number of conspecific neighbours for a group was calculated by adding up the expected values for each individual species in a given group. The observed number of conspecific nearest neighbours for a species group was the sum of the numbers of observed conspecific nearest neighbours for each species in that group. In total there were two single species and two combined species groups (Figure 6.3).

The Chi Square value was calculated for each individual species and each species group. Because one observed number was compared to one expected value, the degrees of freedom was 1, and the corresponding critical value was 3.841.

51 out of the 400 trees measured had conspecific nearest neighbours. A *t*-test was used in order to determine whether there was a significant difference between the distances separating conspecific nearest neighbours and those separating non-conspecific nearest neighbours. If conspecific adults are generally further apart than non-conspecifics it would support the Janzen-Connell model that conspecifics repel each other (Connell 1971; Janzen 1970).

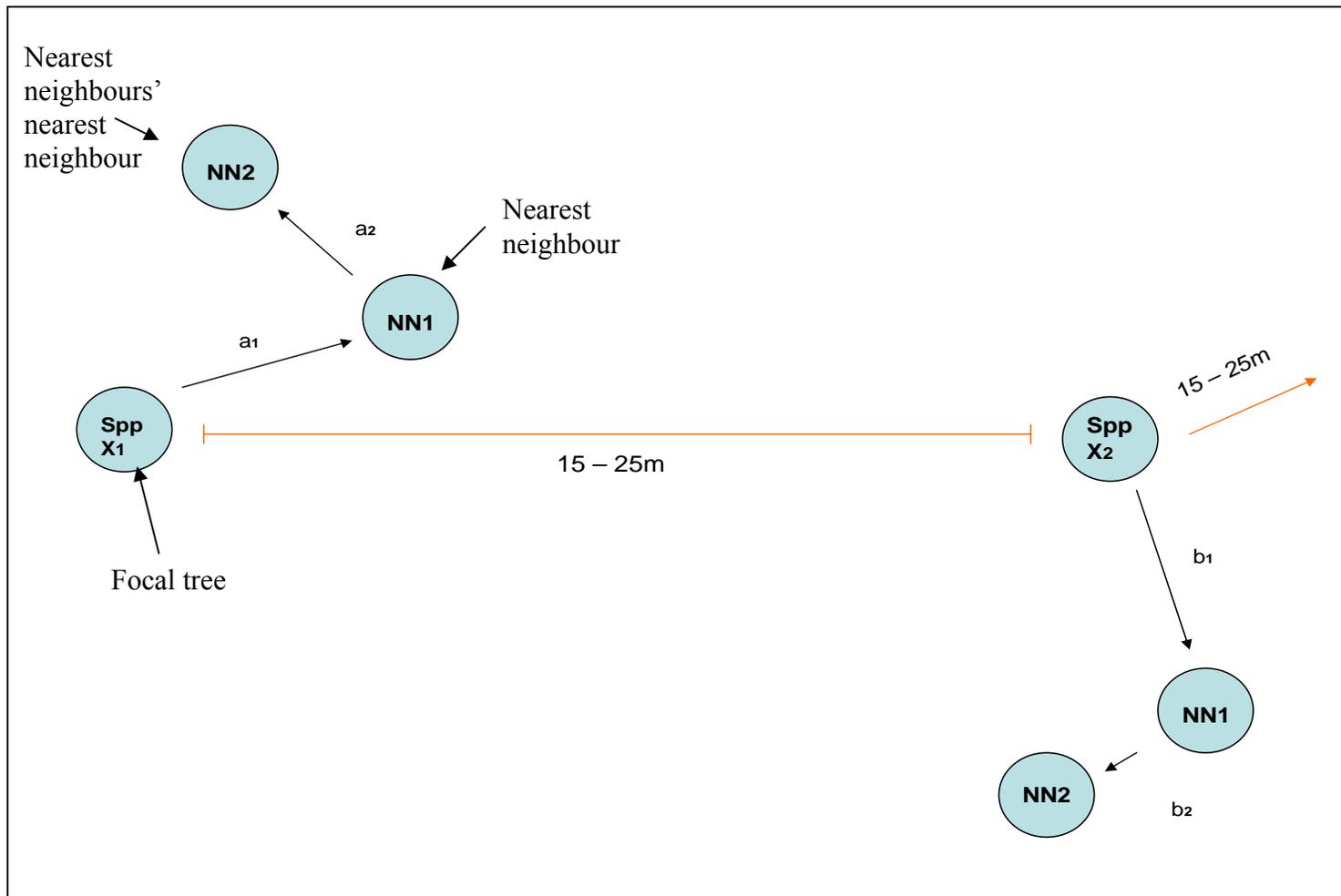


Figure 6.1 Method used for measuring clumping: Focal trees were between 15m-25m apart. Focal trees species' identities were determined, the distance to their nearest neighbour was measured and its species identity determined and the distance to that neighbour's nearest neighbour was also measured and its species identity determined.

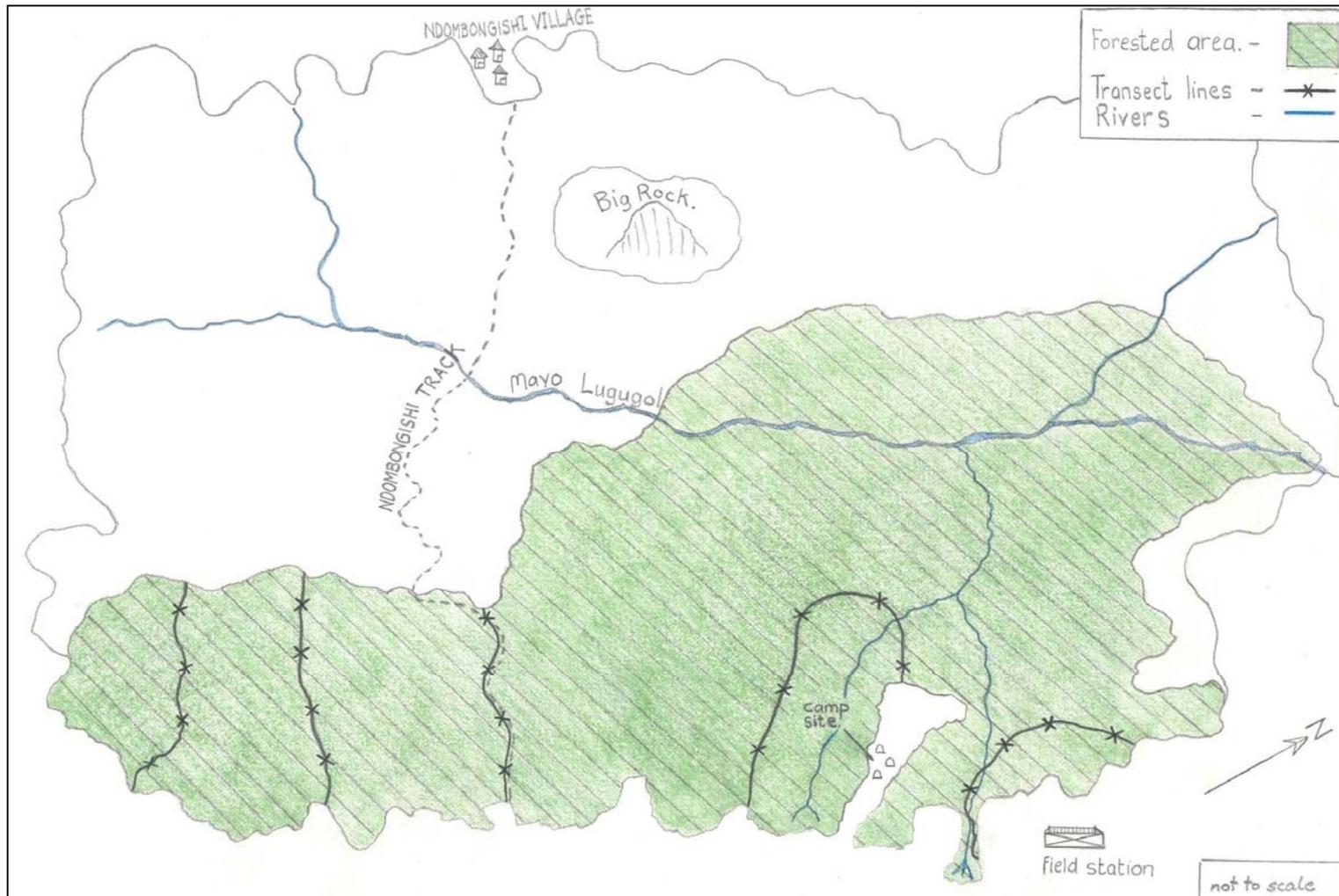


Figure 6.2 Position of transects in the forest along which clumping of tree species was measured

6.3 RESULTS

The mean distance between conspecific nearest neighbours was 4m and the mean distance between non-conspecific neighbours was 3.9m. The two tailed t-test result for a significant difference between the distances among conspecific and non-conspecific nearest neighbours was not significant at 0.05 significance level ($p = 0.67$).

The two most commonly observed species *Anthothena noldeae* and *Carapa procera* both had more conspecific nearest neighbours than would be expected to occur by chance alone, but Chi square tests for significant differences between the expected and observed values were not significant (Figure 6.3). Combined, *Strombosia scheffleri* and *Garcinia smeathmannii* had a significantly greater number of conspecific nearest neighbours than would be expected to occur by chance alone. The combined group of 40 species had a lower than desired expected value of 5, but this difference was negligible (Figure 6.3). In addition a far greater number of conspecific nearest neighbours were observed than was expected, and this difference was statistically significant (Figure 6.3).

Table 6.1 Expected number of conspecific nearest neighbours for each species or species' group, the observed number and Chi square test results for a significant difference between the two values. Bold Chi square values are greater than the critical value.

Species and species' groups	n	Expected no. of conspecific nearest neighbours.	Observed no. of conspecific nearest neighbours.	Observed > Expected ?	Chi-square value	d.f.	Critical Value.
<i>Anthonotha noldeae</i>	57	8.12	13	Yes	2.93	1	3.841
<i>Carapa procera</i>	51	6.5	8	Yes	0.36	1	3.841
Group 1 *	60	5.34	10	Yes	4.06	1	3.841
Group 2 **	232	4.97	20	Yes	45.53	1	3.841

* Group 1	<i>Strombosia scheffleri</i> , <i>Garcinia smeathmannii</i> .
** Group 2	<i>Chrysophyllum albidum</i> , <i>Isolona pleurocarpa</i> , <i>Macaranga occidentalis</i> , <i>Olex subscorpioidea</i> , <i>Santiria trimera</i> , <i>Polyscias fulva</i> , <i>Trichilia welwitschii</i> , <i>Syzgium guineense</i> subsp. <i>bamendae</i> , <i>Celtis gomphophylla</i> , <i>Tabernaemontana contorta</i> , <i>Rauvolfia vomitoria</i> , <i>Ficus</i> sp. (a), <i>Ficus volgellii</i> , <i>Hannoa klaineana</i> , <i>Trema orientalis</i> , <i>Alangium chinense</i> , <i>Symphonia globulifera</i> , <i>Dasylepis racemosa</i> , <i>Oxyanthus speciosus</i> , <i>Vitex doniana</i> , <i>Khaya grandifoliola</i> , <i>Drypetes gossweileri</i> , HMC600, <i>Beilschmiedia mannii</i> , *HMC623, HMC650, <i>Anthocleista volgelii</i> , <i>Nuxia congesta</i> , H190?, HMC638, <i>Dombeya ledermannii</i> , <i>Zanthoxylum leprieurii</i> , <i>Entandrophragma angolense</i> , <i>Newtonia buchananii</i> , <i>Deinbollia pinnata</i> , <i>Schefflera abyssinica</i> , <i>Anonaceae</i> sp., <i>Canthium</i> sp., <i>Rauvolfia</i> sp., <i>Ficus</i> sp. (b).

* HMC collecting number. Herbarium specimens are held at the Royal Botanical Gardens Kew, and are awaiting identification.

6.4 DISCUSSION

The two most common tree species which could be considered individually, *Anthonotha noldeae* and *Carapa procera*, showed a non-significant, but greater number of nearest neighbours than would be expected from a random distribution of adult trees of each species.

The two groups of species (Group 1 and Group 2) had a significantly greater number of conspecific nearest neighbours than expected. This suggests that at least some tree species in Ngel Nyaki show clumped distributions. The evidence for this may have been stronger if a greater spatial scale than just nearest neighbours (such as the next closest tree than the nearest neighbour) was used to determine clumping. This is because many of the study species used in this project appeared to be more abundant in certain areas of the forest (*pers. obs*).

This finding is consistent with more recent findings in intensively studied tropical forests which demonstrate that tree species distributions are better described by random or clumped models (Hyatt *et al.* 2003).

The fact that many tree species seemed to be localized may reflect their “niche requirements” (Hubbell & Foster 1990; Wright 2002). Wright (2002) reported that a number of studies have shown tree species to be non-randomly distributed with respect to micro-topographic gradients in drainage, moisture and nutrients. Hubbell & Foster (1990), working on a long term demographic study of woody plants on Barro Colorado Island in Panama, found that about half of the 239 tree species included in their analysis exhibited statistically significant habitat correlations with identified topographic or edaphic features in their 50ha plot.

On a larger scale Terborgh *et al.* (2002) studied tree species distributions related to four edaphically distinct divisions among plots over the south-eastern Peruvian landscape. These authors found that among 426 of the more common species they observed, 26% were restricted to one of the four edaphic divisions. In addition (Terborgh *et al.* 2002) pointed out that their findings may have been an underestimate because it is possible that more common species are able to occupy a greater range of edaphic conditions than rare species.

Another explanation for tree species clumping may be that the large numbers of seeds falling near conspecific parent trees overwhelm distance and density dependant differences in per capita recruitment so that recruit density is greatest where seeds were initially most numerous

(Wright 2002; Hubbell 1980). The fact that many tree species in tropical forests show clumped or random distributions is considered to be evidence against the Janzen-Connell hypothesis (Hyatt *et al.* 2003; Okuda *et al.* 1997; Clark & Clark 1984; Hubbell 1980).

However, this pattern is not necessarily contradictory to the predictions of the Janzen-Connell hypothesis (Gilbert 2006; Clark & Clark 1984). True tests of the Janzen-Connell model do not rely on static analyses of the spatial distributions of conspecific adult trees, but rather look at the changes in the degree of clumping over time compared to the initial distribution of seeds and seedlings (Gilbert 2006; Clark & Clark 1984).

The greater than expected numbers of conspecific nearest neighbours found in this study indicate survival near to conspecifics does not fall to zero and that establishment and survival to maturity in the immediate vicinity of conspecifics is possible. Some degree of clumping of conspecifics is a reasonable expectation of the Janzen-Connell model, as Janzen (1970) predicts that adults of a given tree species are only more regularly distributed than if the probability of a new adult appearing at a point in the forest were proportional to the number of seeds arriving at that point. In addition Janzen (1970) predicted that conspecifics growing in close proximity to each other will have overlapping seed shadows, and the increased seed abundance will increase the probability of conspecific seedlings becoming established in that area. Therefore, theoretically, over time, given spatial and temporal variation in host specific predator abundances (Connell 1971), synchronous conspecific seeding events (Janzen 1976), tree fall gaps, and microsite availability (Wright 2002), windows of opportunity will occur for conspecific seedlings to become established in the area. The higher seed input at areas away from parents because of overlapping seed shadows, together with windows of opportunity, would favour increased clumping of conspecifics over time because of increased seed input in the area (Hammond & Brown 1998). In support of this argument Schupp (1992) found that seed survivorship beneath parent trees of *Faramaea occidentalis* in Panama increased with increasing adult density. Additionally (Wright 2002) explains that if a superior competitor becomes sufficiently abundant it may escape dispersal and recruitment limitation, which Wright thought may explain why *Trichilia tuberculata* comprises 13% of all canopy trees on Barro Colorado Island in Panama.

The findings in this investigation show that at least some species in Ngel Nyaki are likely to have clumped distributions. However the two individually tested species, *Antinotha noldeae* and *Carapa procera*, did not have significantly greater numbers of conspecific nearest neighbours than is expected to occur by chance alone (Table 6.1), which may indicate that these two species are more regularly spaced than would be expected by their seed shadows. Combined, *Strombosia scheffleri* and *Garcinia smeathmanni* (Group 1), and Group 2 (composed of 40 species) had a significantly greater number of conspecific nearest neighbours than would be expected to occur by chance alone. It is unlikely that this indicates that all these species showed clumped distributions, but probably reflects the clumped distribution of some of them. The regular spacing of conspecific adult trees as described by Janzen (1970) may still apply to the majority of the species in Ngel Nyaki forest. The clumping of some species is unlikely to be evidence against the Janzen-Connell hypothesis.

An additional process by which clumping may result while the Janzen-Connell model still applies, is when unpredictable evolutionary shifts lead to greater resistance of tree species to their natural enemies (Givinish 1999). In this way a tree species' distribution may change in its degree of clumping over time, and at times be less clumped because of the activities of host specific seed / seedling predators as predicted by the Janzen-Connell model.

Due to the fact that clumping to some degree in some species can be expected by the Janzen-Connell hypothesis (Clark & Clark 1984), it is not possible to reach a strong conclusion as to whether or not the degree of clumping observed in Ngel Nyaki is evidence against the Janzen-Connell hypothesis.

CHAPTER 7: GENERAL DISCUSSION AND CONCLUSION.

7.1 GENERAL DISCUSSION

The Janzen-Connell hypothesis predicts that host specific enemies cause seedling mortality to be highest under parent / conspecific adult trees (Janzen 1970; Connell 1971).

Seedling abundance at different distances away from the parent tree.

The significant ANCOVA result in Chapter 3 indicated that, across the three species studied, small seedlings are more abundant under parent trees than further away, and larger seedlings and saplings are more abundant further away from parent / conspecific adult trees than underneath them. This result supports the hypothesis that the Janzen–Connell model applies in Ngel Nyaki and possibly West African montane forests in general. This is because the more abundant larger seedlings and saplings at distances away from parent / conspecific adult trees indicates that more seedlings have grown, and thus survived, for a longer time there. However there are a number of reasons besides host specific enemies that may have caused seedling survival to be lowest under parent / conspecific adult trees. These reasons include allelopathy (Taiz & Zeiger 1998; Wright 2002; Janzen 1970), increased interspecific competition among high densities of seedlings under parent trees (Wright 2002; Duncan 1991; Connell 1971), local depletion of critical nutrients by the parent / conspecific adult tree or particularly effective shading by the adult crown (Clark & Clark 1984) and dense leaf litter layers under parent trees (Molofsky & Augspurger (1992) (for more details see Chapter 3).

Planted seedling survival at different distances away from conspecific adult trees.

For the experimentally planted seedlings (Chapter 5), although non-significant, two of the three species studied, *Deinbollia pinnata* and *Entandrophragma angolense*, showed lowest survival under conspecific adult trees three months after they had been planted (Figure 5.3; Figure 5.5). Additionally, experimentally planted *D. pinnata* seedlings under conspecific adult trees showed the least height increase over three months (Figure 5.7), and the experimentally planted *E. angolense* seedlings under conspecific adult trees showed the greatest height decrease over three months (Figure 5.8). Although non-significant, these results also suggest that seedling survival or performance is lowest under parent / conspecific adult trees. The significant ANCOVA result (Chapter 3), and the non-significant but suggestive results of Chapter 5, indicate that seedling survival is increased away from parent / conspecific adult trees, but they do not reveal the cause of seedling mortality.

Herbivory at different distances from parent / conspecific adult trees.

The Janzen-Connell hypothesis predicts that host specific herbivores are of major importance among host specific enemies in causing seedling survival to be lowest under parent / conspecific adult trees (Connell 1971; Janzen 1970).

The hypothesis that seedling leaf herbivory is highest under parent trees was tested in chapters 4 and 5. The results were all non-significant (Table 4.1 - 4.3; Table 5.6) and species showed differing trends (Figure 4.3 - 4.5; Figure 5.9 – 5.11).

Measuring seedling herbivory, or survival, at a single point in time as I did in Chapters 3 and 4 may not reveal the pattern predicted by the Janzen-Connell model. This is because host specific seedling predators may not have been present or abundant at the exact time of the experiment because they have been affected by previous adverse environmental conditions (Connell 1971), or because their host seedlings have been in short supply at some point in time prior to making the measurements (Janzen 1970). One of the three

species in Chapter 4, *Pouteria altissima* showed a decrease in herbivory with distance from parent / conspecific adult trees (Figure 4.3), although this trend was not significant (Table 4.1). For the experimentally planted seedlings tested in Chapter 5, by month three all three species showed highest seedling herbivory close to conspecific adult trees (Figure 5.9 – 5.11), although this result was not significant (Table 5.6). Other reasons why the study species may not have revealed that herbivory was highest under parent trees include: chemical defenses in leaves and tough, thick leaves with thick cell walls which deter a broad spectrum of herbivores (Givinish 1999), production of an ephemeral super abundance of edible leaf tissue to satiate herbivores (Clark & Clark 1991), sparse seedling distributions (Janzen 1970) and herbivory by generalist herbivores who do not concentrate their feeding under parent trees (Janzen 1970) (for more details see Chapter 4 and 5). Therefore herbivory being highest near to parent trees may become evident when measurements are made over a longer time. Also herbivory might only be important for species whose seedlings leaves do not contain chemical defenses and / or are not sufficiently thick and tough.

A high diversity of host specific seed / seedling predators in the tropics, and that all or the majority of tree species in the tropics have a variety of host specific predators, as predicted by Janzen (1970) and Connell (1971) may not be necessary to cause survival to be lowest under parent trees. Seed and young seedling densities are highest under parent trees (Janzen 1970; Connell 1971) and many generalist herbivores respond simply to high densities of seeds and seedlings (Schupp 1990; Forget 1993; Greenwood 1985; Glanz *et al.* 1982 as cited in Hammond & Brown 1996; Clark & Clark 1984; Janzen 1970) and thus feed preferentially under parent / conspecific adult trees. I propose that host specific and generalist herbivores work synergistically over time with factors such interspecific competition, allelopathy, depletion of nutrients and particularly effective shading under parent/ conspecific adult trees, and possibly non-specific effects such as leaf litter (Augspurger 1992) and falling debris (Clark & Clark 1989; Aide 1987), to cause seedling

survival to be lowest under parent trees. Recruitment does not fall to zero under parent trees (Wright 2002). Recruitment is made possible under parent trees by a number of factors including temporal availability of light gaps (Augsburger 1984; Hammond & Brown 1996), suitable microhabitats (Wright 2002), temporal reductions in host specific enemies (Connell 1971), satiation of predators (Janzen 1971, 1976; Clark & Clark 1991) and chemical and structural defenses of seeds and seedlings (Givinish 1999). Therefore, the probability of seedling recruitment under parent / conspecific adult trees is actually higher than is generally expected by many authors who have tested the model (Hammond & Brown 1996; Clark & Clark 1989). This idea is supported by the results of Chapter 6 (Testing whether or not tree species in Ngel Nyaki show clumped distributions.) that across all species studied there were more conspecific nearest neighbor adult trees than would be expected by chance alone. Results of this study suggest that seedlings do become established under parent / conspecific adult trees, but over time the probability of a seed becoming a mature sapling is lowest under parent / conspecific adult trees. In support of Janzen's (1970) model the survival of seedlings would not be expected to be proportional with the amount of seeds falling in an area, a greater proportion of seeds would become established seedlings at distances away from parent / conspecific adult trees.

The majority of insects are host specific to a number of species in the same genus (Novotny *et al.* 2002). Therefore they may only be host specific to a particular species in a genus when their seedlings are abundant (Hammond & Brown 1996; Connell 1971). For example, after a number of trees in an area have set seed and their young seedlings are abundant, host specific insects may be chemically attracted to them (Hammond & Brown 1996). Under this scenario, host specific seedling herbivores may only be important in causing high seedling mortality under parent / conspecific adult trees when one of their host species' seedlings are sufficiently abundant. When the host species' seedlings that were abundant have suffered mortality, and their numbers have been

sufficiently reduced, the host specific predators may then switch to another species in the genus if they have become abundant. The pressure on a given species from host specific enemies may thus be less continuous and intense than predicted by the Janzen-Connell model. Consequently, there will be numerous opportunities through time where seedlings can become established near to their parent trees. Such a scenario may have led to the large inconsistencies in results of the Janzen–Connell model (i.e. Romo *et al.* 2004; Hammond & Brown 1996; Burkey 1994; Clark & Clark 1984) and thus influenced Hyatts' (2003) conclusion that further testing of the Janzen – Connell model is unnecessary.

Seasonal dry forests such as Ngel Nyaki are unfavourable to desiccation intolerant insects and fungi (Givinish 1999) which could be significant because insects are the most important host specific enemies of seeds and seedlings (Hammond & brown 1996; Connell 1971; Janzen 1970). Host specific predator abundances may oscillate with the seasons and respond to the abundances of their hosts which will be highest in the wet season (Coley & Barone 1996). They may also switch between hosts when their abundances decline (Hammond & Brown 1996), and this may explain why there are no evident differences between the trends shown by wet forest trees versus those of dry habitat trees (Clark & Clark 1984). Whether the pressure from seedling herbivores is continuous or not, when abundant, seedlings would suffer high mortality from host specific enemies and this effect may be strong enough over time to cause increased seedling survival with distance from parent / conspecific adult trees (Wright 2002).

The significant result in Chapter 3 indicates that seedling survival is enhanced at distances away from parent / conspecific adult trees. The results of tests for increased survival at distances away from parent / conspecific adult trees for experimentally planted seedlings in Chapter 5 were non-significant for all three species. Nevertheless for two of the three species, *Deinbollia pinnata* and *Entandrophragma angolense*, the non-significant trends showed increased survival and performance at distances away from

parent conspecific adult trees (Figure 5.3; Figure 5.5). Therefore the results of this study suggest that the prediction of the Janzen-Connell model that seedling survival is greatest at distances away from parent / conspecific adult trees applies in Ngel Nyaki. Highest seedling mortality under parent / conspecific adult trees alone will maintain tree species diversity in Ngel Nyaki (Connell 1971; Janzen 1970; Paine 1966). Despite this support, the importance of host specific seedling enemies, as predicted by the Janzen-Connell model, in causing highest seedling mortality under parent / conspecific adult trees could not be determined from the results in this study. All tests of herbivory being highest under parent / conspecific adult trees were non-significant. Nevertheless four species (*P. altissima*, *E. angolense*, *D. pinnata* and *Sterculia setigera*) out of the total of six study species, despite being non-significant, showed a decrease in herbivory with distance from parent / conspecific adult trees (Figure 4.3; Figure 5.9-5.11). This does indicate that host specific herbivory may be an important cause of seedling mortality being highest under parent / conspecific adult trees but the evidence is weak. Studies which have detected distance or density dependant seedling mortality in nature have not determined the relative importance of host specific enemies in causing this pattern (*pers. obs*; Clark & Clark 1984). I suggest that further testing of the Janzen-Connell model should involve determining the relative importance of host specific enemies as a mortality agent for naturally occurring seedlings that suffer highest mortality under parent / conspecific adult trees.

7.2 CONCLUSION

The results of this study indicate that seedling survival increases at distances away from parent / conspecific adult trees in Ngel Nyaki. Support for the prediction that host specific herbivores are the main cause of seedling mortality under parent / conspecific adult trees was not borne out. Non-significant trends in herbivory showed that herbivory decreased with distance for four out of six species studied. This may indicate that host specific herbivory is important in causing highest seedling mortality under parent / conspecific adult trees in Ngel Nyaki. The effect from host specific herbivory may not be

as strong as predicted by the Janzen-Connell model for non- seasonal wet tropical lowland forests because Ngel Nyaki is a dry seasonal forest. This is because many insects are dessication intolerant and host specific pest pressure on seedlings in wet tropical forests would be constant. Nevertheless the host specific herbivores that may be present in Ngel Nyaki are likely to work in synergy with other factors to cause highest seedling mortality under parent / conspecific adult trees. Seedling mortality being highest under parent / conspecific adult trees is likely to maintain tree species diversity in Ngel Nyaki.

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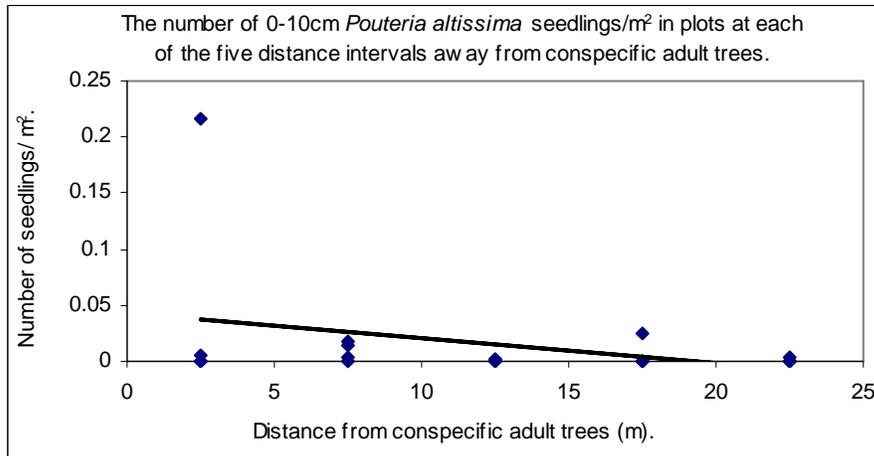


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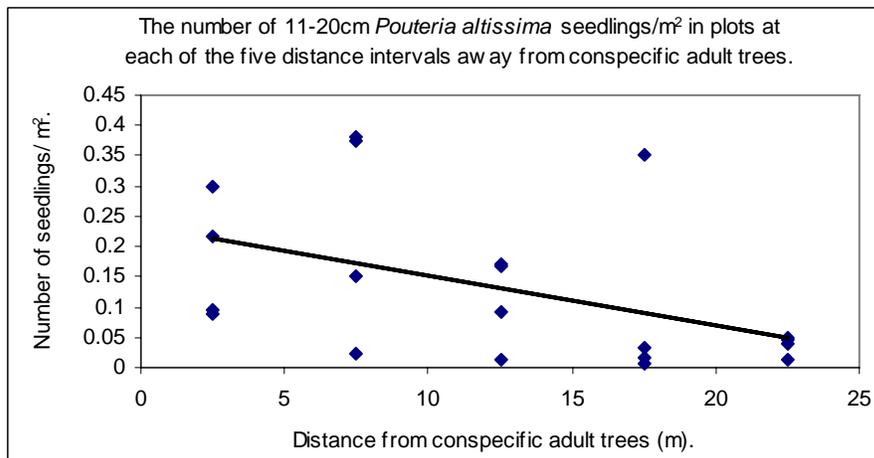


Figure 1 (b).

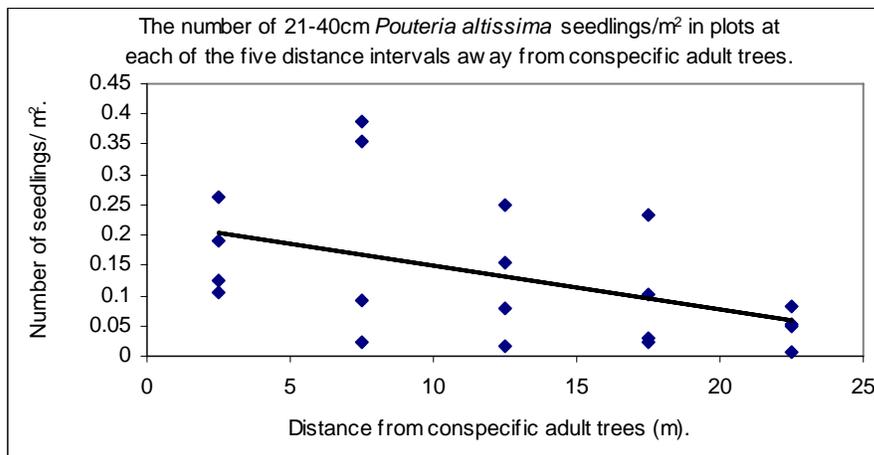


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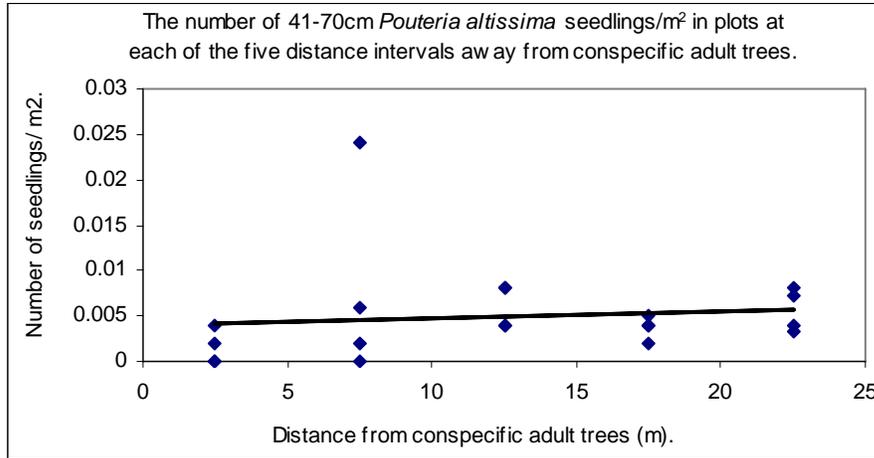


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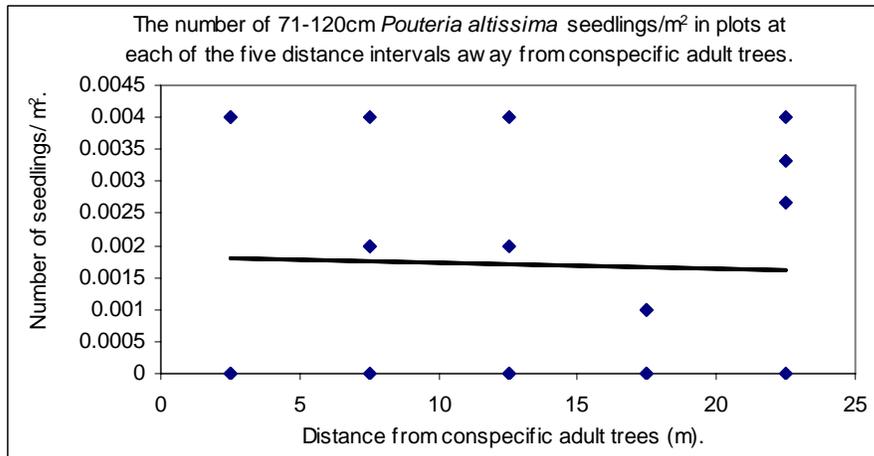


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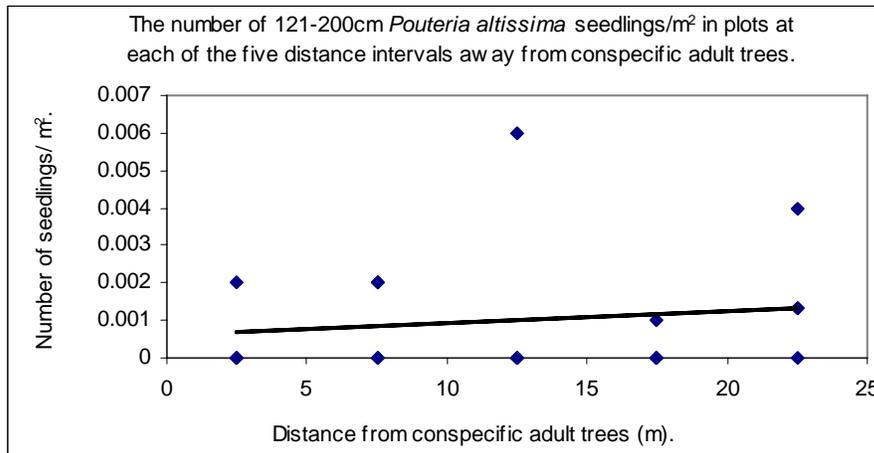


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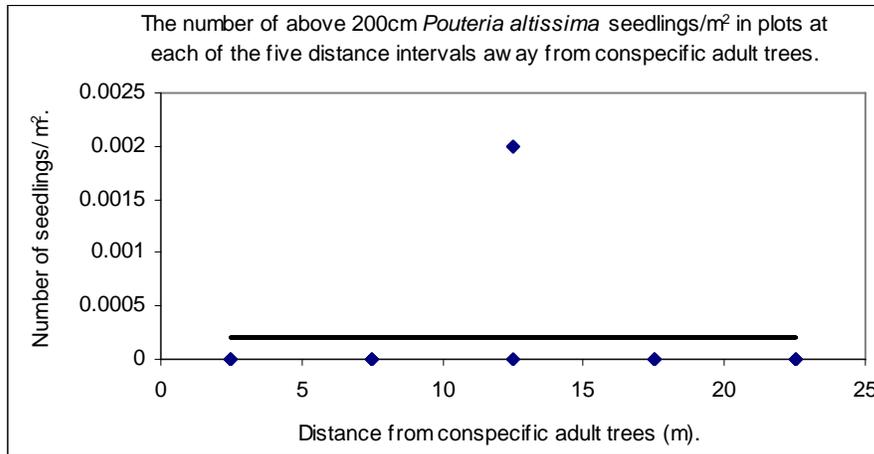


Figure 1 (g).

Figure 1 (a-g) *Pouteria altissima*: regression plots for abundance of seedlings at each distance away from parent conspecific adult trees for each height category. Regression slopes show a trend of changing from being negative for seedlings in the smaller height categories to being positive for seedlings in the larger height categories.

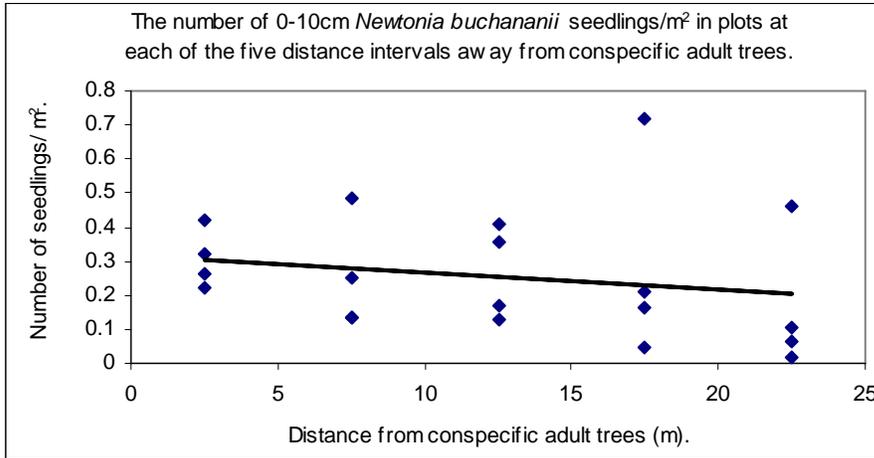


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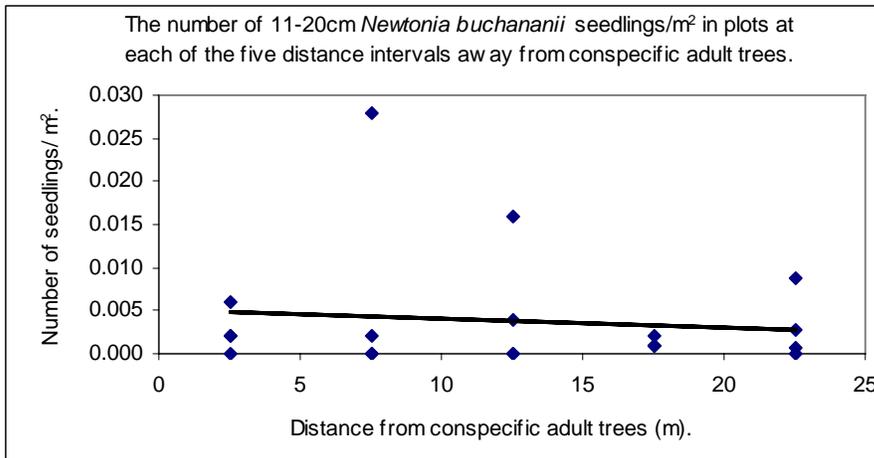


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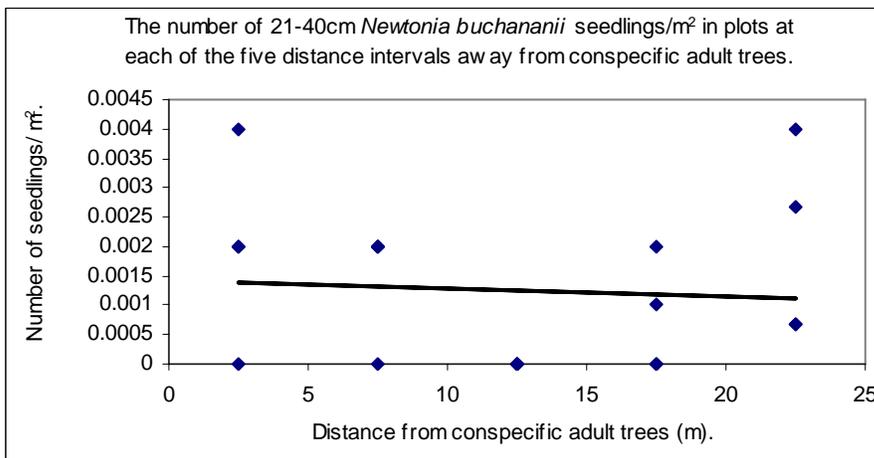


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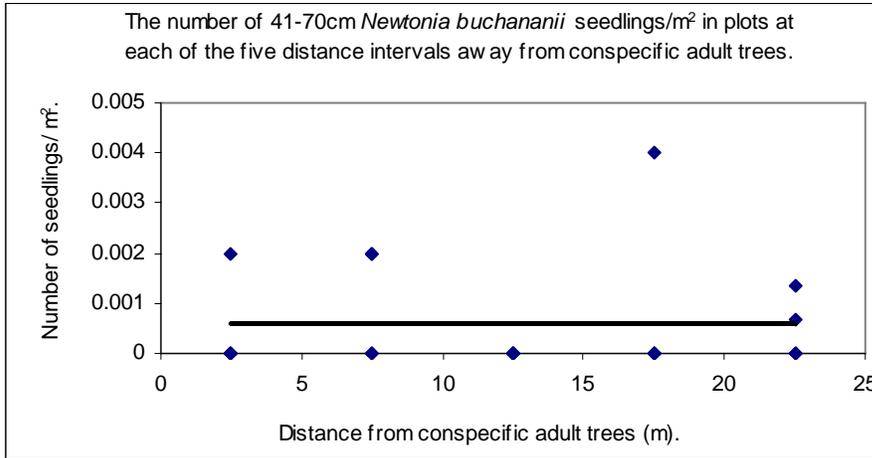


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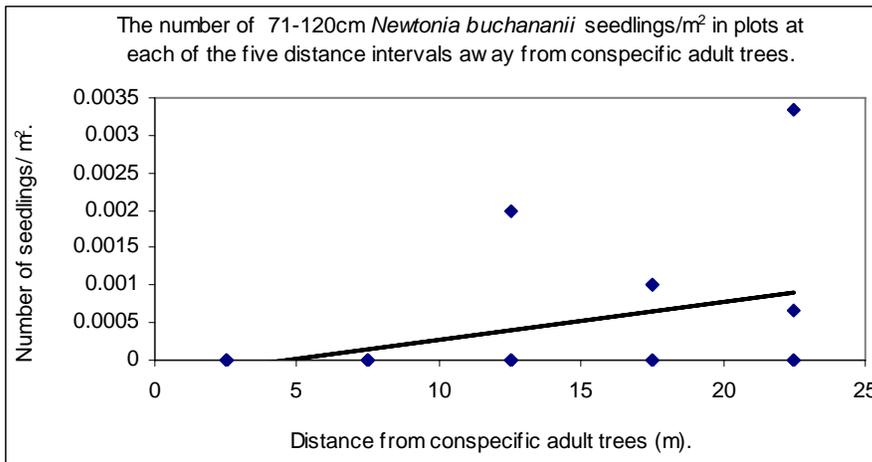


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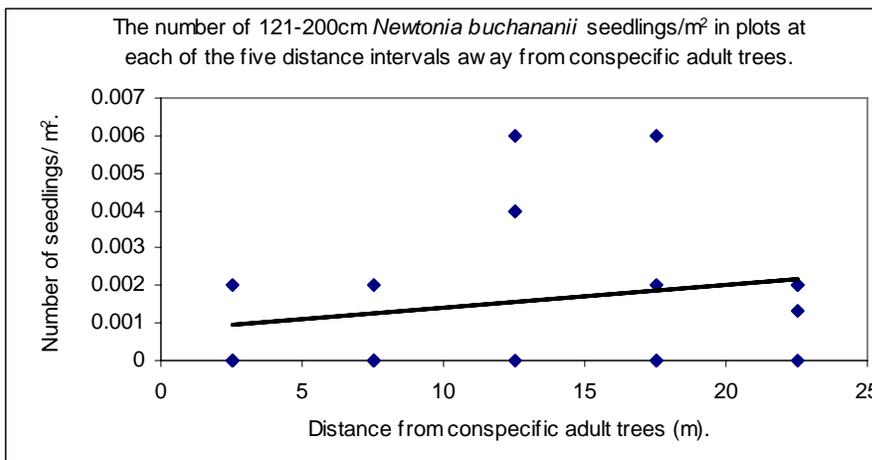


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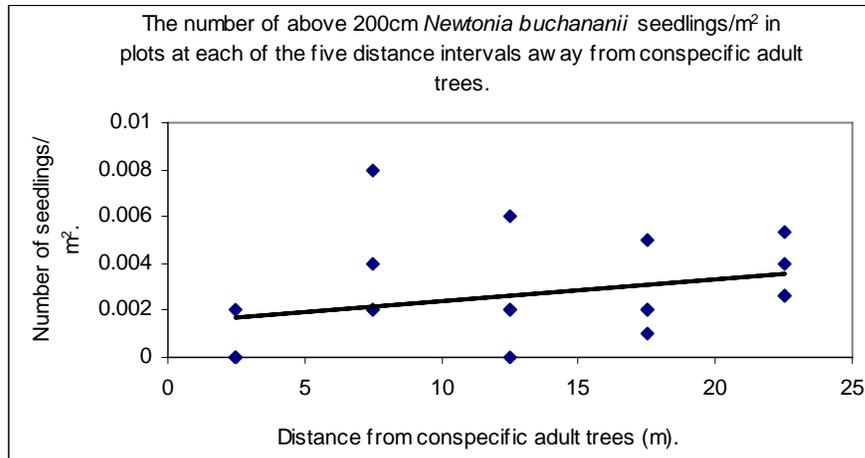


Figure 2 (g).

Figure 2 (a-g) *Newtonia buchananii*: regression plots for the abundance of seedlings at each distance away from parent conspecific adult trees for each height category. Regression slopes show a trend of changing from being negative for seedlings in the smaller height categories to being positive for seedlings in the larger height categories.

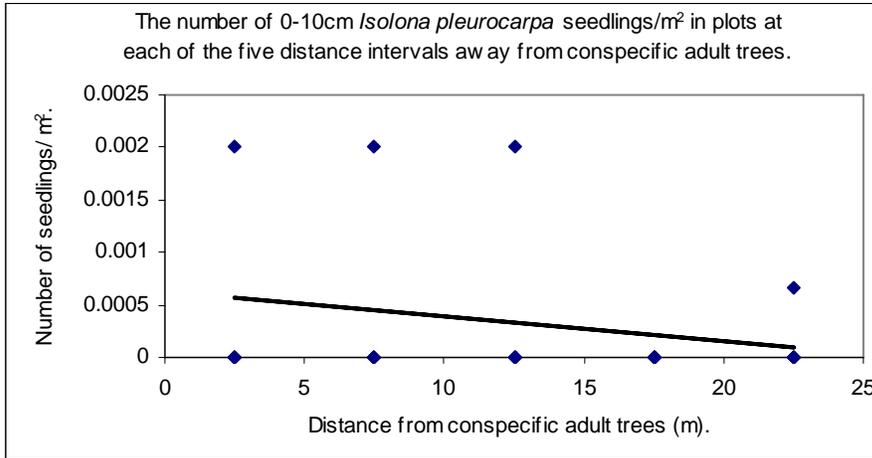


Figure 3(a).

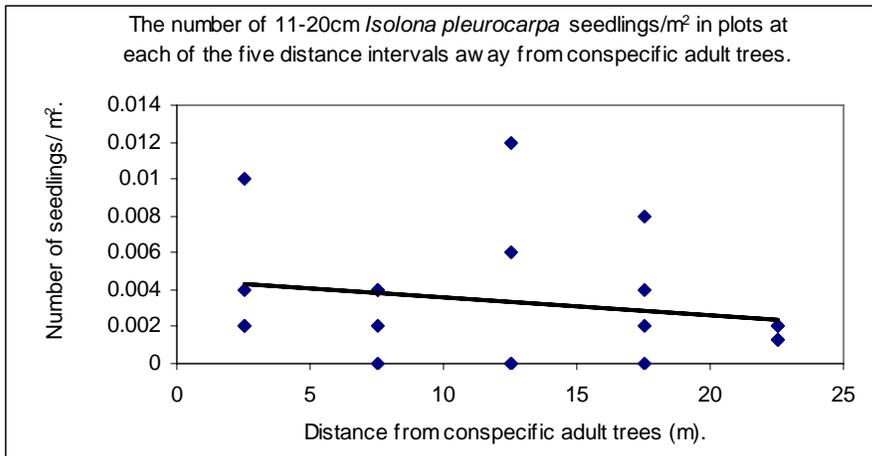


Figure 3(b).

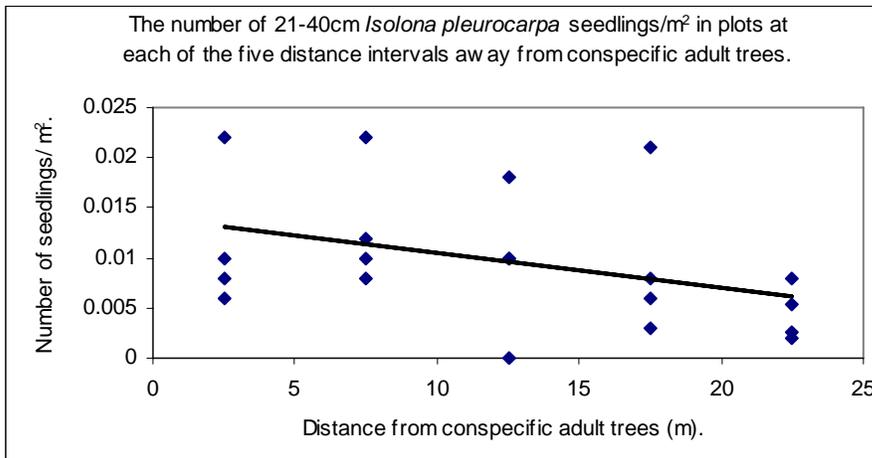


Figure 3(c).

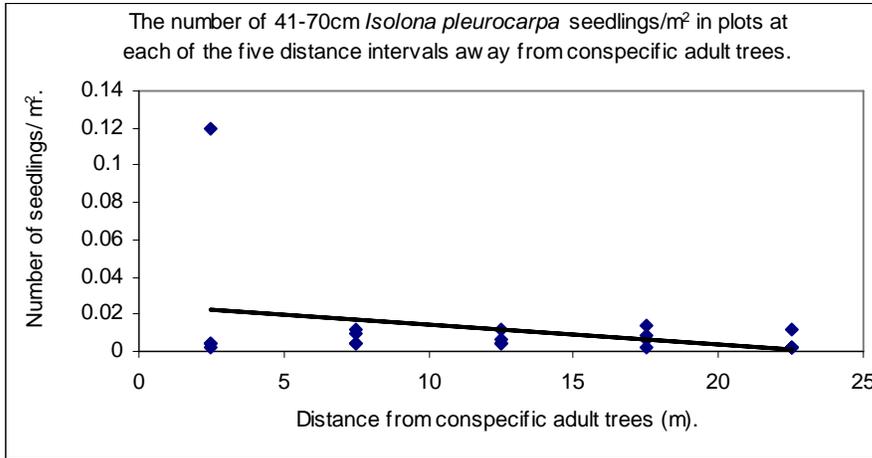


Figure 3(d).

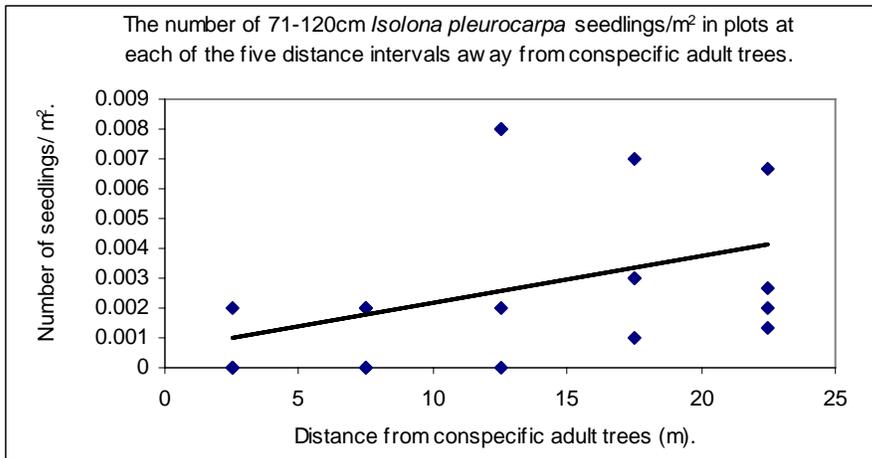


Figure 3(e).

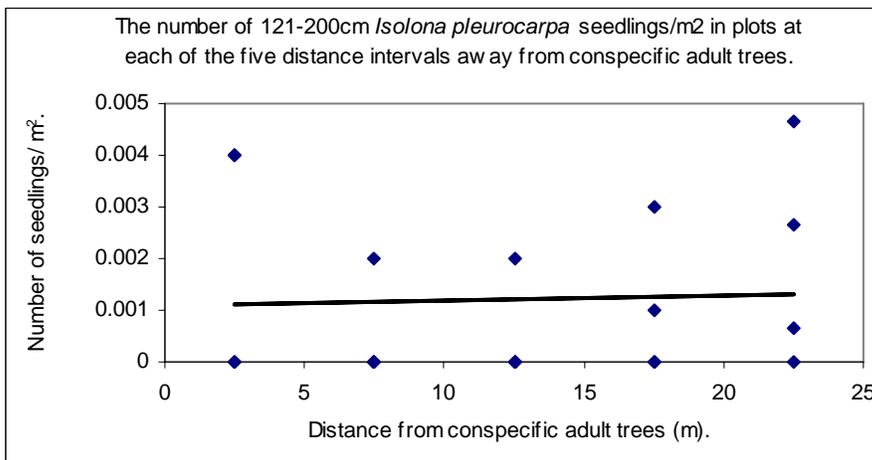


Figure 3(f).

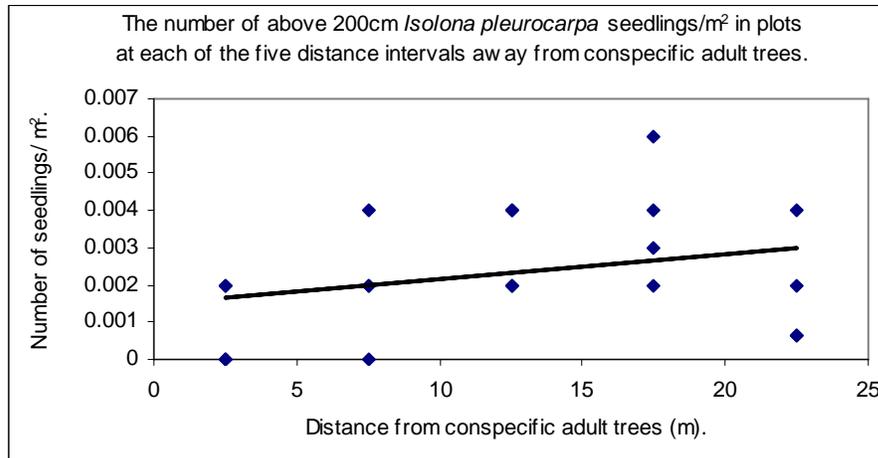


Figure 3(g).

Figure 3 (a-g) *Isolona pleurocarpa*: regression plots for the abundance of seedlings at each distance away from parent conspecific adult trees for each height category. Regression slopes show a trend of changing from being negative for seedlings in the smaller height categories to being positive for seedlings in the larger height categories.