THE DECLINE AND RESTORATION OF RIPARIAN AND HILLTOP FORESTS
IN THE SERENGETI NATIONAL PARK, TANZANIA

by

Gregory J. Sharam

BSc., Dalhousie University, Halifax, Nova Scotia, 1994
M.Sc., University of British Columbia, Vancouver, British Columbia, 1997

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN
THE FACULTY OF GRADUATE STUDIES
(Zoology)

UNIVERSITY OF BRITISH COLUMBIA

© Gregory J. Sharam, 2005
ABSTRACT

The riparian and hilltop forests of Serengeti National Park, Tanzania, have been in rapid decline since the early 1970s. Fifty percent of riparian forests and 85% of hilltop forests have been converted to grassland in that time. This thesis investigates the causes of this decline and the conditions under which forests will stabilize and recolonize grassland areas.

Fire is the main cause of decline, particularly affecting the upwind side of rivers and removing seedlings and canopy trees at the forest-grassland boundary. The effects of fire depend on the type of forest and forest edge. Closed-canopy forests with dense dripline edges are more resistant to fire than open-canopy, advancing edges. Mortality of seedlings and canopy trees in closed-canopy forests increased only when stands were burned in four successive years, while seedlings and canopy tree mortality occurred after only one year of burning in forests with open-canopy advancing edges.

Germination of forest trees within forests is limited by grass abundance and conditions in the grassland, but is increased by recent fires, floods and grass removal. Subsequent survival and growth of seedlings is limited by fires at the forest periphery and by antelope browsing. Survival of large trees is reduced by fire and by elephants; however, elephant damage was insufficient to limit replacement of the forest canopy although elephants did damage canopy trees.

Seedling establishment is poor in the grassland adjacent to forests, despite the removal of fire, grass and antelope browsers. However, isolated stands of savanna trees can act as nurse trees and facilitate the establishment of riparian forests by excluding grass, fire and browsers, and increasing dry season soil moisture. Moreover, current forest stands probably developed from previous nurse stands. The history of Serengeti forests is reviewed and its implications for forest conservation and management are discussed.
# TABLE OF CONTENTS

ABSTRACT ......................................................................................................................... ii
LIST OF FIGURES ............................................................................................................. vi
LIST OF TABLES ............................................................................................................... ix
ACKNOWLEDGEMENT ................................................................................................. xi

CHAPTER 1 An introduction to the decline of the Serengeti riparian and hilltop forests . . 1

CHAPTER 2 Riparian and hilltop forests and in Serengeti National Park, Tanzania;

are the effects of savanna fires dependant on forest edge type? ................................. 21

Introduction .................................................................................................................... 21
Methods ........................................................................................................................... 23
Results ............................................................................................................................. 32
  Patterns of forest decline ............................................................................................... 32
  Survival of large trees in three forest edge types .......................................................... 33
  Large tree survivorship with and without fire .............................................................. 33
  Large tree survivorship with repeated burns ............................................................... 36
  Expansion of bushes at the forest periphery ............................................................... 36
  Seedling survival at the forest edge ............................................................................ 38
  Grass fuel load across the forest-savanna boundary ................................................... 38
  Fuel combustibility and forest type ............................................................................ 42
  Fire frequency and extent ............................................................................................ 42
  Late dry season grass water content ........................................................................   42

Discussion ....................................................................................................................... 45

Conclusion ....................................................................................................................... 49

References ....................................................................................................................... 50

CHAPTER 3 The effects of antelopes, elephants, and fire on riparian and hilltop forests

of the Serengeti ecosystem, Tanzania. ........................................................................... 52

Introduction .................................................................................................................... 52

Methods ........................................................................................................................... 56

Results ............................................................................................................................. 62
  Forest density by size class ........................................................................................... 62
  Seedling response to impala, elephants and fire ........................................................... 62
  Survival of large trees ................................................................................................. 67
  Interactions between elephants, antelopes and fire .................................................... 71
## List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-1</td>
<td>Aerial view of riparian forests along one of the Mara River tributaries (Ngurimi River) near the Kenya-Tanzania border, Serengeti National Park, Tanzania.</td>
<td>2</td>
</tr>
<tr>
<td>1-2</td>
<td>Location of riparian and hilltop forests within the Serengeti ecosystem.</td>
<td>3</td>
</tr>
<tr>
<td>1-3</td>
<td>Major River systems in East Africa and locations of known riparian forest systems. (Modified from Medley and Hughes, 1996)</td>
<td>4</td>
</tr>
<tr>
<td>1-4</td>
<td>The structures of the three types of Serengeti riparian and hilltop forests. Arrow indicates the &quot;edge&quot; of the forest; the maximum extent of forest tree canopy.</td>
<td>9</td>
</tr>
<tr>
<td>1-5</td>
<td>Aerial photograph of Mara River tributary (Ngurimi River) riparian forest patch, with size reduction through time. Photo shows forest cover in 1972, with 1959 and 2000 coverage overlayed.</td>
<td>12</td>
</tr>
<tr>
<td>2-1</td>
<td>Location of riparian and hilltop forests within the Serengeti ecosystem.</td>
<td>25</td>
</tr>
<tr>
<td>2-2</td>
<td>The structures of the three types of Serengeti riparian and hilltop forests. Arrow indicates the edge of the forest; the maximum extent of forest tree canopy.</td>
<td>27</td>
</tr>
<tr>
<td>2-3</td>
<td>Experimental setup of permanent transects for canopy tree survival, tree seedling manipulations in riparian and hilltop forests, and grass biomass measurements.</td>
<td>31</td>
</tr>
<tr>
<td>2-4</td>
<td>Canopy tree survival in Grumeti riparian, Mara riparian and Mara Hilltop forests. Survival is split by transect through the forest and size class. (Error bars ± 1 SD).</td>
<td>34</td>
</tr>
<tr>
<td>2-5</td>
<td>Survival of trees in hilltop forests exposed to fire, protected from fire, and individuals in fire plots that were observed to be scorched. (Error bars ± 1 SD).</td>
<td>35</td>
</tr>
<tr>
<td>2-6</td>
<td>Forest edge trees and bushes of Grumeti riparian, Mara riparian, and Mara Hilltop forest (species combined) yearly survival and proportion undamaged under treatments of burning 0, 1, 2, &amp; 3 consecutive years. (Error bars ± 1 SD).</td>
<td>37</td>
</tr>
<tr>
<td>2-7</td>
<td>Survival of forest seedlings in plots that have been burned and protected from fire in two consecutive years.</td>
<td>39</td>
</tr>
<tr>
<td>2-8</td>
<td>Mean yearly survival of seedlings in Grumeti riparian, Mara riparian, and Mara Hilltop forest patch edges that have been exposed to and protected from fire for two years. (Error bars ± 1 SD).</td>
<td>40</td>
</tr>
<tr>
<td>2-9</td>
<td>Survival rates of seedlings in Mara riparian forests at increasing distance from the forest-grassland boundary. Arrow indicates the edge of the forest; the maximum extent of forest tree canopy. (Error bars ± 1 SD).</td>
<td>41</td>
</tr>
<tr>
<td>Section</td>
<td>Description</td>
<td></td>
</tr>
<tr>
<td>---------</td>
<td>-------------</td>
<td></td>
</tr>
<tr>
<td>2-10</td>
<td>Fuel loads (dry weight) outside and inside Grumeti riparian, Mara riparian, and Mara hilltop forests. Arrow indicates the edge of the forest; the maximum extent of forest tree canopy. (Error bars $\pm$ 1 SD).</td>
<td></td>
</tr>
<tr>
<td>2-11</td>
<td>Percent moisture during the middle of the dry season for grass outside and inside Grumeti riparian, Mara riparian, and Mara hilltop forests. Percent moisture is total weight/dry weight. Arrow indicates the edge of the forest; the maximum extent of forest tree canopy. (Error bars $\pm$ 1 SD).</td>
<td></td>
</tr>
<tr>
<td>3-1</td>
<td>Location of riparian and hilltop forests within the Serengeti ecosystem, and location of Serengeti and Rubondo National Parks in East Africa.</td>
<td></td>
</tr>
<tr>
<td>3-2</td>
<td>Experimental setup of permanent transects for canopy tree survival and density estimates in riparian and hilltop forests.</td>
<td></td>
</tr>
<tr>
<td>3-3</td>
<td>Densities of principal Serengeti riparian and hilltop thicket species, and of canopy species of Rubondo Island forests. (Error bars $\pm$ SD).</td>
<td></td>
</tr>
<tr>
<td>3-4</td>
<td>Yearly survival rates of seedlings with herbivores (H) and inside herbivore exclosures (EX) in three different types of broad-leaved forest, Serengeti National Park, Tanzania. (Error bars $\pm$ SD).</td>
<td></td>
</tr>
<tr>
<td>3-5</td>
<td>Growth rates (height) of seedlings with herbivores (H) and inside herbivore exclosures (EX) in three types of broad-leaved forest in Serengeti National Park, Tanzania. Growth rate was reduced or made negative by antelope browsing on the apical meristem. (Error bars $\pm$SE).</td>
<td></td>
</tr>
<tr>
<td>3-6</td>
<td>Yearly survival rates of large trees (&gt;0.75m) with fire and without fire, and elephant damage. Elephant damage was characterized by removing branches and stripping leaves from branches. (Error Bars $\pm$SD).</td>
<td></td>
</tr>
<tr>
<td>3-7</td>
<td>Yearly survival rates of large trees (&gt;0.75m) with and without fire and elephant &quot;pushed over&quot; damage. &quot;Pushed over&quot; damage occurs when elephants damage the main trunk of the tree, resulting in some but not all broken wood, thus the tree could, potentially survive. (Error bars $\pm$SD).</td>
<td></td>
</tr>
<tr>
<td>3-8</td>
<td>Yearly survival rates of large trees (&gt;0.75m) with and without fire and herbivory damage by impala. Impala herbivory was limited to browsing of forest trees below 1.6 m. (Error bars $\pm$SD).</td>
<td></td>
</tr>
<tr>
<td>4-1</td>
<td>Location of riparian and hilltop forests within the Serengeti ecosystem.</td>
<td></td>
</tr>
<tr>
<td>4-2</td>
<td>Experimental setup of seedling monitoring transects and germination plots in riparian and hilltop forests.</td>
<td></td>
</tr>
<tr>
<td>4-3</td>
<td>Density of Grumeti river, Mara river, and Mara hilltop forest canopy tress at increasing distance from the forest-grassland boundary (0 m) to the river or patch centre at 85-95 m. Arrow indicates forest edge; the maximum extent of forest tree canopy. (Error bars $\pm$ SD).</td>
<td></td>
</tr>
</tbody>
</table>
4-4 Density of tree seedlings as a function of distance from the forest - grassland boundary; distance increases as one travels into the forest. Arrow indicates forest edge; the maximum extent of forest tree canopy. 93

4-5 The number of new seedlings per metre per year in each River, Central, Inside Edge and Grassland transects of Grumeti riparian, Mara riparian, and Mara Hilltop forests. Arrow indicates forest edge; the maximum extent of forest tree canopy. (Error bars + SD) 97

4-6 The number of new seedlings per m² per three month season in the Mara riparian forests. Short Rains are November-January, Long Rains are February-April, Early Dry is May-July, Late Dry is August-October. (Error Bars + SD) 98

4-7 Survival of forest canopy tree seedlings with grass present, and removed, with grass removed and antelopes excluded inside forests and in the adjacent grassland. No seedlings survived in the Grassland + Grass present treatment. (Error Bars + SD) 100

5-1 *Acacia polyacantha* stand on the Kimarishi River (tributary of the Grumeti River): (A) *Acacia polyacantha* stand canopy trees, (B) edge of riparian forest, (C) understory of dense bushes in *A. polyacantha* stand 111

5-2 Location of riparian and hilltop forests within the Serengeti ecosystem 113

5-3 The relationship between density of forest seedlings and area of *Acacia polyacantha* stands along the Grumeti River, Serengeti National Park. (n=75 stands) 119

5-4 The mean density of forest seedlings, and mean understory percent covers of grasses, herbs, and bushes in *Acacia polyacantha* stands. Medium sized patches were approximately 100 m², and large patches > 650 m². (n=75 stands) (Error bars = ±SD seedling density) 120

5-5 Distance between seedlings of riparian forest trees and the nearest *A. polyacantha* trees and nearest bushes within *A. polyacantha* stands. (n=327 seedlings) 121

5-6 Current position (July 2001) of *Acacia polyacantha* stands superimposed on photo taken from Kimerishi Hill of the riparian forests along the Orangi River, June 1980 123

5-7 Survival of *Euclea divinorum* seedlings in riparian areas of the Mara River; with and without fire and browsing, and with and without grass present. The grass present treatment is equivalent to the unburned, with browsers treatment. (Error bars ± SD) (average survival of 214 seedlings in 12 plots) 125

5-8 Growth rate of *Euclea divinorum* seedlings in riparian areas of the Mara River with and without fire and browsing, and with and without grass present. The grass present treatment is equivalent to the unburned, with browsers treatment. (Error bars ±SD) 126
Population growth rate of canopy trees in *Croton* thickets and closed canopy riparian forests under conditions of (i) no elephants, antelope, or fire, (ii) with elephant, (iii) with antelope, and (iv) with fire.

List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>The mean size of 20 forest patches on the Grumeti River, Mara River tributaries, and Mara Hilltops in 1972, the number of these forest patches surviving in 2000, the remaining area of surviving patches, and the total area remaining of the 20 forest patches in 2000</td>
<td>32</td>
</tr>
<tr>
<td>2-2</td>
<td>Number of forest patches on the leeward and windward side of the Grumeti River in 1972 and 2000</td>
<td>33</td>
</tr>
<tr>
<td>2-3</td>
<td>Forest edge average growth rates (cm/year) across 15 sites by forest type</td>
<td>38</td>
</tr>
<tr>
<td>2-4</td>
<td>Duration when grass adjacent to forest blocks was ignitable during the dry season. Each forest block was visited every 7 days, yielding an average error of 3.5 days to each date</td>
<td>42</td>
</tr>
<tr>
<td>3-1</td>
<td>The proportions of (A) trees attacked by elephants, (B) that survive afterwards, and (C) survival of un-attacked trees in each size class larger than seedlings (0-0.75 m) in the Grumeti River, Mara River, and Mara Hilltop forests</td>
<td>67</td>
</tr>
<tr>
<td>3-2</td>
<td>The proportions of (A) trees pushed down by elephants, (B) that survive afterwards, and (C) survival of un-attacked trees in each size class larger than seedlings (0-0.75 m) in the Grumeti River, Mara River, and Mara Hilltop forests</td>
<td>69</td>
</tr>
<tr>
<td>3-3</td>
<td>The proportions of (A) trees attacked by antelope, (B) that survive afterwards, and (C) survival of un-attacked trees in each size class larger than seedlings (0-0.75 m) in the Grumeti River, Mara River, and Mara Hilltop forests</td>
<td>69</td>
</tr>
<tr>
<td>3-4</td>
<td>Total mortality rates per year (probability of attack X survival probability) for elephant attacked trees (Ele), elephant &quot;pushed over&quot; trees (PO), and antelope attacked trees (A) in Grumeti River, Mara River, and Mara hilltop forests</td>
<td>73</td>
</tr>
<tr>
<td>4-1</td>
<td>The percent ground, grass, and canopy cover (± SD) where naturally occurring seedlings were found and the mean forest ground, grass, and canopy cover (± SD) for Grumeti riparian, Mara riparian and Mara hilltop forests</td>
<td>94</td>
</tr>
<tr>
<td>4-2</td>
<td>The distance between naturally occurring seedlings and the nearest canopy tree and nearest bush (± SD), and the mean distance between canopy trees and bushes (± SD) for Grumeti riparian, Mara riparian and Mara hilltop forests</td>
<td>94</td>
</tr>
</tbody>
</table>
4-3 Number of seedlings per square metre at the end of the wet season in riparian forests with and without flooding during that wet season. Standard deviations in brackets...

4-4 The number of new seedlings in areas following fires and in areas without fires in Grumeti and Mara riparian forest, and Mara hilltop forest. Standard deviations in brackets...

4-5 Proportion of Core to Edge forest seedlings found in four forest transects; near river (except in hilltops), central forest, inside forest edge, and in grassland...

4-6 Mean number of new seedlings in forest plots at the end of the wet season with and without grass removed from the experimental plot Averages are across 9 treatment plots in each of three focal study patches, of each forest type. (Standard deviations are in brackets)

6-1 The effects of antelopes, elephants, fire, floods, grass removal, and canopy gaps on the population growth rate of Croton thickets and closed riparian forests via changes in germination rate, seedling growth and survival, and large tree survival. Each treatment was conducted in the absence of other effects: thus antelope are assumed to be removed when the effects of elephants are varied, unless otherwise stated.
ACKNOWLEDGEMENTS

Research of an international nature requires the cooperation and assistance of many people. In Tanzania, my research was made possible by the Tanzanian Commission for Science and Technology, the Tanzania Wildlife Research Institute and Tanzania National Parks. Frankfurt Zoological Society provided infrastructure in the field. In particular, I would like to thank Justin Hando, Chief Park Warden of Serengeti National Park.

My supervisors at UBC, A.R.E. Sinclair and Roy Turkington, provided insight, direction and the opportunity to work in Serengeti. I thank both of them for their support. My supervisory committee members, Jamie Smith, Dolph Schluter and Valerie Lemay provided many useful criticisms and comments.

In Tanzania, I would like to thank Dr. Simon Mduma for his guidance and forbearance with a novice student in the bush. My field assistant and co-worker, Mzee Steven Makatcha, deserves thanks for his hard work and motivation. I also thank Ali Nkwabi, Sanders Moore, Jumapili Shabani, Nelson Ole Kwai, Sita Mustafa and Ephrahim Wangomo for data collection help, and Mzee Dorino, M. Azali, and M. Ole Robo, my armed guards, for keeping me safe in the field. Sebastian Chua was of enormous help in identifying many of my trees.

My deepest thanks to Aerin Jacob, for her support, tolerance and sense of humour in the face of this undertaking. Thanks to my friends for their digging, mailing, laughing and commiserating which has seen me through. My gratitude to my parents, for their encouragement, sense of adventure, and curiosity which got me into this in the first place.

There is a tree native to Turkistan,
Whose hard, cold cones,
Not being wards to time,
Will open only in a forest fire.
I knew the Pheonix was a vegetable.
-William Empson

Come away, and stop banging on that tree. There is a leopard in it.
- Steven Makatcha
Chapter 1 An introduction to the decline of the Serengeti riparian and hilltop forests.

Introduction

Natural forest fragments occur in riparian grasslands (Figure 1-1) throughout the tropics, where they provide habitat for a variety of plant and animal species and increase the biodiversity of savanna ecosystems dramatically (Medley 1992; Medley and Hughes 1996; Kellman et al. 1998). Riparian and hilltop forests are found in the Serengeti ecosystem of Tanzania and Kenya (Figure 1-2) and across East Africa (Figure 1-3) (Medley et al. 1996). Outside protected areas, forests are under heavy pressure as a source of firewood and building materials. Despite their high biodiversity and rapid loss, the dynamics of these forests in East Africa are poorly understood. In Serengeti, riparian and hilltop forests have been declining in both area and number since 1970, apparently due to natural processes (Chapter 2). In this thesis, I examine the dynamics of Serengeti riparian and hilltop forests. I quantify the processes that reduce and enhance survival and recruitment of forest trees. My goal is to gain insights into the ecology of natural forest fragments and their future management.

Forests in Serengeti are subject to a wide variety of natural disturbances which remove canopy trees and reduce recruitment, including fire, elephant damage, and antelope browsing. The effects of individual disturbances have been studied in similar forests to those in Serengeti, in South Africa (Van Wilgen et al. 1990), Uganda (Chapman and Chapman 1999a), Belize (Kellman and Meave 1997), and Venezuela (Biddulph and Kellman 1998), but not with all of these disturbances acting in combination. Forests are prone to grassland fires, which can enter forests and either directly remove canopy trees, or reduce canopy cover by preventing seedling recruitment (Kellman et al. 1997). The effects of fire, however, can be mediated by conditions at the forest edge including increased moisture and reduced grass biomass (Biddulph et al. 1998). These in turn may be affected by the type and structure of the forest boundary. In savannas, elephants reduce Acacia (L.) woodland tree cover when elephant density is high, and limit recruitment of woodlands by removing seedlings (Laws 1970; Norton-Griffiths 1979; Dublin 1986; Dublin et al. 1990; Lock 1993). Antelope, primarily impala (Aepyceros melampus), limit growth rate and recruitment of Acacia seedlings in Serengeti and Manyara National Parks (NP), Tanzania (Belsky 1984; Prins and van der Jeugd 1993). Each of these factors, or combinations of them, may be causing the decline of riparian and hilltop forests in Serengeti.
Figure 1-1. Aerial view of riparian forests along one of the Mara River tributaries (Ngurimi River) near the Kenya-Tanzania border, Serengeti National Park, Tanzania.
Figure 1-2 Location of riparian and hilltop forests within the Serengeti ecosystem.
Figure 1-3 Major River systems in East Africa and locations of known riparian forest systems. (Modified from Medley and Hughes, 1996)
A second aspect of forest dynamics is recruitment of new trees inside forests and into the adjacent grassland to allow the forests to replace canopy trees lost to disturbance or senescence and expand into the grassland. Recruitment of forest seedlings in grassland areas is often poor, despite fire suppression (Chapman and Chapman 1996; Biddulph et al. 1998; Hoffmann et al. 2004). In some cases, forests that have been converted to grassland have remained grassland for over a century (Chapman et al. 1996). Low seedling survival may be due to high sunlight, low soil moisture (Kellman 1984; Kellman 1985; Hoffmann et al. 2004), competition with grass (Chapman et al. 1999b; Williams 2000), herbivory by rodents (Duncan and Duncan 2000; Holl et al. 2000), and low seed dispersal (Meave and Kellman 1994; Chapman et al. 1999b; Holl et al. 2000). Alternatively, cool fires and flooding may increase germination rates of forest trees (Medley et al. 1996; Kellman et al. 1997; Williams 2000). Others have reported a large increase in germination and seedling survival below bird roosts and savanna trees in the grassland, presumably due to reduced competition from grass and increased seed rain (Chapman et al. 1999a; Holl et al. 2000; Holl 2002). Thus, seedlings may only recruit under special conditions both within the forests and in the adjacent grassland.

In this thesis, I ask two questions: 1) what processes are causing the decline of Serengeti forests, and 2) under what conditions can forests recruit new trees both inside the forests and in the adjacent grasslands? In this chapter I describe: (i) the Serengeti ecosystem, (ii) riparian forests in East Africa and Serengeti, (iii) savanna woodland dynamics, and (iv) what is known about riparian forest dynamics. I then propose hypotheses to account for forest decline and recruitment, and describe how these hypotheses are tested in subsequent chapters.

The Serengeti Ecosystem

The Serengeti ecosystem is a mosaic of open grasslands and woodlands covering 25 000 Km$^2$ of north western Tanzania and south western Kenya (Figure 1-2). The ecosystem is defined by the seasonal migration of wildebeest (*Connochaetes taurinus*). The ecosystem is composed of the core areas of Serengeti National Park in Tanzania and Masai Mara National Reserve in Kenya. Serengeti NP is surrounded by the Ngorongoro Conservation Area, Maswa Game reserve, and the Loloindo, Grumeti, and Ikongoro Game Controlled Areas in Tanzania. Masai Mara NR is surrounded by Group Ranches in Kenya. Serengeti was established as a game reserve in the southern
and eastern Serengeti National Park (NP) in 1929, and areas were added in 1940, 1951, 1959, 1965 and 1967 to form the present park (Sinclair 1995b).

The climate of Serengeti is semi-arid with mean maximum temperatures of 27-28°C in Seronera. Minimum temperatures vary from 16°C in the wet season (November-April), to 13°C in the dry season (May-September). Rainfall occurs bimodally with the "short rains" occurring in November-December and the "long rains" occurring in February-April. A rainfall gradient follows an altitudinal gradient across the park, with the highest altitude and annual rains in the north of the park (1950m, 1200 mm/year), and lowest in the south (1600m, 500 mm/year) (Sinclair 1995b).

The Masai Mara is composed of a series of plains and mesas. South of the Mara River (Figure 1-2), northern Serengeti is characterized by a series of generally north-south hills and river valleys ranging from 100-250m elevation. Central Serengeti is composed of low, rolling hills, while the western corridor of the park is a plain with low hills between the Grumeti and Mbalageti Rivers. The south east of the park is a flat, treeless plain where the grassland vegetation is maintained by a concretion layer in the soil that is of recent volcanic origin. Soils follow a gradient in clay composition from hilltops to valley bottoms. Hilltop soils are generally stony, thin, and well-drained with a low clay content. Valley bottom soils are depositional areas with high clay and sand content and are poorly drained.

The northern hilly region of Serengeti supports a woodland of *Terminalia mollis* (C. Lawson), *Combretum molle* (R. Br. Ex G. Don) and tall grass. Forests occur in some valleys and in disjunct hilltop thickets on ridges and hilltops. The central and western parts of Serengeti support mixed stands of *Acacia clavigera* mainly in well drained sites and *A. drepanolobium* (Harms.), and *A. kirkii* (Engl.) in poorly drained sites. The western corridor of the park supports similar stands in hilly areas and open grassland in plain areas.

The most common herbivore in the ecosystem is the wildebeest (*Connochaetes taurinus*) with a population of approximately 1.4 million (Mduma et al. 1999). Other grazers include zebra (200,000) (*Equus burchelli*) and Thompson's gazelles (440,000) (*Gazella thomsonii*) (Sinclair 1995b). Browsers are also common, particularly in riparian forests, including impala (74,000) (*Aepyceros melampus*) (Campbell and Borner 1995), and smaller numbers of bushbuck (*Tragelaphus scriptus*), steinbuck (*Paphicerus campestris*), and dikdik (*Madoqua kirkii*). Elephants (*Loxodonta africana*) range widely within the ecosystem, and are often observed in riparian forests.
Riparian forests in Africa

Riparian forest patches similar to those in Serengeti occur on many rivers throughout East Africa (Medley et al. 1996; Young 1996) (Figure 1-3), West Africa (Martin 1991), and South Africa (Coates Palgrave 1983). Forests similar to the Mara hilltop *Croton* spp. thickets occur in montane areas of Kenya (Hughes 1990), Uganda, Rwanda (Lejju et al. 2001), and Ethiopia (Teketay 1992).

The current distribution of riparian and hilltop forests in East Africa is thought to be a consequence of historic expansions of Central African lowland forests, and montane forests from the mountainous areas surrounding Lake Victoria (Livingstone 1982; Medley et al. 1996). Central African forests increased in extent ca 14 000 BP during a warm, wet period from central Africa to the Indian Ocean. They retreated west as the climate cooled ca 6 000 BP (DeBrusk 1998). Montane forests expanded to lower altitudes at about the same time (Jolly et al. 1997). Both forest types have retreated further during the last 3 000 years as drier conditions and human set fires have increased (Livingstone 1982). Riparian and hilltop forests are therefore remnants of central African and montane forest expansions and now function as refugia for species that do not otherwise exist in the savanna ecosystem (Livingstone 1982; Medley et al. 1996).

Forests outside reserves in East Africa are in jeopardy due to logging, particularly for long straight poles for building (Pers Obs.). Riparian areas are also used heavily by pastoralist’s cattle (Medley et al. 1996).

Riparian forests in Serengeti

Riparian forests within the Serengeti ecosystem occur on the floodplain created by the Grumeti River in the west, and in the steeper valleys of the Mara River tributaries on the south side of the Mara River. Small riparian patches also occur along the Mbalageti and Orangi Rivers in the west of the park. Hilltop thickets of *Croton dichogamus* occur in the north of the park and in the bordering Masai Mara Game Reserve in Kenya (Figure 1-2). The Grumeti River meanders along a broad, flat floodplain through the lowest elevations in the park, while Mara River tributaries occur at the highest elevations in the park in rolling hills and gullies.

The riparian and hilltop forests in Serengeti fall into two groups based on structure and species composition. The first group consists of the riparian forests in the west of the park, on the Grumeti, Mbalageti, and Orangi Rivers. These forests have a homogenous closed canopy, a “hard” boundary with the grassland, and are composed of
species from Central Africa and coastal areas of East Africa (Dale and Greenway 1961; Beentje 1994). The second group is composed of the Mara tributary riparian forests and Mara hilltop forests. Mara riparian forests are composed of two distinct zones, a dense closed canopy core and an open canopy boundary zone composed of fire-tolerant species. Mara hilltop forests are similar in species composition in the open canopy boundary zone of Mara riparian forests. The trees in Mara forests also occur in montane areas of Kenya, Uganda and Rwanda (Dale et al. 1961; Beentje 1994).

*Grumeti River riparian forest*

The Grumeti forests have a dense canopy, low numbers of bushes, and grass occurs only in canopy gaps and at the periphery (Figure 1-4). The forest edge has a distinct "hard boundary" with the grassland composed of overhanging canopy trees, bushes, and young canopy trees. The most abundant canopy species are *Lecaniodiscus fraxinifolius* (Baker), *Elaeodendron buchananii* (Loes) [Cassine buchananii Loes.], *Diospyros abyssinica* (Hiern) F. White [Maba abyssinica (Hiern)], and *Ziziphus pubescens* (Oliv.). These forests occur at the lowest elevation in the ecosystem (1200m), and have the lowest annual rainfall (740mm), and highest mean temperature (17°C).

*Mara River tributary riparian forest*

These forests occur in two distinct bands: a closed canopy band 50-100m wide adjacent to the river, followed by a 50-75m semi-closed canopy band that borders the grassland (Figure 1-4). The closed canopy core is composed of *Diospyros abyssinica*, *Drypetes gerrardii* Hutch. [Drypetes battiscombei Hutch.], *Ekebergia capensis* Sparrm. [Ekebergia meyeri Presl ex C. DC.], *Olea africana* Mill. [Olea europaea L., Olea chrysophylla Lam.], and *Ficus* (L.) trees, with an understory of *Croton dichogamus* Pax., *Teclea trichocarpa* (Engl.) Engl., and *Strychnos* sp. The semi-closed canopy band is composed of canopy *Euclrea divinorum* (Hiern) subsp. *keniensis* (R.E. Fries) de Wit [Euclrea keniensis (R.E. Fries)] trees, and an understory of *Croton dichogamus*. The Mara region of Serengeti has the highest elevation within the park ecosystem (1950m), the highest rainfall (1200mm), and lowest mean temperature (12°C).
Figure 1-4. The structures of the three types of Serengeti riparian and hilltop forests. Arrow (↓) indicates the “edge” of the forest; the maximum extent of forest tree canopy.
Mara Hilltop forest

On some hilltops within the Mara watershed, hilltop forests or "thickets" cover areas from 1-5 ha. and consist of a dense matrix of 2-3m *Croton dichogamus* and *Teclea trichocarpa* bushes with interspersed emergent (6-15m) *Euclea divinorum*, *Diospyros abyssinica*, and *Olea africana* trees (Figure 1-4). The Mara hilltop forests closely resemble the outer band of the Mara riparian forests.

History and ecology of the Savanna Matrix

The *Acacia* woodlands of Serengeti have undergone large changes in density during the last century (Dublin 1986; Dublin 1995; Sinclair 1995a). Since the riparian and hilltop forests exist within a matrix of savanna woodlands and grasslands, an understanding of the history of savanna dynamics in Serengeti is relevant to understanding the causes of forest decline.

The savanna matrix of *Acacia* and *Terminalia* species has undergone two periods of mass-establishment in the last century. Dense woodlands were established at the beginning of the 20th century, declined mid-century, and rose again since the late 1970's. The first records from Serengeti at about 1900, describe the area as a savanna parkland (references in Dublin (1986). Bovine pleuro-pneumonia and rinderpest outbreaks in the 1880s and 1890s reduced both wildlife and cattle in the Serengeti area by more than 90% (Sandford 1919; Mallet 1923; Sinclair 1979). The Masai and WaSekuma people who occupied the area from the Moshi hills in north east Tanzania to Serengeti in north west Tanzania, were pastoralists, almost completely dependant on cows. The removal of cows caused high mortality and emigration of these people (Ford 1971). Such emigration reduced seasonal burning of grassland areas to improve dry season forage for cows during the period 1890-1930 (Dublin 1986). In addition, the ivory trade, which peaked in the 1880's, removed elephants from many parts of East Africa, including the Serengeti (Spinage 1973). With the removal of both fire and elephants, *Acacia* species exhibited a pulse of establishment and formed dense woodlands over much of Serengeti and Masai Mara (Sinclair 1995b; Sinclair et al. 2005).

Following this mass establishment, the Serengeti woodlands began a slow decline from the 1930s through the 1970s (Sinclair 1995a), resulting by 1970 in a parkland of grass and a few large trees. Elephant damage to adult trees and seedlings was initially thought to be the cause of woodland decline following the immigration of elephants into the ecosystem in the 1930s and subsequent build-up of numbers through the 1960s. Norton-Griffiths (1979), however, demonstrated that frequent, hot fires were the principal
cause of woodland decline and that elephants played a secondary role. From 1950-70 high rainfall and few herbivores (populations remained low after the rinderpest epidemic) allowed extensive, hot fires to burn over much of Serengeti and Masai Mara, often twice of three times per year (Norton-Griffiths 1979). Dublin (1986, Dublin 1990) found in Masai Mara that only fire, not elephants, can convert a woodland into a grassland. Once in a grassland state, however, either elephants or fire are able to maintain that grassland state.

The wildebeest population increased dramatically during from 1963 to 1977 (Mduma et al. 1999) and their grazing reduced the grass fuel load and thus fire frequency (Norton-Griffiths 1979, Sinclair 2005). This combination of factors has led to a second mass establishment of Acacia trees that began in the late 1970s (Sinclair 1995a).

**History of the riparian and hilltop forests in Serengeti**

Much less historical information is available concerning the riparian and hilltop forests of Serengeti. Reports indicate no mass establishments of trees. Instead forests appear to have declined gradually throughout this period, largely by erosion of the forest edge by fire (Figure 1-5).

The earliest records of forests are from hunters and game wardens between 1905 and 1913 who described an open parkland with Croton thickets on hilltops in the Masai Mara, "...an open, grassy rolling country. Here and there are low, rocky, circular outcroppings hillocks crowned with green thickets... The thickets [Croton dichogamus] are nowhere continuous, and one can always march around them" (White 1915). During the 1930’s the photographers Martin and Osa Johnson described extensive Croton thickets on hilltops of northern Serengeti, as did the first Royal Air Force aerial survey of the area in 1950 (Dublin 1986). Whether the Croton thickets increased with the Acacia woodlands due to infrequent fire and elephants in the early 1900’s is unknown.

In 1975, Herlocker described the riparian and hilltop forests during a comprehensive mapping of Serengeti and proposed that they had once been much more extensive. He classified riparian forests and hilltop forests as “Evergreen forests” and “Semi-Deciduous Bushland” (Herlocker 1975). Evergreen forest occurred, “on alluvial soils…along rivers and…as small relics scattered on deep sandy loam soils of broad ridge tops [in the north of Serengeti]”. “Evergreen Forest has a high water demand and is easily destroyed by burning. Therefore it generally occurs on sites which provide a large amount of ground water and some protection against grass fires.”
Figure 1-5 Aerial photograph of Mara River tributary (Ngurimi River) riparian forest patch, with size reduction through time. Photo shows forest cover in 1972, with 1959 and 2000 coverage overlayed.
Combretum molle-Terminalia mollis woodland, which covers most of the northern part of Serengeti on hills and hillsides was reported to replace evergreen vegetation under conditions of frequent fires in Kenya (Glover and Trump 1970). Herlocker (1975), thus proposed that evergreen vegetation (riparian forests) had once occurred over large areas where Combretum molle-Terminalia mollis woodland was found in 1972. This idea is consistent with the view that riparian forests in East Africa are relicts of closed canopy forest which extended over East Africa 10 000 years BP and has been gradually declining since (Livingstone 1982). However, there is no evidence to support the idea that riparian forests recently covered much of northern Serengeti, nor any records of forests composed of the same species types covering such a large and seasonally dry area in Tanzania or Kenya. However, distribution patterns of forest birds have been interpreted as evidence for more extensive forests in the past (Moreau 1966).

Hilltop Croton thickets were described by Herlocker as “Semi-deciduous bushland”, a thicket type once common in Eastern Narok District of Kenya (Glover et al. 1970) and Southwest Kenya Highlands (Langdale-Brown et al. 1964). Semi-deciduous bushland is easily destroyed by fire, and may be replaced by Acacia clavigera and Acacia gerrardii. It was thus proposed to be an early successional step toward A. clavigera stands, and must have once covered a large area of Serengeti in the region between the Mara and Grumeti Rivers (Figure 1-2) (Herlocker 1975). It is now known that A. clavigera establishes directly into grasslands due to a reduction in fire frequency (Dublin 1986), and this assumption of former distribution of Croton thickets may be erroneous.

The first quantitative evidence of forest decline is from Norton-Griffiths (1979) who compared aerial photography taken in 1958 and 1972 of the northern portion of Serengeti. He reported a 20% decline in “bush thicket”, largely hilltop Croton forest, and a 6% decline in riparian forest cover; 1.43% and 0.47% decline per year respectively. Norton-Griffiths (1979) modeled the effects of fire and elephants on Acacia woodland dynamics. He showed that fire was removing sufficient Acacia seedlings to limit recruitment and so cause a decline in woodland Acacia populations (Norton-Griffiths 1979), although no data were available to model the riparian and Croton/hilltop forests.

From 1950-1982, the Croton/hilltop thickets in Masai Mara park, adjoining the northern Serengeti, declined rapidly in both size and percent cover (Dublin 1986). The average percent cover of the extant thickets declined 38% (from 77% to 39%) over the same time period (Dublin 1986). Both the absolute and relative loss rates of Croton thicket percent cover increased from a low of 0.25-0.4 %/yr. during the 1950’s to a high
of 1.4-3.2% in the following decades until 1982, indicating that an accelerated rate of decline of these forests began in about 1960. The average area of individual Croton thickets declined 33% from 4.12 km$^2$ to 2.80 km$^2$ during the same period (Dublin 1986).

In the following section, I summarize each chapter in the thesis and briefly describe my principal findings.

Chapter 2: Fire

The importance of fire in limiting both seedling and adult survivorship of savanna Acacia species suggests that it may also be an important determinant of riparian and hilltop forest survivorship. Fires entered forest patches, leaving fire scars on standing trees. Fires also appear to have killed canopy trees creating openings that allowed grass to grow (G. Sharam pers obs.). In Chapter 2, I examine: (i) whether fire is the cause of forest decline, (ii) the mechanism by which fire erodes forest edges, (iii) the influence of forest boundary type on susceptibility to fire, (iv) whether the time between successive burns affects tree mortality rate, (v) the lateral spread of forests in the absence of fire, and (vi) the mechanisms by which forests exclude grassland fires.

Grassland fires remove both seedlings and canopy trees at the forest edge, and can erode the forest edge if fires are more frequent than every third year. Fire is excluded from forests by low grass content and high moisture content in the surface litter during the dry season. Thus, dense forest boundaries exclude infrequent fires better than open boundaries, but at high fire frequencies, all forest boundaries are equivalent. Lateral spread of the forest by tree canopies is slow, and is halted by fires as infrequent as once every four years.

Chapter 3: Elephant and antelope herbivory

While damage to large Acacia trees in savanna is the most obvious sign of elephants, measurements showed that the majority of trees removed are in the 0-0.75m and 0.75m-2m size classes (Croze 1974a; Croze 1974b; Dublin 1986). Elephants have been reported to control the recruitment of a variety of tree species, including Acacia clavigera in Serengeti NP (Dublin 1986; Dublin et al. 1990; Dublin 1995), Acacia erioloba (E. Meyer) in Chobe NP, Botswana (Barnes 2001), and Acacia spp., Capparis tomentosa (Lam.) and Dichrostachys cinerea (L., Wight & Arn.) in Queen Elizabeth NP, Uganda (Lock 1993). Impala have also been proposed as limiting the recruitment of Acacia trees in Manyara NP, Tanzania (Prins et al. 1993) and Chobe NP, Botswana
Elephant damage to larger trees and signs of impala browsing on seedlings were observed in Serengeti riparian and hilltop forests.

In Chapter 3, I examine the question of whether elephant and impala reduce the survival and growth of seedlings of forest trees, and whether herbivory interacts with fires to further reduce survival. In order to test these ideas, I made the following predictions: (i) seedling mortality by elephants is high, (ii) canopy tree mortality by elephants is high, (iii) seedling mortality by impala is high, and (iv) there are interactions between damage to seedlings by impala, elephants and fire. Impala browsing reduced seedling survival and effectively stopped seedling growth, while the effects of elephant herbivory and damage were negligible. There was no interaction between mortality due to herbivory and fire damage.

Chapter 4: Germination and establishment of tree seedlings: the effects of flooding and grass competition

Some researchers have found that despite fire suppression, forest trees fail to recruit in grassland areas (Duncan et al. 2000), due to low soil nutrients in grassland areas (Kellman 1984), limited seed rain (Holl et al. 2000), seed herbivory by rodents (Duncan et al. 2000), desiccation (Hoffmann et al. 2004), and competition with grass (Bowman and Panton 1993; Berkowitz et al. 1995; Holl et al. 2000; Bendfeldt et al. 2001; Hoffmann et al. 2004). In addition, riparian tree seeds have undergone pulses of germination in forests following fires in Belize (Kellman et al. 1997), and floods of the Tana River, Kenya (Hughes 1990).

In Chapter 4, I examine the distribution of naturally occurring seedlings following floods and in relation to grass abundance, and examined the germination and survival rate of seeds under the experimental conditions of with and without grass, browsers, recent fires, and floods. Recent fires, floods, and grass removal increased the germination rate of seeds, while removal of browsers increased the subsequent survival of seedlings. No experimental treatment allowed germination in the grassland adjacent to forests, but removal of both grass and browsers allowed small numbers of planted seedlings to survive.

Chapter 5: Establishment of forest tree seedlings under nurse trees in the savanna

It has been proposed that forest seedlings can only establish into grassland areas when associated with a “nurse” tree below which seed rain is higher, grass density is
lower and soil moisture is higher (Kellman and Miyanishi 1982; Bowman et al. 1993; Holl et al. 2000; Otsamo 2000; Loik and Holl 2001; Holl 2002; Hoffmann et al. 2004).

In Chapter 5, I examine: (i) whether riparian forest tree seedlings can establish under the canopies of savanna "nurse" trees, and (ii) under what conditions nurse trees are able to establish in riparian grassland. The nurse species *Acacia polyacantha* established along the Grumeti River in the late 1970s likely due to a reduction in fire. Large stands of *A. polyacantha* facilitate the establishment of riparian forest seedlings by excluding grass, fire, browsers, and elephants, while individual canopy trees and small stands were unable to support seedlings. Another potential nurse species, *Euclea divinorum*, did not establish in grassland areas when fires are reduced, and appears to also be limited by browsing. Stands of pioneer species, particularly *A. polyacantha*, may make good management tools for establishing riparian forests and degraded stands in other areas of Africa.

Chapter 6 Decline and establishment in closed canopy forests of Serengeti; the cumulative effects of fires, elephants, antelope browsing, floods, and grass competition.

In Chapter 6, I examine whether the effects of disturbance and herbivory on germination and survival are sufficient to limit forests from replacing lost canopy trees. Fire at even low frequencies, and impala browsing are able to limit recruitment of forest seedlings, while elephants did not reduce survival sufficiently to limit forests until they reached densities 4-5X those found today. The positive effects of floods, recent fires, and grass removal on germination are unable to balance the negative effects of fires and impala. Thus, forests can only establish under nurse trees (Chapter 5) and forests can subsequently survive only when fire frequency and antelope numbers are low.
References


Chapter 2 Riparian and hilltop forests in Serengeti National Park, Tanzania; do effects of savanna fires depend on forest edge type?

Introduction

Closed canopy forests are often found in tropical savannas as islands of high species diversity. Forests are subject to frequent grassland fires, limiting their distribution to fire refugia such as hilltops, fire shadows, and riparian areas (Geldenhuys 2005). Forests decline during periods of frequent fires, and some forests expand when fires are removed (Dunham 1989; Kellman and Meave 1997; King et al. 1997; Biddulph and Kellman 1998). In the Serengeti ecosystem, riparian forests along the Grumeti and Mara Rivers, and hilltop forests near the Mara River have been declining since the early 1970s, likely as a consequence of fire.

The patterns of forest loss in Serengeti can provide evidence of whether fire is causing forest decline. Riparian forests are exposed to more frequent fires than grassland areas due to both higher grass fuel load in riparian areas and the linear shape of forest patches (Kellman et al. 1997). As early as the 1970s, Norton-Griffiths (1979) noted that hilltop and riparian forests in the north of Serengeti were being converted to grasslands. Between 1958 and 1972, fragmented, open canopy, and linear-shaped patches of Croton/hilltop thickets in Serengeti changed to grassland more frequently than did round patches (Norton-Griffiths 1979). Dublin (1986) reported that the rate of loss of Croton thicket increased after 1960, and that Croton thickets were declining in both percent cover and in total area by 2-3% per year.

Fire appears to be the main determinant of riparian and hilltop forest distribution. Closed canopy Central African and montane forests in East Africa have declined during the last 6000 years, largely due to immigration of people and the corresponding increase in fire frequency (Jolly et al. 1997). Forested riparian areas in Brazil and Australia were found to have less charcoal in soil cores from periods when fires were frequent than forested non-riparian areas, suggesting that continuous forests retreat to riparian areas when fire frequency is high (Bassini and Becker 1990; Hopkins et al. 1993).

Fire erodes forest edges in Venezuela, and South Africa (Kellman et al. 1997; Geldenhuys 2005). Riparian and hilltop forests are often composed of trees common in continuous forests and which are very susceptible to fire (Uhl and Kauffman 1990). Fires are observed at the edges of riparian and hilltop forests in Serengeti, leaving fire...
scars on standing trees. Fires also appear to have killed canopy trees, creating openings that allow grass to grow (G. Sharam, Pers Obs.)

Fires burn up to riparian forests and then are driven along them by the wind, and forests occur more frequently in the lee of wind-driven fires on the downwind side of rivers (Kellman et al. 1997). Montane forests also occur in fire shadows on the leeward side of ridgelines and streams (Geldenhuys 2005). Higher survival of forest patches on the downwind side of rivers would be consistent with fire causing forest decline in Serengeti.

Fires at the forest boundary can either remove seedlings and limit recruitment, or remove larger trees and change the forest structure. Tropical forest trees lack thick, insulating bark and can be killed by ground fires of even moderate intensity, unlike savanna tree genera such as Acacia, Terminalia, Dichrostachys, etc. (Uhl et al. 1990). Despite the susceptibility of large trees to fire, most tropical forest fragment research shows that the effect of fire is to reduce the survival of seedlings and thus limit recruitment of new forest trees (Unwin et al. 1985; Biddulph et al. 1998).

The boundary between forest and grassland is highly variable between forest types, and its particular combination of characteristics may exclude grassland fires or allow them to penetrate into the forest interior (Biddulph et al. 1998). Few previous studies describe the type of forest edge, and Murcia (1995) found no studies that compared the effects of fire on different edge types. Human-made forest fragments are particularly susceptible to fire, and managing them effectively requires a thorough understanding of how the forest edge type responds to fire (Uhl and Buschbacher 1985). Three different forest edges are found in Serengeti. Two follow Ranney's criteria (1981): cantilevered (Grumeti riparian) and advancing (Mara riparian), with an additional edge type I describe as "open advancing" (Mara hilltops).

Few experiments have been conducted to look at the effects of varying the frequency of repeated burning on forest edges. Different types of forest edges expose different parts of trees and bushes to grassland fires. Dense cantilevered edges expose only the ends of their branches to fire, while advancing edges expose the trunks of trees to fire and may be more susceptible to repeated burning.

Many forest fragments do not expand into grassland areas, as seedlings are susceptible to fires, and seedling recruitment continues to be poor despite removal of fire (Duncan and Duncan 2000). Seedling recruitment may be limited by seed dispersal (Holl et al. 2000), and by physiological constraints (Eriksson and Ehrler 1992). Forests
may expand by lateral growth of branches, creating a micro-environment with limited grass and good conditions for seedling establishment. Lateral growth depends on the growth rate of the ends of branches, which are also removed by fire.

Forest edges exclude grassland fires by a variety of methods, including topological protection and shrubby boundaries (Unwin et al. 1985), high moisture content in live foliage (Van Wilgen et al. 1990). The forest edge may also exclude fire by reducing the amount of burnable grass in the edge, maintaining a high moisture content in the grass via shading (Biddulph et al. 1998). These effects may not be true for all forest edge types, particularly those with very open canopies.

In this chapter I examine the effects of fire on riparian and hilltop forests and the influence of forest edge type on forest erosion rates by:

1. Observing the number and type of forest patches that have survived between 1972 and 2000 on the leeward and windward side of rivers to determine if fire is causing forest decline.
2. Burning forest patches and measuring the survival of seedlings and canopy trees to determine the mechanism by which fire erodes forest edges.
3. Observing both the relative loss rates of the three forest types 1972-2000, and survival rates of tagged trees under similar burning regimes to measure the influence of forest boundary type on fire susceptibility.
4. Repeatedly burning the grassland adjacent to forests and monitoring the survival of tagged trees to measure the effects of successive burns on tree mortality rate.
5. Repeat measuring of the maximum extent of the forest edge from a fixed point and manipulating the number of consecutive years that the adjacent grassland is burned, to estimate the rate of lateral forest spread.
6. Measuring the burnable biomass of and moisture content of grass across the forest boundary during both the wet and dry seasons to assess the mechanisms by which forests exclude grassland fires.

Methods

Study Site

The Serengeti Ecosystem is a mosaic of open grasslands and woodlands covering 25 000 km² of north western Tanzania and south western Kenya (Figure 2-1). Riparian forests within Serengeti National Park (NP) occur on the broad floodplain created by the Grumeti River in the west, and in the steeper valleys of the Mara River
tributaries on the south side of the Mara River. Dense thickets occur on hilltops to the south of the Mara River (Figure 2-1).

**Grumeti riparian forests**

The Grumeti River riparian forests grow as patches and strips along the Grumeti River in the western corridor of Serengeti NP. Forests typically extend 200-400m along the river and 100-150m from the river into the grassland. The canopy of the forest is closed with low light levels and is made up largely of *Lecaniodiscus fraxinifolius*, *Elaeodendron buchanii*, and *Ziziphus pubescens*. The forest edge is a “hard” boundary, with a dense row of bushes and tree branches of *Ziziphus pubescens* and *Grewia bicolar* (Figure 2-2). This boundary is thick enough to reduce light levels to as low or lower than the forest canopy in the centre of the forest patch. Soils are sandy and typical of floodplain levee forest soils (Medley and Hughes 1996).

Outside the forest/grassland boundary are seasonally dry swamps and a dense belt of riparian grasses, composed chiefly of *Panacum maximum*. Beyond the riparian grass belt are savanna grasses, typified by *Themeda triandra*, *Digitaria macroblephara*, *Pennisetum meziamum*, and *Sporobolus* spp. Serengeti park rangers and managers report that fires burn the edges of these forests every 2-4 years. Fires are more common on the southern side of the largely east-west running river, as the only road in the area is to the south and predominant winds carry seasonally lit fires to the river (G. Sharam pers obs. 2000).

**Mara riparian forests**

The Mara riparian forests range in size from 50 X 50 m to 200 X 600 m and grow as patches in the confluences of streams along the southern tributaries of the Mara River. Mara riparian forests are different from the Grumeti riparian forests in that they are composed of two distinct belts of vegetation (Figure 2-2). The first belt is immediately adjacent to the river and is similar to the Grumeti riparian forests in patch density and low light levels. It is composed chiefly of *Diospyros abyssinica*, *Drypetes abyssinica*, *Eckiburgia capensis*, *Olea africana*, and *Ficus* spp. canopy trees.
Figure 2-1. Location of riparian and hilltop forests within the Serengeti ecosystem.
The second, or outer, band is 20-40 m wide and is unlike Grumeti forests in its open canopy structure of *Euclea divinorum* and *Olea africana*, higher grass content and higher proportion of bushes such as *Croton dichogamus*, *Techlia trichocarpa*, and *Strychnos* sp. The outer band dominant trees have an open canopy structure, small leaves, and little ability to block sunlight from reaching the ground. The forest understory and adjacent riparian area are dominated by the grass *Setaria spheculata*, while the savanna proper is composed largely of *Hyparrhenia filipendula*, *Themida triandra*, *Sporobolus pyramidalis*, and *Heteropogon contortus*. Soils are deep and less sandy than the Grumeti riparian forests.

There is little information on how often the Mara riparian forests have burned. However, the frequency of fires appears to be lower than that of the Grumeti river due to the lack of roads in the area for park rangers to light fires. Fires that do occur are generally lit by cattle thieves covering their tracks or game poachers burning areas adjacent to riparian forests to attract animals to their snares (G. Sharam *pers obs.* 1998-2001).

*Mara hilltop forests*

Hilltops and ridges south of the Mara river have thickets of *Croton dichogamus* and *Techlia trichocarpa* with emergent canopy trees of *Diospyros abyssinica*, *Euclea divinorum*, and *Driedes abyssinica*. Dense hilltop thickets resemble the outer band of Mara riparian forests with fewer canopy trees (Figure 2-2). Soils are thin and rocky/gravely in these forests. Grass occurs throughout at low densities. Fires occur often in these hilltop forests, as roads run along ridge tops from which rangers light fires. Fires lit by poachers in riparian areas burn up to hilltop areas, exposing the hilltops to a higher burn frequency than valleys, every 1-2 years in some areas (G. Sharam *pers obs.* 1998-2001).
Closed canopy forests with a hard grassland boundary. Forest is homogeneous with a strip of hydrophytic species at river and dense bushes at grassland edge.

Closed canopy forest with a catena of tree types grading from closed canopy through open Euclea canopy to grassland. Note the mixture of grass and shrubs under the open canopy.

Hilltop thickets of bushes and tree species from the river forests. Grass is found only within opened areas of the bush matrix. Tree seedlings are found only in dense bush areas.

Figure 2-2. The structures of the three types of Serengeti riparian and hilltop forests. Arrow (↑) indicates the edge of the forest; the maximum extent of forest tree canopy.
Patterns of forest loss

Twenty forest patches were identified in 1972 aerial photos in each of the three forest types: Grumeti River riparian, Mara River tributary riparian, and Mara hilltop forests. Forest size in 1972 was calculated by geo-referencing the aerial photos, and calculating the forest polygon area using Arcview Geographic Information Systems (GIS) (ESRI products, version 4.0). Forest size in 2000 was obtained by visiting each forest patch, walking the perimeter of the forest with a handheld Garmin 12XL Global Positioning System (GPS) and recording the track-log, from which the polygon area was calculated. Error in estimation of position using the GPS was no more than 2.6 m.

In order to examine the persistence of forests on the windward and leeward sides of rivers, aerial photographs from 1972 were compared with the present day distribution of Grumeti riparian forests. Forest patches were chosen in 1972 aerial photographs on the windward and leeward side of a 10 km section of the Grumeti River. As forests with different shapes and sizes may have survived at different rates, forest patches were divided into three categories of “belts”, “patches”, and “bows”. Belts are linear forests following the river course (minimum 50 m X 100 m). Patches are smaller and roughly square or round forests (approximately 25 m X 25 m). Bows are similar in size to patches, but are located behind river oxbows and are largely protected from fire. The number and percent area of forests remaining on the three river types between 1972 and 2000, and the proportions of forest patches on the windward and leeward sides of the Grumeti river were compared using Chi-square tests.

Canopy tree survival with fire

The effect of grassland fires on the survival of forest trees was measured using tagged trees in burned and unburned areas of forest patches. Trees were tagged in six study forest patches on each of the Grumeti and Mara Rivers, and in the Mara Hilltops. To measure the distance that fires penetrated into forest patches, trees were tagged in four roughly parallel transects at increasing distance from the forest centre, of 1000 trees each, in September 1998. The transects were identified as: A) River transect, running parallel and 10 m from the river (only in the two riparian forests); B) Central transect, parallel to and 50 m from the forest edge; C) Inner Edge transect, running 5 m inside the forest boundary, and D) Outer Edge transect consisting of trees directly adjacent to the grassland (Figure 2-3). Tagged trees were divided into 6 size classes: 1) seedlings < 0.75 m high (considered separately in a following section); 2) 0.75-1.5 m; 3) 1.5-3 m; 4)
3-5 m; 5) 5-8 m; and 6) >8 m high. Tagged trees were monitored every two months for three years and the condition of each tree was noted.

In each forest type, three patches with tagged trees were exposed to fire, and three were protected from fire as a control. All forest patches were protected from natural grassland fires by a 3 m wide fire-break running 100 m along, and 5 m from the forest edge. Fire breaks were constructed by cutting grass in the early dry season (May). The grass was allowed to dry for two weeks, and then burned while the surrounding grass was still green. Fire treatments were conducted by burning the area inside the fire breaks during the late dry season (August 1999, 2000, 2001) when the grass was dry. The survival of trees in the four transects within burned and control treatments were compared using Kaplan-Meier survival curves and the Log-Rank tests are reported (Zar 1974).

Repeated burns

The effect of repeated burns of tree survival was measured on trees at the forest edge that were burned 1) zero, 2) once, 3) twice, or 4) three times in four years. Control and Burned trees from the previous section were used as burned (1) zero and three times (4) treatments. Burned once (2) and twice (3) treatments consisted of two additional groups of 1000 tagged trees along the outer edge of the Fire treatment forest patches. These additional treatments were protected by fire breaks and burned during the late dry season (August: Burned once – 1999, Burned twice – 1999, 2000).

Seedling survival

The survival of seedlings of canopy trees (<0.75 m) was measured in three treatments in each forest type: 1) forest core - fire, 2) forest edge - fire, and 3) forest edge + fire (Figure 2-3). These treatments were carried out in different ways in the three forest types due to differences in seedling density. In each forest type, plots were established in three replicate study forests. In Grumeti forest patches where seedlings were abundant, seedlings were tagged (n=100 per plot) in three forest core plots, three plots on the forest edge where the canopy was intact, and in three plots at the forest edge where the canopy was removed and grass was allowed to invade (for a total of 9 plots of each type). After one year, four of the nine edge plots with grass were burned in the late dry season (August 2000, 2001). The other edge plots were protected by fire breaks and served as treatment controls.
Seedlings on the Mara riparian forests were monitored by tagging seedlings (n=250) in a single 50 m wide belt transect extending from the grassland edge to the river in each patch, in November 1998. Fire plots were set up in riparian forest patches parallel to the control areas. Both control and fire treatment areas were protected by fire breaks, and the fire treatments were burned in the late dry season (August 1998, 1999, 2000).

Hilltop forests were too small to contain both burned and unburned treatments. Three separate hilltop forest patches were chosen as controls and three as Fire treatments. Seedlings were tagged (n=150) in each forest at varying distance from the edge in March 2000. Each forest was surrounded by a fire break and for Fire treatments, the entire forest block inside the fire break was burned in the late dry season (August 2000 and 2001). Survival of seedlings was compared using Kaplan-Meier survival curves and Log-Rank tests.

Rates of edge expansion and contraction

The rates of forest edge expansion and contraction were found by measuring the distance between the forest edge and a series of markers each year in each forest type. Thirty concrete blocks were placed approximately 3 m inside the edge of forest patches and the distance between each block and the maximum extent of the forest edge bush layer was measured. I measured the rate of edge expansion at five fire frequencies in the burning treatment areas: 1) not burned; 2) burned once, 3) burned twice, 4) burned three, and 5) burned four times in four years. The growth rates (cm/yr) were compared using ANOVA, t-tests, and exponential regression. Data were transformed when necessary to ensure normality.
Figure 2-3 Experimental setup of permanent transects for canopy tree survival, tree seedling manipulations in riparian and hilltop forests, and grass biomass measurements.
Measuring grass biomass and moisture content

Grass biomass and moisture content were measured in the wet and in the dry season in each of the three forest types. Three transects were established perpendicular to the forest/ grassland edge in each of nine study forests (three of each type). A series of plots (30 X 30 cm) were sampled at five m intervals along a 60 m transect that ran perpendicular to the forest edge (30 m into the forest and 30 m into the grassland) for a total of 12 plots per transect. An additional plot was sampled at 75 m into the grassland to measure grass biomass outside the riparian areas. All of the grass and leaf litter and plant material in each plot was collected (in January and June 2000 and 2001), weighed, dried in paper bags in the sun and then re-weighed to measure dry biomass and calculate percent water content. Biomass and water content were compared between sites using ANOVA, and inside and outside of forests using t-tests.

Results

Patterns of forest decline

All three riparian and hilltop forest types in Serengeti NP declined by ≥ 48% from 1972 – 2000 (Table 2-1). Open canopy Mara hilltop patches declined the most (92%), and Grumeti closed canopy forests declined the least (48%).

Table 2-1 The mean size of 20 forest patches on the Grumeti River, Mara River tributaries, and Mara Hilltops in 1972, the number of these forest patches surviving in 2000, the remaining area of surviving patches, and the total area remaining of the 20 forest patches in 2000.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>Average forest patch size in 1972</th>
<th>Number of patches remaining in 2000 (%)</th>
<th>Average area of surviving patches remaining '72-00</th>
<th>Total area remaining in 2000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grumeti River</td>
<td>0.46 ± 0.52 ha</td>
<td>14 (70%)</td>
<td>75 ± 11%</td>
<td>52%</td>
</tr>
<tr>
<td>Mara River</td>
<td>2.8 ± 1.1 ha</td>
<td>17 (85%)</td>
<td>41 ± 18%</td>
<td>34%</td>
</tr>
<tr>
<td>Mara Hills</td>
<td>3.9 ± 1.6 ha</td>
<td>6 (30%)</td>
<td>28 ± 24%</td>
<td>8%</td>
</tr>
</tbody>
</table>

Fewer forest patches persisted on the windward side of the Grumeti River than on the leeward side of the river between 1972 and 2000 (p=0.001, \( \chi^2_{0.05,2}=8.25 \)), but there was no effect of forest type on the number surviving (p=0.23, \( \chi^2_{0.05,2}=2.61 \)) (Table 2-2).
Table 2-2 Number of forest patches on the leeward and windward sides of the Grumeti River in 1972 and 2000.

<table>
<thead>
<tr>
<th>Aspect</th>
<th>Forest type</th>
<th>1972</th>
<th>2000</th>
<th>% Surviving</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leeward</td>
<td>Oxbow</td>
<td>14</td>
<td>10</td>
<td>71</td>
</tr>
<tr>
<td>Leeward</td>
<td>Patch</td>
<td>38</td>
<td>28</td>
<td>74</td>
</tr>
<tr>
<td>Leeward</td>
<td>Belt</td>
<td>21</td>
<td>14</td>
<td>66</td>
</tr>
<tr>
<td>Windward</td>
<td>Oxbow</td>
<td>17</td>
<td>6</td>
<td>35</td>
</tr>
<tr>
<td>Windward</td>
<td>Patch</td>
<td>36</td>
<td>9</td>
<td>25</td>
</tr>
<tr>
<td>Windward</td>
<td>Belt</td>
<td>18</td>
<td>7</td>
<td>38</td>
</tr>
</tbody>
</table>

*Belt forests are at least 50m wide by 100m long, Patches are at least 25 X 25 m and Oxbow forests are sheltered in river oxbows where the forest edge is protected by a swamp. As Belt forests are converted to grassland, they first become Patches and are further reduced in size to an Oxbow forest or disappear entirely.

**Survival of large trees in three forest edge types**

All three forest types had similar high survival of trees in the forest core areas (p=0.26, Log-Rank, $\chi^2_{0.05,2}=10.27$) (Figure 2-4). However, riparian and hilltop forests had different patterns of survival with increasing distance from the forest core. Both riparian forest types had consistently high survival within forests (Inner edge, Central, and River transects) (Grumeti R: p=0.096, Log-Rank, $\chi^2_{0.05,2}=4.67$; Mara R: p=0.056, Log-Rank, $\chi^2_{0.05,2}=6.16$), and lower survival on the edges of forests (Outer edge transect) (Grumeti R: p=0.002, Log-Rank, $\chi^2_{0.05,1}=10.14$; Mara R: p=0.023, Log-Rank, $\chi^2_{0.05,1}=9.37$). Tree survival was similar inside riparian forest types (p=0.26, Log-Rank, $\chi^2_{0.05,1}=10.27$), but lower in the core of hilltop forests (p=0.041, Log-Rank, $\chi^2_{0.05,1}=16.29$). Hilltop forests also showed lower survival in both forest Outer and Inner edge compared to the forest interior (Central transect) (p=<0.0001, Log-Rank, $\chi^2_{0.05,1}=67.89$).

**Large tree survivorship with and without fire**

Sufficient large trees were burned for statistical analysis only in the Mara Hilltop Forests. Tree survival was lower in burned plots than unburned plots in hilltop forests, where entire forest patches were protected from fire and others burned three times in four years (Figure 2-5) (p<.001, Log-Rank, $\chi^2_{0.05,1}=21.14$). Within the burn treatment, fire reduced the survival of smaller trees more than larger trees (p=0.001, Log-Rank, $\chi^2_{0.05,1}=18.35$, size classes 2&3 compared to 4,5&6).
Figure 2-4 Canopy tree survival (%) in Grumeti riparian, Mara riparian and Mara Hilltop forests. Survival is split by transect through the forest and size class. (Error bars ± 1 SD)
Figure 2-5. Survival (%) of trees in hilltop forests exposed to fire, protected from fire, and individuals in fire plots that were observed to be scorched. (Error bars ± 1 SD)
Not all trees were burned within the Mara Hilltop Fire treatment, but the individual trees that were scorched had lower survival than the average among trees in the Fire treatments (p=0.005, Log-Rank, \( \chi^2_{0.05,1} = 12.30 \)). The largest size class was almost entirely made up of \textit{Diospyros abyssinica} emergent canopy trees. Large \textit{Diospyros} either died immediately from fire damage (21%), or were “scorched” with the outer half of their crowns dying back. Trees that were scorched two or three years in a row died in approximately 80% of cases.

\textit{Large tree survival with repeated burns}

The size distribution of trees on the outer edges of forest patches was bimodal, with peaks in the 1.5-3 m and 5-8 m size classes. I will henceforth refer to these as “bushes” and “trees” (Figure 2-6). The effects of repeated burns increased with the degree of canopy openness of forest patches. Dense Grumeti dripline edges suffered damage to trees and mortality to bushes after three consecutive years of burning compared to unburned trees (p=0.024, Log-Rank, \( \chi^2_{0.05,1} = 11.14 \)). Closed canopy Mara riparian forests with advancing edges had the same effect after only two years of burning (p=0.018, Log-Rank, \( \chi^2_{0.05,1} = 16.35 \)), while open canopy Mara hilltop forests did so after a single year of burning (p=<0.003, Log-Rank, \( \chi^2_{0.05,1} = 9.68 \)).

The pattern of increasing mortality of bushes with repeated burns was also different between forests. Mean survival in both advancing edge forests declined in a linear fashion with repeated burns (Mara R: \( r^2 = 0.942, p=0.001, \text{Survival} = -0.079 \times \text{years burned} + 1.06 \); Mara Hills: \( r^2 = 0.96, p=0.001, \text{Survival} = -0.14 \times \text{years burned} + 1.15 \)), and exponentially in dripline forests (Grumeti riparian) (\( r^2 = 0.65, p=0.002, \text{Survival} = 0.942 - 0.0146 \times \text{Years burned} \)).

\textit{Expansion of bushes at the forest periphery}

The forest edge expanded into the grassland in all forest types via the lateral expansion of bushes at an average rate of 10 cm per year when fire was removed for four years (Table 2-3). Expansion rates declined to zero when forest edges were burned both one and two years out of four (p=0.043, t-test, \( t_{0.05(2)} = 3.874 \)). Overall, expansion rates declined exponentially with increasing fire frequency (\( R^2 = 0.821, p=0.039, \text{ANOVA, } F_{0.05(2),8,60} = 52.37 \)), and there was no significant difference in the rates of forest edge expansion and contraction between forest types (p=0.49, ANOVA, \( F_{0.05(2),8,60} = 3.874 \)).
Figure 2-6 Forest edge trees and bushes of Grumeti riparian, Mara riparian, and Mara Hilltop forest (species combined) yearly survival and proportion undamaged under treatments of burning 0, 1, 2, & 3 consecutive years. (Error bars ± 1 SD)
Table 2-3 Forest edge average lateral growth rates (cm/year) across 15 sites by forest type. (± SD)

<table>
<thead>
<tr>
<th></th>
<th>Grumeti riparian</th>
<th>Mara riparian</th>
<th>Mara hilltops</th>
</tr>
</thead>
<tbody>
<tr>
<td>No fire</td>
<td>10 ± 5</td>
<td>12 ± 8</td>
<td>7 ± 11</td>
</tr>
<tr>
<td>Fire 1 of 4 years</td>
<td>5 ± 21</td>
<td>13 ± 17</td>
<td>10 ± 4</td>
</tr>
<tr>
<td>Fire 2 of 4 years</td>
<td>-2 ± 14</td>
<td>4 ± 19</td>
<td>-14 ± 27</td>
</tr>
<tr>
<td>Fire 3 of 4 years</td>
<td>-47 ± 22</td>
<td>-31 ± 65</td>
<td>-76 ± 52</td>
</tr>
<tr>
<td>Fire 4 of 4 years</td>
<td>-92 ± 38</td>
<td>-65 ± 52</td>
<td>-120 ± 75</td>
</tr>
</tbody>
</table>

*Seedling survival at the forest edge*

Seedling survival in Fire treatment areas was lower than unburned areas in all three forest types combined (p=<0.000, Log-Rank, $\chi^2_{0.05,1}=42.4$), and in each individual forest type (Figure 2-7 & 2-8) (Grumeti: p=<0.0001, Log-Rank, $\chi^2_{0.05,1}=67.1$; Mara R: p=0.0035, Log-Rank, $\chi^2_{0.05,1}=8.504$; Mara Hills: p=0.0134, Log-Rank, $\chi^2_{0.05,1}=6.11$). Not all seedlings were burned or scorched in the Fire treatment areas. Survival of individual burned seedlings in both riparian forest types was zero, and 0.09 % in hilltop forests.

Seedling survival was also lower at the forest edges than in the forest interiors, even in fire control areas p=0.02, Log-Rank, $\chi^2_{0.05,1}=5.18$. This low survival is likely due to competition with grass. Seedlings in Mara riparian forests had low survival within 20 m of the forest edge, where grass biomass was high (Figure 2-9).

*Grass fuel load across the forest-savanna boundary*

Fuel loads (grass + leaf litter) varied across the forest boundaries of the three forest types based on topography and canopy density. Hilltop areas with typically stony, dry soil, had the lowest fuel loads of the three forest types outside the forest (p=0.031, ANOVA, $F_{0.05(2),6,24}=6.07$; p=0.019, Tukey-Kramer HSD, $q_{0.05,3,24}=4.51$), while riparian areas had similar, high fuel loads (p=0.28, Tukey-Kramer HSD, $q_{0.05,3,24}=1.28$) which increased within 15 m of the forest edge (p=0.0214, t-test, $t_{0.05(26)}=4.864$). Fuel load inside forests was lower in hilltop and closed canopy riparian forests (Grumeti), and higher in open canopy riparian forests (Mara) (p=0.022, ANOVA, $F_{0.05(2),6,3}=5.01$; p=0.016, Tukey-Kramer HSD, $q_{0.05,3,27}=3.65$). Only closed canopy forests (Grumeti) showed a sharp decline in fuel load at the forest boundary (Figure 2-10).
Figure 2-7 Survival of forest seedlings in plots that have been burned and protected from fire in two consecutive years.
Figure 2-8 Mean yearly survival of seedlings in Grumeti riparian, Mara riparian, and Mara Hilltop forest patch edges that have been exposed to and protected from fire for two years. (Error bars ± 1 SD)
Figure 2-9 Survival rates of seedlings in Mara riparian forests at increasing distance from the forest-grassland boundary. Arrow (↑) indicates the edge of the forest; the maximum extent of forest tree canopy. (Error bars ± 1 SD)
Figure 2-10 Fuel loads (dry weight) outside and inside Grumeti riparian, Mara riparian, and Mara hilltop forests. Arrow (↑) indicates the edge of the forest; the maximum extent of forest tree canopy. (Error bars ± 1 SD)
Fuel combustibility and forest type

Grass inside and outside of all forests had similar, high moisture content during the wet season (Dec-April) (p=0.597, ANOVA, \(F_{0.05(2),5121}=5.43\)) and averaged 290 ± 42% moisture (calculated as wet mass/dry mass). During the dry season (July), grass moisture content was low (~ 20%) >15 m from the forest edge in all sites (Figure 2-11) (p=0.172, ANOVA, \(F_{0.05(2),236}=1.28\)), and higher (~ 60%) near the edge (<15 m) of riparian forests (p=0.001, ANOVA, \(F_{0.05(2),236}=7.721\)). Mara forests, with open canopy and clayey soils contained grass with high moisture content (p=0.041, ANOVA, \(F_{0.05(2),56}=3.26\); p=0.022, Tukey-Kramer HSD, \(q_{0.05,2,56}=1.48\)), while both Grumeti and hilltop forests on sandy/stony soils did not.

Fire frequency and extent

No fires entered the Grumeti riparian forests during the four study years despite frequent fires in the adjacent grassland. Of the 24 fires reaching the edge of the Mara riparian forests, five entered it. The maximum extent of these fires into Mara riparian forests was 3.5 m. Fires entered hilltop thickets in 11 of 17 cases, penetrated to 10 m in some cases, and burned 10-15% of the forest area.

Flammability of grass during the dry season

Grass dried and was burnable in the savanna matrix and in dry hilltop forests (two years of four) early in the dry season, but riparian areas would only burn in the late dry season. During the late dry seasons of 1999-2001, riparian grasses dried to a combustible state an average of 37 days per year on the Grumeti River, and in two out of three years for an average of 15 and 60 days in Mara riparian and hilltop forests respectively (Table 2-4).

<table>
<thead>
<tr>
<th>Year</th>
<th>Grumeti riparian</th>
<th>Mara riparian</th>
<th>Mara hilltop</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>August 6 - 22</td>
<td>Did not burn</td>
<td>August 2 - August 19</td>
</tr>
<tr>
<td>2000</td>
<td>July 9 - August 27</td>
<td>July 23 - August 15</td>
<td>July 6 - August 16</td>
</tr>
<tr>
<td>2001</td>
<td>June 28 - September 15</td>
<td>August 3 - 12</td>
<td>June 12 - August 21</td>
</tr>
</tbody>
</table>
Figure 2-11 Percent moisture during the middle of the dry season for grass outside and inside Grumeti riparian, Mara riparian, and Mara hilltop forests. Percent moisture is total weight/dry weight. Arrow (↑) indicates the edge of the forest; the maximum extent of forest tree canopy. (Error bars ± 1 SD)
Discussion

Fires are currently eroding the edges of riparian and hilltop forests, and are likely the principal cause of forest decline in Serengeti. Forests have declined more rapidly on the windward side of rivers where fires are more common. The density of the forest edge determines the forest's resistance to fire, with dense dripline edges having the lowest mortality when fires were infrequent and requiring successive burns before the mortality of bushes and trees increased. Open, advancing edges contained more dry grass which dried earlier in the dry season, and may have caused higher mortality due to fire. Erosion of the forest edges occurred through removal of canopy trees and seedlings. Fires were excluded from riparian forests during the early and mid-dry seasons due to high water content in grass, but fires could burn the forest edge during the late dry season when water content in grass was lowest. In general, dense bushy dripline forest edges were better able to exclude grass and thus fire, although the frequency and timing of burning events had the greatest control over survival of forest edge trees and ultimately the persistence of forest patches.

The mechanism by which fire erodes forest edges

Fires erode the forest edges by killing both seedlings and canopy trees, with a more pronounced effect on seedlings than adult trees. The effect of fire is limited to the outer edge of forest patches (Figure 2-4). Fire was not observed to enter into forest core areas.

Seedlings in burned areas survived less well than seedlings in unburned areas (Figures 2-7 & 2-8). Nearly all burned seedlings died. Other researchers have found positive effects of fire, including removal of forbs, increased germination, and increased seedling survival (Kellman et al. 1997). I did not find a positive effect of fire, as there was no increase in seedling density or seedling survival in previously burned areas. Many researchers report that seedling mortality due to fire is the main structuring force on woodland, savanna and riparian communities (Norton-Griffiths 1979; Unwin et al. 1985; Dublin 1986; Goldammer and Siebert 1990; Kellman et al. 1997; Higgins et al. 2000; Roques et al. 2001; Hoffmann et al. 2004). Both savanna trees and natural riparian forests have high canopy tree survival when burned (Kellman et al. 1997; Higgins et al. 2000), unlike human-produced forest patches, which are susceptible to fire (Uhl et al. 1985; Uhl et al. 1990). The high mortality of canopy trees in this study may be a product of more frequent or hotter burns than in other study sites. In general, few
researchers have reported grass biomass at the time of burns, from which fire intensity can be calculated.

The influence of forest boundary type on fire susceptibility

Forests with “advancing edges” declined more rapidly than forests with “cantilevered” edges. Grumeti riparian forests with cantilevered edges had the highest survival rate of forest patches and the highest percent cover remaining between 1972 and 2000 (Table 2-2). Mara hilltop forests with open advancing edges had the lowest survival of patches and lowest percent cover remaining during the same period.

The distance into the forest that fires could penetrate and burn seedlings differed between forest types. The cantilevered edge of Grumeti riparian forests and limited grass undergrowth effectively stopped fires from entering this forest type. Seedlings were not exposed to fire until the forest edge was removed and grass was allowed to grow in around the seedlings. Thus, the results for Grumeti riparian forests are not representative of the natural forest system, where adult tree mortality would have to occur in order for seedlings to be exposed to fire.

Seedling mortality in Mara riparian areas only occurred when the area was burned in the late dry season and fire was able to enter the forest. When fire entered, it did so patchily and for no more than 1-2 m. Mara hilltop areas with the most open canopy experienced the smallest decrease in seedling survival in burned areas (Figure 2-8). Mara hilltops also had the lowest grass fuel load (Figure 2-10), suggesting that a reduction in fuel load commonly observed on rocky hilltops may function as fire refugia allowing those forests to persist.

The survival of seedlings in the Mara riparian forest was distinctly higher in core areas of the forest than on the forest edge where grass biomass was high and fires were excluded from the forest edge (Figure 2-9). Thus suggests that seedling survival is reduced by both grass competition and fire on the forest edge.

Fires entered forests with open canopies and high grass content to a greater depth than closed canopy forests, although no fire entered any forest more than 5 m. Fire penetrated Mara riparian forests more deeply (2-3 m) than Grumeti forests which effectively excluded fires. Mara hilltop forests had the most open canopy, and fire entered these forests the most frequently and to the greatest depth (5-8 m). While fires can enter forests with open canopies, mortality rates of canopy trees inside the forests (forest inner edge transect) due to fire were low (Figure 2-4). This suggests that the
effects of fires are limited to the outer forest edge and fires are not important forces for structuring forest interiors.

**Successive burns and tree mortality rates**

Curvilinear models of years burned vs. survival fit the survival data of both Grumeti and Mara riparian forests better than linear models, indicating an increasing rate of mortality with each successive burn, while a linear model best fit the survival of Mara hilltop trees. This result suggests that fire resistance of trees in these forests types is not dependant on thick, insulating bark as in the *Acacia* species (Uhl *et al.* 1990), but instead on a layer of bush branches creating a microclimate that protects each tree and the forest edge. These bush branches are removed or reduced when grassland fires burn the forest edge, increasing the likelihood of fire reaching the tree trunk, at which point the tree dies. This explains why the greater lag time before damage and mortality effects were observed on the Grumeti river. This interpretation of a dense bushy forest edge calls into question previous views of forest “hard” boundaries indicating a fire-intolerant forest type (Herlocker 1975). Results for *Croton* hilltop forests indicated that there is a linear increase in mortality with successive burns. *Croton* bushes are fastigiate (narrow and tall) and have a sparse canopy and do not overhang the area around them (G. Sharam *pers obs.*). Thus, there is no shading and reduction in grass fuel load below *Croton* edge trees, providing fuel and direct access to the stem of the plant, resulting in damage and mortality after the first fire episode.

**The lateral spread of forests in the absence of fire**

The rate of lateral bush growth at the forest edge was slow, averaging 10 cm per year when the forest was protected from fire (Table 2-3). Growth and loss rates were similar between forest types. Lateral growth rates were zero in all forest types after only one year of burning. At three and four years of burning out of four, forests shrank at 0.70 m and 1 m per year. All forest types showed an exponentially increasing loss rate with increasing burn frequency. Thus, fire damage is not spatially additive. This effect may be caused by the slow removal of insulating branches around forest edge trees and bushes, followed by the death of the bush, ultimately leading to an increase in the rate of forest edge contraction.

Forest edges did not advance rapidly into the grassland with removal of fire. It is likely that fires may naturally occur in subsequent years, as a result of grouping of dry
years due to climatic events such as El Nino. If a forest is burned for three consecutive years, it would take 3-10 years to recover the ground lost to these fires. The forest edge in some areas has retreated by 100 m in the last 30 years, a distance requiring 1000 years to recover. This slow rate of forest edge growth suggests that lateral growth of the forest is too slow to allow the forest to recover from large disturbances and underlines the need to understand the processes of forest establishment into the grassland. It also supports the idea that forest decline and expansion are likely separate processes (Chapman and Chapman 1999; Chapman et al. 1999).

The mechanisms by which forests exclude grassland fires

Forests are not consistently protected from fire in a single manner. Dense forest edges have lower levels of grass within the edge bushy layer. Riparian forests are protected from fire by moist conditions. Despite this, late season fires can erode forest edge trees and bushes. The most consistent defense that forests have is low burnable biomass within the forest, which limits entry by grassland fires.

Fuel load declined at the forest boundary on the Grumeti river, but not in Mara riparian forests, where grass levels were high at and inside the forest boundary (Figure 2-10). Grass biomass was much higher outside riparian forests than hilltop forests (Figure 2-10), likely due to increased soil moisture in riparian areas (Medley et al. 1996). The closed canopy and dense bush layer of the Grumeti river limited grass growth at the forest edge so effectively that no grass understory existed at the forest boundary. This effect was a consequence of competition with canopy trees and bushes. When canopy trees and bushes on the forest edge were removed, grass rapidly invaded these areas. This result contrasts with studies in Venezuela (Biddulph et al. 1998), where there was no reduction in grass at the forest boundary, and in many cases an increase in fuel load. The open canopy of the Mara riparian areas in contrast, allows grass to grow as an understory. Despite this fact, the high grass moisture content inside Mara riparian forests prevented these grasses from burning until late in the dry season.

Management implications

Riparian areas are targeted by poachers during the late dry season when the greatest “green flush” occurs after burning. The green flush attracts herbivores that can be caught by snaring. Large-scale fires lit by cattle thieves and pastoralists outside the park are also most common in the late dry season. While the frequency of these fires
may not change over the dry season, the area burned increases as the dry season proceeds (G. Sharam pers obs.), exposing more riparian and hilltop areas to fire in the late dry season. Thus, the most common types of grassland fires strike forest patches in the late dry season when they are most vulnerable.

Conclusion

The three types of forest in Serengeti National Park, Tanzania, respond differently to fire. Closed-canopy, dripline edges (Grumeti riparian forests) do not allow fires to enter forested areas and must be burned more frequently before there is severe mortality. Forests with open-canopy and advancing edges (Mara riparian and hilltop forests) are less tolerant of burning. One mechanism here is that closed edges and canopies reduce the amount of grass present in the understory, limiting fire entry. From '98-01, fire returned more frequently than the forest could resist. Its ability to remove adult canopy trees at the forest edge suggests that it may be the main cause of riparian and hilltop forest decline in Serengeti.
References


Chapter 3 The effects of antelopes, elephants, and fire on riparian and hilltop forests of the Serengeti ecosystem, Tanzania.

Introduction

Riparian and hilltop forests in East Africa are naturally fragmented islands of closed-canopy Central African forest and montane forest species. In the last 30 years, the decline of the riparian and hilltop forests in Serengeti National Park, Tanzania, and Masai Mara Reserve, Kenya, has approached 80% in some areas (Chapter 2).

Central African forests extended from Central Africa to the Indian Ocean during a warm wet period ca 14 000 BP, and then retreated as the climate cooled ca 6 000 BP (DeBrusk 1998). Montane forest species expanded from the mountainous areas surrounding Lake Victoria to lower altitudes during this cooler period 6 000 BP (Jolly et al. 1997). Both forest types retreated during the last 3 000 years as drier conditions prevailed and the frequency of human-set fires increased (Livingstone 1982). Riparian and hilltop forests are assumed to have persisted as remnants of the Central African and montane forest expansions, and they now function as refugia for species that could not otherwise exist in the savanna ecosystem (Livingstone 1982; Medley and Hughes 1996).

Riparian and hilltop forests throughout the dry tropics are generally composed of continuous forest canopy species. They exist within a grassland matrix often with abundant herbivores and frequent fires. Herbivores may limit regeneration in a variety of forest types and plant communities, including rodents in montane Africa (Chapman et al. 1999b) and Central America (Holl et al. 2000), goats in Hawaii (Cabin et al. 2000), and deer in N. America (Potvin et al. 2003), Japan (Tsujino and Yumoto 2004), and New Zealand (Husheer et al. 2003). In African savanna, both elephants (Loxodonta africana) and antelopes, principally impala (Aepyceros melampus), reduce regeneration of Acacia trees, the most frequent canopy trees in the savanna biome (Dublin 1986; Roques et al. 2001). Elephants in Zambia cause savanna woodland decline by removing large trees (Caughley 1976). Both impala and elephants are common in the riparian and hilltop forests of Serengeti (G. Sharam pers obs., 1998-2001). In addition, circumstantial and experimental evidence suggested that grassland fires on forest edges reduced survival of both seedlings and adults of canopy trees (Chapter 2; Kellman and Meave 1997; Biddulph and Kellman 1998; Chapman and Chapman 1999a). Forests elsewhere decline during periods of frequent fires (Bassini and Becker 1990; Hopkins et al. 1993), and some forest types expand when fires are removed (Kellman et al. 1997).
Elephants

In East Africa, research on the influence of elephants on tree populations has largely focused on reduced Acacia recruitment in woodlands. Elephants affect Acacia populations variably at different rainfall levels (Laws 1970; Corfield 1973; Dublin 1986; Dublin et al. 1990; Dublin 1995). In very dry areas such as Tsavo National Park (NP), Kenya, elephants are primarily browsers on savanna trees because the herb layer is sparse. Elephants consume trees and reduce tree numbers but are then limited by their food. This reciprocal limitation was seen in the 1970's when Acacia tree numbers reached low levels, elephant numbers subsequently declined, and new Acacia seedlings began to recruit (Corfield 1973).

In wet areas, such as Queen Elizabeth NP, Uganda, elephants are primarily grazers on abundant grasses and only browse on trees during the driest parts of the dry season. Elephant numbers remain high with this abundant primary food source, despite declining tree numbers which can be entirely removed from the system by elephants. Thus, at high rainfall levels, elephants do not live in equilibrium with trees (Laws 1970).

At intermediate rainfall levels, such as in Serengeti, both elephant browsing and dry season fires control Acacia seedling recruitment. Without abundant dry season herbaceous forage, elephants cannot reach population levels high enough to remove all of the adult trees. At high frequency, fires can remove large Acacia trees and sufficient seedlings that tree populations decline and a grassland state is reached (Dublin 1986; Dublin et al. 1990). Thus, Acacia trees exist with elephants in two states, one at high tree density not limited by elephants and another at low tree density limited by elephants (Dublin et al. 1990; Sinclair 1995). According to this "savanna multiple states hypothesis", elephants cannot reduce the population of Acacia trees to low numbers, nor can they control recruitment at high tree numbers. Only fire can convert an Acacia woodland state to grassland. Once trees drop to low densities, however, both elephants and fire can limit tree recruitment (Dublin et al. 1990).

There have been two large scale pulsed recruitments of Acacia trees in Serengeti, both connected with changes in elephant populations and fire frequency. The first began in 1889 with the introduction of rinderpest, a cattle disease from Asia. Cattle, buffalo, wildebeest, impala, and other ungulates were severely reduced, as were the human pastoralists. Dublin (1986) proposed that, with a reduction in livestock and thus people, fire frequency fell. At the same time, elephants numbers had been greatly
reduced in large areas of East and Southern Africa by the ivory trade (Spinage 1973; Sinclair 1979). This combination of reduced fire frequency and elephant numbers allowed Acacia trees to establish in the grassland.

A second pulse of recruitment occurred during the late 1970's when fires and elephants were again reduced in Serengeti. Grass fuel load declined at this time due to an increase in the wildebeest population to 1.4 million following elimination of the disease rinderpest in the surrounding villages (Mduma et al. 1999). Seasonal rains also changed (due to El Nino) so that grass was not dry enough to burn in the dry season (Sinclair 1995). At the same time, poaching reduced elephants by 83% in Serengeti from 2400 to 400 (Dublin 1986; Dublin et al. 1990).

Antelopes

While reduction of fire and elephants may allow Acacia seedlings to establish, disease can also play a role. Prins and van der Jeugd (1993) showed that the exact timing of a pulse of Acacia recruitment in Lake Manyara NP, Tanzania, coincided with a local reduction in impala numbers from an anthrax outbreak. They also found that woodland encroachment in Manyara NP preceded the removal of elephants by poachers in 1987. Moreover, two other Acacia pulsed recruitments in Manyara and surrounding region coincided with large epidemics in the impala population (Prins and van der Jeugd 1993). Browsers also reduced survival and growth rate of Acacia species in Serengeti (Belsky 1984), Masai Mara Game Reserve, Kenya (Dublin 1986), and Chobe NP, Botswana (Barnes 2001).

Broad-leaved tree species can constitute 30-50% of impala diet, particularly in the dry season (Rodgers 1976; Cerling et al. 2003). Impala are often found in riparian and hilltop forests of Serengeti where they are the most abundant browser. Groups exceed 50 animals, and signs of browsing and clipping are common on seedlings and small trees.

Fire

Grassland fires can prevent recruitment of Acacia seedlings (Norton-Griffiths 1979), and so transform a woodland to a grassland-dominated system (Dublin 1986; Dublin et al. 1990). Fires can kill adult trees although they rarely do in Serengeti. Seedlings are vulnerable even to “cool” fires (Uhl and Kauffman 1990). Closed riparian
and hilltop forests of broad-leaved species are likely to be more susceptible to fire than Acacia species due to their thin bark (Uhl et al. 1990).

The most common types of fires in riparian and hilltop forests are “edge fires”, where a grassland fire burns up to the edge of the forest. Fires can enter open canopy hilltop forests to a small degree when the grass inside the forest is dry (Chapter 2). Tree mortality along the forest edge increases and forest patches are eroded if fire recurs more often than two out of four years (Chapter 2). Thus, at high fire frequencies, fire can account for the decline of riparian forests. Fire damage may also interact with herbivory or elephant damage to increase the decline rate of forests (Norton-Griffiths 1979; Dublin 1986).

As in the Acacia savanna system, recruitment and survival of riparian and hilltop forests may be limited by a single factor such as fire, elephants or browsing alone. Alternatively, as in the savanna multiple state hypothesis, two or more factors may have to change for regeneration to occur; such as both fire and elephants, (Dublin et al. 1990), or both fire and impala browsing (Prins et al. 1993).

In this chapter I examined the demography of riparian and hilltop forests in Serengeti NP and compared it with the demography of a stable forest on Rubondo Island NP, Tanzania. I treated Rubondo Island as a control because fire, elephant damage and impala were low or absent. I made the following predictions concerning the impacts of ungulate herbivory:
1) Seedling mortality due to elephants is high;
2) Canopy tree mortality due to elephants is high;
3) Seedling mortality due to impala will is high; and
4) There are interactions between damage to seedlings by impala, elephants and fire.
Methods

Study Site

Serengeti

The Serengeti ecosystem is a mosaic of open grassland and woodland types covering 25,000 km² of northwestern Tanzania and southwestern Kenya (Figure 3-1). Riparian forests are found within the Serengeti National Park (NP) on the floodplain created by the Grumeti river in the west of the park, and in the steeper valleys of the Mara River tributaries on the south side of the Mara River. Dense hilltop thickets are found mainly on the hills to the south of the Mara River with a few on the north side.

The Grumeti forests are distinct in species composition from the other sites. However, the Mara hilltop thicket appears to be a sub-community related to components of the Mara riparian community. Forests on Rubondo Island closely resembles Grumeti forest in species composition and structure.

Grumeti riparian forests

The Grumeti riparian forests grow as patches and strips along the Grumeti River in the western corridor of Serengeti NP. Forests typically extend 100-150m from the river into the grassland, and 200-400m along the river. The canopy of the forest is made up largely of *Lecaniodiscus fraxinifolius* (Baker), *Elaeodendron buchananii* (Loes), and *Ziziphus pubescens* (Oliv.). This dense canopy results in low under canopy light levels.

Mara riparian forests

The Mara riparian forests grow as patches in the confluences of streams and along the southern tributaries of the Mara River, and vary from 50 X 50 m to 200 X 600 m in area. Unlike the Grumeti forests, the Mara riparian forests are composed of two distinct bands of vegetation. The band adjacent to the river is similar to the Grumeti riparian forests in stand density and low light levels. It is composed chiefly of *Diospyros abyssinica* (Hiern) F. White, *Drypetes garrardii* Hutch., *Ekebergia capensis* Sparrm., *Olea africana* Mill., and *Ficus* trees.

The second band is 20-40m wide and has an open canopy structure of *Euclea divinorum* (Hiern) subsp. *keniensis* (R.E. Fries) de Wit and *Olea africana*, higher grass content and higher proportion of bushes such as *Croton dichogamus* Pax., *Teclea trichocarpa* (Engl.) Engl., and *Strychnos* spp. The dominant trees have an open crown,
small leaves, and little ability to block sunlight from reaching the ground. Soils are deep (>0.25 m) and less sandy than the Grumeti riparian forests

**Mara Hilltop Forests**

Hilltops and ridges south of the Mara River have thickets like the outer band of Mara riparian forests, but with fewer canopy trees. They are composed of *Croton dichogamus* and *Teclea trichocarpa* with emergent canopy trees of *Diospyros abyssinica*, *Euclea divinorum*, and *Drypetes abyssinica*. Soils are thin (<0.05 m) and rocky/gravelly.

Dublin (1986) showed that Mara hilltop thickets declined 1950 - 1982 from a total area in the Mara Reserve of 4.2% to 2.8% over the 32 years, which resulted in loss rates of 0.5% to 3.2% per year. Percent cover of individual forests declined from 80% to 40% in this same period, a process which has continued since 1982.

**Rubondo Island**

Rubondo Island National Park is a 240 km$^2$ island located in the south west of Lake Victoria, Tanzania (Figure 3-1). The topology is composed of alternating bands of sandy low-lying areas and low hills (60-80 m), with four larger hills rising 300 m. The annual temperature is 19-26 °C, and the rainfall 1200 mm which occurs bi-modally, as in the north of Serengeti. The forest on Rubondo Island NP covers 80% of the island, and is composed of diverse, largely Central African species (Beentje 1994). The herbivore population is composed of 20-30 elephants, and larger numbers of bushbuck (*Tragelaphus scriptus*) which are browsers, and sitatunga (*Tragelaphus spekii*) which browse on swamp vegetation. Seedlings of canopy trees are abundant and do not show evidence of browsing on the apical meristem (G. Sharam *pers obs.* 2001).

I sampled forest areas in the north of the park and in the semi-deciduous forest on the east side of the park which are similar in density and species composition to Grumeti riparian forests. This area is composed largely of *Diospyros abyssinica*, *Lecaniodiscus fraxinifolius*, *Celtis africana* Burm. f. [*Celtis kraussiana* Bernh.], and *Elaeodendron buchananii*. 
Figure 3-1. Location of riparian and hilltop forests within the Serengeti ecosystem, and location of Serengeti and Rubondo National Parks in East Africa.
**Tree density by size class**

Tree density was measured in three focal forests chosen in each forest type using belt transects through forest patches from grassland to river. Trees were divided into six classes based on height: 1) 0-0.75 m (seedlings), 2) 0.75-1.5 m, 3) 1.5-3 m, 4) 3-5 m, 5) 5-8 m, and 6) >8 m. Transects were 1m wide for the seedling size class, 2m wide for all larger size classes, and 80-140m long. Measurements in the four forest types were made in November 1998 (Mara riparian), July 1999 (Grumeti riparian), June 2000 (Mara hilltops) and September 2001 (Rubondo Island) (Figure 3-2). Additional transects were measured until the variation (S.D.) in density per tree size class was less than 20%, generally with 9-13 transects per patch.

**Seedlings**

The impact of antelope herbivory on seedlings (trees under 0.75 m tall) was measured by comparing seedlings in sites with and without antelopes. Antelope were excluded by thorn fencing around individual tagged seedlings or groups of tagged seedlings, depending on the forest type. In Grumeti forests, where seedling density was high, thorn fences 1.6 m tall were built around groups of seedlings. Three thorn fences 4 X 4 m were built around 50-75 seedlings each in the three Grumeti experimental forest patches, for a total of nine replicates. In both the Mara River and Mara hilltop forests, where seedlings are less dense, individual thorn fences were built around each of 35 seedlings per forest patch, in three forest patches in the Mara riparian, and six patches in the Mara hilltops. In sites with antelopes, seedlings were tagged (250 per forest patch) and left exposed to antelope attack. Seedling height was measured every two months for three years, and observations were made on the health. Since elephants did not eat the 10 X 12 cm metal tags yearly surveys searched the study plots and surrounding area extensively for discarded metal tags.

Data were censored if elephants, antelopes, or fire damaged the thorn fences. Approximately 80% of fences remained intact after three years.
Figure 3-2 Experimental setup of permanent transects for canopy tree survival and density estimates in riparian and hilltop forests.
Large Trees

Trees larger than seedlings (size classes 2-6) were tagged in three transects of 1000 trees each in each of three study forests on the Grumeti and Mara Rivers in June 1999 and October 1998 respectively (Figure 3-2). Size classes were the same as those used for density estimates. Large trees were tagged in two transects of 250 trees each in the six Mara hilltop study forests in March 2000 (Figure 3-3). The health of the trees and damage by antelopes and elephants were recorded every two months for three years on the Grumeti and Mara Rivers and for two years in the Mara hilltops. Types of damage recorded were:

1) Antelope herbivory: any herbivore damage that removed leaves or browsed branches or twigs. I recorded the height of all apical shoots that had been browsed.
2) Elephant damage: the removal of branches, removal of leaves by stripping branches, and gouging of the bark and trunk of trees.
3) Elephant “pushed-down”: damage caused by an elephant pushing a tree until the trunk cracked or broke, or the root stock was torn on one side. Pushed-down trees were bent to >45° angle (usually 90°).

Interactions with fire

Mara hilltop forest patches were divided into two either burned or unburned treatment groups of three forests each. Fire breaks were burned around all of the forests at the beginning of the dry season (May), and one group of forests was burned inside the firebreak in the late dry seasons of 2000 and 2001. Seedlings with herbivore exclusion fences were revisited immediately after the fire and fences were repaired if damaged by fire.

Statistical analyses

The variation between density classes within a patch was determined by single factor analysis of variance (ANOVA) with species as the factor. Density estimates of the three Serengeti forests and Rubondo forests were compared using ANOVA and Tukey-Kramer Honestly Significant Different (HSD) test. Samples were first confirmed to have equal variances and transformations were conducted as required to ensure normality.

Seedling growth was compared between treatment groups for each size class using Kaplan-Meier growth curves, and the Log-Rank test result was reported. Growth rates of seedlings were compared between forest type and herbivore treatments using t-
tests and ANOVA. The contributions of fire and herbivore damage to tree survival were assessed using parametric regression on Cox's proportional hazards of survival times.

Results

*Forest density by size class*

The densities of all size classes larger than seedlings was similar between the three forest types of Serengeti NP and the forests on Rubondo Island. Densities between forest types ranged from 85-420 stems/ha (p=0.193, ANOVA, F_{0.05,12,160}=11.69, using transects within forests as replicates) (Figure 3-3). Seedling densities, however, were much higher on Rubondo Island than the three Serengeti NP forest types (p<0.001, ANOVA, F_{0.05,3,170}=5.004; p=0.011, Tukey-Kramer HSD, q_{0.05,3,170}=2.46). The average seedling density on Rubondo Island was 8-14 times higher than the next larger size class (0.75-1.5 m) ranging in density from 1022-8600/ha (p<0.001, t_{0.05(2)12}=6.052). Seedling densities in Serengeti NP, however, were similar to the density of the next larger size class, ranging from 12-216/ha (p=.442, t_{0.05(2)46}=0.77) (Figure 3-3).

*Seedling response to impala, elephants and fire*

Seedlings of canopy trees in Serengeti survived less well than all other size classes in all forest types combined (p<0.001, Log-Rank, \chi^2_{0.05,1}=288.85, using average survival within focal forests as replicates, n=9 forests). Seedlings in antelope exclusion plots survived better than seedlings exposed to herbivory in all three forest types combined (p<0.001, Log-Rank, \chi^2_{0.05,1}=414.91), and in each individual forest (Grumeti R: p<0.001, Log-Rank, \chi^2_{0.05,1}=240.18; Mara R: p<0.001, Log-Rank, \chi^2_{0.05,1}=33.65; Mara hilltops: p<0.001, Log-Rank, \chi^2_{0.05,1}=40.52) (Figure 3-4). Seedlings exposed to herbivory had survival rates 40-60% of protected seedlings (0.46 - 0.57 % per year, and 0.77 - 0.93 % per year respectively). Where antelopes were excluded, seedling survival was similar in Grumeti and Mara riparian forests (p=0.21, Log-Rank, \chi^2_{0.05,1}=3.15, n=6 forests), and survival in both was higher than in the Mara hilltop forests (p=0.0002, Log-Rank, \chi^2_{0.05,1}=13.79, n=9 forests) (Figure 3-4).
Figure 3-3  Densities of principal Serengeti riparian and hilltop thicket species, and of canopy species of Rubondo Island forests. (Error bars ± SD)
Figure 3-4 Yearly survival rates (%) of seedlings with herbivores (H) and inside herbivore exclosures (Ex) in three different types of broad-leaved forest, Serengeti National Park, Tanzania. (Error bars ± SD)
In Mara hilltop forests where seedlings were exposed to ± herbivory and ± fire, fire also reduced seedling survival (p=0.0046, Log-Rank, $\chi^2_{0.05,1}=8.25$). However, there was no interaction between fire and herbivory (p=.546, Likelihood-ratio test, $\chi^2_{0.05,1}=0.365$) (Figure 3-4).

Seedlings protected from antelope grew (vertically) faster than those exposed to browsing in all forest types (p=0.001, t-test, $t_{0.05(2),7}=11.28$, using focal forests as replicates) (Figure 3-5), which were not different from zero (p=0.723, t-test, $t_{0.05(2),7}=6.39$). Average growth rates of protected seedlings ranged from 4.9 - 21.2 cm/yr. In Mara hilltop forests, where fire was an additional variable, seedlings that survived in burned plots grew as well as unburned seedlings (p=0.379, ANOVA, $F_{0.05,3,6}=0.971$). There was no interaction between fire and herbivory (p=0.689, ANOVA, $F_{0.05,3,6}=0.373$) (Figure 3-5). Variability in growth rate was higher in browsed plots (SD = 10.7 cm) than protected plots (SD = 4.7 cm) (p<0.001, Bartlett test, $F_{0.05,1,1731}=131.74$, n=1733 plants) (Figure 3-5).

In all three forest types, the number of seedling deaths attributable to elephant damage was too small to calculate survival probabilities for attacked plants (Grumeti R. n=2, Mara R. n=3, Mara Hills n=9). Seedling damage attributed to elephant feeding consisted of plants broken off at the base or missing entirely. Elephant herbivory of seedlings did occur, as aluminum seedling tags were found deformed because of chewing by elephants, but elephants caused a low proportion of total mortality (0.01 - 0.6%).

Where a seedling was removed, and the tag was not found, the seedling’s fate was recorded as “unknown”. An average of 6 ± 5%/year of all seedlings were listed as “unknown”. Ten % of unknown tags were trampled into the ground, removed by mongoose spp. (identified by the teeth marks), or found in poachers’ camps. These deaths/losses were unrelated to seedling survival, and were censored from analysis.

If I assume that all remaining missing seedlings listed as “unknown” were due to elephant feeding, then elephants may have played a role in reducing seedling survival. The “unknown” loss rates of tags were not consistently different between forest types, nor between species. In comparison, if all unknown seedlings were removed by elephants, the resulting mortality estimate of 6 ± 5%/year was much lower than that of antelope browsing (31-36%), and equivalent to that of fire.
Figure 3-5 Growth rates (height) of seedlings with herbivores (H) and inside herbivore exclosures (EX) in three types of broad-leaved forest in Serengeti National Park, Tanzania. Growth rate was reduced or made negative by antelope browsing on the apical meristem. (Error bars ±SE)
Survival of large trees

Trees larger than seedlings were grouped into five size classes. Damage rates by elephants, antelopes, and fire, survival after damage and survival of undamaged trees were calculated separately for each size class.

Rates of elephant attack on Grumeti and Mara riparian trees were similar in all size classes at approximately 10% of trees per year, except the largest size class which experienced less damage at 5% per year (Table 3-1). Mara Hilltop damage rates were three times those in the riparian forests at approximately 30% of trees per year, again with a reduction in the largest size class. There was no difference in elephant attack rate between different transects within forests (p=0.42, Log-Rank, $\chi^2_{0.05,1}=1.72$, n=9 focal forest patches).

Trees damaged by elephants had lower survival rates than undamaged trees in Grumeti riparian forests (p=0.007, Log-Rank, $\chi^2_{0.05,1}=11.61$, n=1001 trees), and Mara hilltop forests (p<0.001, Log-Rank, $\chi^2_{0.05,1}=29.49$, n=1391 trees), but not in Mara riparian forests (p=0.892, Log-Rank, $\chi^2_{0.05,1}=0.0186$, n=978 trees) (Figure 3-6, Table 3-1).

Table 3-1 Proportions of (A) trees attacked by elephants, (B) that survive afterwards, and (C) survival of un-attacked trees in each size class larger than seedlings (0-0.75 m) in the Grumeti River, Mara River, and Mara Hilltop forests.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Grumeti River</th>
<th>Mara River</th>
<th>Mara Hilltops</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>2 (0.75-1.5 m)</td>
<td>0.10</td>
<td>.86</td>
<td>0.87</td>
</tr>
<tr>
<td>3 (1.5-3 m)</td>
<td>0.14</td>
<td>.92</td>
<td>0.93</td>
</tr>
<tr>
<td>4 (3-5 m)</td>
<td>0.08</td>
<td>.98</td>
<td>0.94</td>
</tr>
<tr>
<td>5 (5-8 m)</td>
<td>0.08</td>
<td>.85</td>
<td>0.97 **</td>
</tr>
<tr>
<td>6 (&gt;8 m)</td>
<td>0.05</td>
<td>.80</td>
<td>0.97 **</td>
</tr>
</tbody>
</table>

(* indicates difference in survival between attacked and not attacked groups at $\alpha<0.05$ level, ** at $\alpha<0.001$)
Figure 3-6 Yearly survival rates (%) of large trees (>0.75m) with (■) fire and (□) without fire, and elephant damage (■). Elephant damage was characterized by removing branches and stripping leaves from branches. (Error Bars ±SD)
Proportions of trees “pushed-down" by elephants were similar in all size classes and in all forest types at approximately 4-5%, except the Mara hilltop forests, which had higher damage rates in the 4-6 m and 6-10 m size classes of approximately 8.5% (Table 3-2). Trees pushed down by elephants had much lower survival than trees that were not pushed-down in all forest types (Grumeti R. p<0.001, Log-Rank, $\chi^2_{0.05,1}=42.46$, n=1001 trees; Mara R: p=0.0112, Log-Rank, $\chi^2_{0.05,1}=6.439$, n=978 trees; Mara Hilltops: p<0.001, Log-Rank, $\chi^2_{0.05,1}=124.24$, n=1393 trees) (Figure 3-7, Table 3-2).

Table 3-2 The proportions of (A) trees pushed down by elephants, (B) that survive afterwards, and (C) survival of un-attacked trees in each size class larger than seedlings (0-0.75 m) in the Grumeti River, Mara River, and Mara Hilltop forests.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Grumeti River</th>
<th>Mara River</th>
<th>Mara Hilltops</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>2 (0.75-1.5 m)</td>
<td>0.02</td>
<td>.78</td>
<td>0.87</td>
</tr>
<tr>
<td>3 (1.5-3 m)</td>
<td>0.04</td>
<td>.82</td>
<td>0.94</td>
</tr>
<tr>
<td>4 (3-5m)</td>
<td>0.03</td>
<td>.85</td>
<td>0.96 **</td>
</tr>
<tr>
<td>5 (5-8m)</td>
<td>0.05</td>
<td>.69</td>
<td>0.98 **</td>
</tr>
<tr>
<td>6 (&gt;8m)</td>
<td>0.03</td>
<td>.67</td>
<td>0.97 $\phi$</td>
</tr>
</tbody>
</table>

(* indicates difference in survival between attacked and not attacked groups at $\alpha\leq0.05$ level, ** at $\alpha\leq0.001$. $\phi$ indicates insufficient data for a comparison.)

Trees damaged by antelopes had the widest range of damage rates, from 10% on the Grumeti R. to 50% in the Mara Hilltops (Table 3-3). Antelope damage was limited to the 0.75-1.5 m and 1.5-3 m size classes. The tallest trees with antelope-clipped apical meristems were 1.4 m tall, while lower branch damage was observed on trees up to 3.0 m tall.

Table 3-3 The proportions of (A) trees attacked by antelope, (B) that survive afterwards, and (C) survival of un-attacked trees in each size class larger than seedlings (0-0.75 m) in the Grumeti River, Mara River, and Mara Hilltop forests.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Grumeti River</th>
<th>Mara River</th>
<th>Mara Hilltops</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>2 (0.75-1.5 m)</td>
<td>0.11</td>
<td>.89</td>
<td>0.86</td>
</tr>
<tr>
<td>3 (1.5-3 m)</td>
<td>0.11</td>
<td>.94</td>
<td>0.93</td>
</tr>
</tbody>
</table>

(* indicates difference in survival between attacked and not attacked groups at $\alpha\leq0.05$ level, ** at $\alpha\leq0.001$)
Figure 3-7 Yearly survival rates of large trees (>0.75m) with (■) and without fire (□) and elephant “pushed over” damage (■). “Pushed over” damage occurs when elephants damage the main trunk of the tree, resulting in some but not all broken wood, thus the tree could, potentially survive. (Error bars ±SD)
While browsing by antelopes reduced the growth and survival of seedlings, browsing had little effect on survival of larger trees ($p=0.229$, Log-Rank, $\chi^2_{0.05,1}=1.44$, $n=9$ forests) (Figure 3-8, Table 3-3). However, in some cases browsed trees had higher growth rates than unbrowsed trees ($p<0.001$, Log-Rank, $\chi^2_{0.05,1}=40.24$, $n=677$ trees) (Mara riparian 0.75-1.5 m and 1.5-3 m classes, and Mara hilltop 0.75-1.5 m class).

*Interactions between elephants, antelopes and fire*

Only the Mara hilltop thickets had sufficient numbers of trees with a combination of fire, elephant damage, and antelope herbivory for statistical analysis. Fire and elephant damage (branch breaking) each reduced survival (Fire: $p=0.011$, Likelihood-ratio test, $\chi^2_{0.05,1}=6.46$; Elephant damage: $p<0.001$, Likelihood-ratio test, $\chi^2_{0.05,1}=25.49$, $n=1391$ trees in each test), but there was no interaction between these effects ($p=0.695$, Likelihood-ratio test, $\chi^2_{0.05,1}=0.153$) (Figure 3-6). Fire and elephant "pushed-down" damage each reduced tree survival (fire: $p<0.001$, Likelihood-ratio test, $\chi^2_{0.05,1}=17.04$; elephant: $p<0.001$, Likelihood-ratio test, $\chi^2_{0.05,1}=67.36$), but again with no interaction effect ($p=0.134$, Likelihood-ratio test, $\chi^2_{0.05,1}=2.25$) (Figure 3-7). When fire and antelope herbivory on 0.75-1.5 m and 1.5-3 m trees were examined, only fire reduced survival, herbivory did not and again there was no interaction effect between the two (fire: $p=0.001$, Likelihood-ratio test, $\chi^2_{0.05,1}=15.82$; antelopes: $p=0.329$, Likelihood-ratio test, $\chi^2_{0.05,1}=0.951$; fire X antelopes: $p=0.559$, Likelihood-ratio test, $\chi^2_{0.05,1}=0.341$) (Figure 3-8).

*Total tree mortality*

Total mortality rates (the yearly attack rate X the yearly mortality of attacked trees) were calculated for each size class. Mortality rates due to antelope herbivory were much higher on seedlings (averaging 30%) than larger trees (3.7% per year) ($p=0.0217$, t-test, $t_{0.05(1),22}=3.37$, using average mortality per forest replicate) (Figure 3-4, Table 3-4). Comparisons between seedlings and large trees could not be performed for elephant damage due to low sample size of elephant-attacked seedlings. Mortality rates due to fire were higher for seedlings (15%) than for larger trees (6%). Mortality due to fire is discussed in chapter 2.
Figure 3-8 Yearly survival rates of large trees (>0.75m) with (■) and without fire (□) and herbivory damage by impala (▲). Impala herbivory was limited to browsing of forest trees below 1.6 m. (Error bars ±SD)
Large tree (>0.75 m) mortality rates due to antelopes and elephants varied between 1% and 9%, and were low in both the Grumeti and Mara riparian forests (Table 3-4). Hilltop forests had higher elephant and antelope-induced mortality rates than riparian areas (elephant: \( p=0.042, t\text{-test}, t_{0.05(27)}=2.182 \); antelope: \( p=0.038, t\text{-test}, t_{0.05(27)}=1.891 \); using focal forest patches as replicates), but total mortality rates of large trees were generally low (averaging 3.5% per year).

The mortality rate differed between forest types (\( p=0.021, \) ANOVA, \( F_{0.05,3,24}=1.28 \); using transects within focal forest patches as replicates). Rates were similar between riparian forests (\( p=0.56, \) Tukey-Kramer HSD, \( q_{0.05,3,24}=2.46 \)) and higher in hilltop forests (\( p=0.033, \) Tukey-Kramer HSD, \( q_{0.05,3,24}=6.28 \)), largely due to an increase in elephant feeding damage in the 2nd and 3rd size classes.

Table 3-4 Total mortality rates per year (probability of attack X survival probability) for elephant attacked trees (Ele), elephant "pushed over" trees (PO), and antelope attacked trees (A) in Grumeti River, Mara River, and Mara hilltop forests.

| Size Class | Grumeti River | | | | | | | | Mara River | | | | | | Mara Hilltop | | | |
|-----------|--------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|           | Ele | PO | A | Total | Ele | PO | A | Total | Ele | PO | A | Total | Ele | PO | A | Total |
| 2 (0.75-1.5 m) | 0.014 | .005 | .012 | .032 | 0.021 | .017 | .063 | .101 | 0.103 | .017 | .092 | .212 |
| 3 (1.5-3 m) | 0.011 | .008 | .007 | .026 | 0.026 | .029 | .030 | .085 | 0.078 | .021 | .021 | .120 |
| 4 (3-5m) | .002 | .005 | N/a | .007 | 0.012 | .009 | N/a | .021 | 0.051 | .051 | N/a | .102 |
| 5 (5-8m) | .012 | .014 | N/a | .026 | 0.004 | .014 | N/a | .018 | 0.056 | .043 | N/a | .099 |
| 6 (>8m) | .010 | .011 | N/a | .021 | 0.005 | .002 | N/a | .007 | 0.005 | .025 | N/a | .030 |

Discussion

The low abundance of tree seedlings in Serengeti NP forests suggests that seedling establishment and survival is lower there than in the healthy Rubondo Island forest (Figure 3-3). Seedlings had the lowest survival rate of all size classes in Serengeti. The large numbers of seedlings with apical meristems removed by browsing, and low survival rates and growth rates of seedlings with antelope browsing, suggests that antelopes are the primary cause of these low seedling densities. Thus antelopes are likely the most important component limiting forest growth and self replacement.

Seedling mortality due to antelope

Browsing by antelopes, principally impala, had the largest influence on seedling survival. Impala reduced the survival of forest tree seedlings by an average of 28% per year. Impala browsing in each of the Serengeti forest types accounts for the reduced...
survival of seedlings that are not exposed to fire (Figure 3-4). Impala browsing, particularly of the seedling apical meristems and buds also effectively stops (vertical) seedling growth in all forest types (Figure 3-5). This reduction in growth is observed in both the heights of seedlings through time, and in the growth form of seedlings. Many exposed seedlings appear old, and have small leaves, thick woody stems, and a woody node at the top of the plant with multiple clip marks and scars. This suggests that impala are limiting the recruitment of some seedlings into the next size class by repeatedly removing the apical meristems or buds. Since protected seedlings grow at up to 24 cm/yr, seedlings can escape from browsing pressure in only 5-6 years and reach the maximum clipped height of 1.4m, a possible size escape from impala.

My results provide the first evidence that impala limit populations of broad leaved (non-Acacia) trees by reducing the growth rate and survival of seedlings. Several studies have reported that antelope can reduce the growth rate, but not survival of Acacia erioloba in savanna areas of northern Botswana (Barnes 2001). However, in Botswana, the effect of impala on seedlings was secondary to mortality by elephants. Belsky (1984) reported that antelope browsing limited Acacia spp. seedling growth below 31 cm for three years in Serengeti, but neither fire nor browsing reduced Acacia seedling survival rates. Seedlings grew rapidly (6-15.6cm/year) when antelopes were removed. It was not known which species of antelope was the main browser in Belsky's (1984) study, because Grant's gazelle (Gazella granti), Thomson's gazelle (Gazella thomsonii), dikdik (Madoqua kirkii) and impala were all present. Moreover, Dublin (1986) reported that seedlings of Acacia spp. exposed to antelope browsing in Masai Mara Game Reserve declined in mean height by 3 cm/yr., while protected seedlings grew by an average of 4 cm/yr. Despite the growth limitation due to antelopes reported in Belsky's (1984) study, Acacia trees successfully established over much of Serengeti during the period of mid-1970's through mid-1980's (Sinclair 1995). It has been proposed that Acacia seedling recruitment in Serengeti is controlled by fire (Packer et al. 2005); thus when periods of low fire occur, sufficient Acacia seedlings may establish to dilute the effects of antelopes.

In addition, for impala to successfully limit Serengeti forest regeneration, they must maintain both high and constant browsing pressure on seedlings. Impala numbers have declined periodically due to disease, such as anthrax in Manyara NP, Tanzania (Boshe and Malima 1986), and both brucellosis (Madsen and Anderson 1995) and foot and mouth disease (Bengis et al. 1994) in Kruger NP, South Africa (Keet et al. 1996).
In Grumeti riparian forests, there was no difference in the survival of trees attacked and not attacked by impala in the second (0.75-1.5m) and third (1.5-3m) size classes (Table 3-3). In contrast, trees that were attacked by impala in these size classes had higher survival in Mara riparian and hilltop forests than those that were not attacked. This result was consistent between plant species. Higher survival of browsed individuals may be a consequence of browsers choosing to feed on fast growing individuals (Mysterud et al. 2001). Slower growing trees of the same species often have lower nutrients and higher chemical defenses (Almeida-Cortez et al. 2004) which may reduce impala feeding. This result suggests that observational studies on mortality and fates of plants may be biased by browser forage choice when compared to manipulation studies.

*Seedling and large tree mortality due to elephants*

Elephant herbivory of seedlings in riparian and hilltop forests occurred at low rates during this study, ranging from 0.01 to 0.6% of seedlings per year. At these rates, damage by fire, impala browsing and unexplained causes were each higher than damage caused by elephant feeding. Dublin (1986) reported much higher elephant damage rates of seedlings in *Acacia* woodlands of 4%, than my estimates in forests. There is also no evidence that the tops of seedlings were broken or torn off, or that elephant attack on seedlings reduced growth rates. On the basis of this information, it appears that elephants, while important in savanna *Acacia* communities, do not play a large part in reducing seedling densities of riparian and hilltop forests.

Observer errors may cause elephant feeding damage to be underestimated. Seedlings killed by fire or other factors are easy to detect due to the remaining seedling stem, flagging tape at the base of the seedling, or tag attached near the top of the plant. Elephant damage is obvious in cases where the elephant strips branches and leaves off the seedling. Elephants can also consume the entire plant, including the tag, which is crushed and discarded, leaving obvious teeth marks on the tag. However, an underestimate may occur when a seedling is removed entirely, including the tag. When seedlings whose mortality was listed as “unknown” are attributed to elephant browsing, then $6 \pm 5\%$ /year of seedlings were removed by elephants, a value similar to that of Dublin (1986) for *Acacia* woodland seedlings.

There is evidence, however, that suggests elephants avoid forest tree seedlings as a forage type. During the three years of the antelope exclusion experiments, twelve of 192 thorn branch antelope exclosures were damaged or pushed over by elephants.
Antelope browsing marks showed that the leaves, twigs, and bark of these fast growing seedling were rapidly consumed once the exclosures were opened, but not by elephants. Given that antelopes preferred seedlings inside exclosures and that elephants could have easily accessed these seedlings but chose not to, suggests that elephants do not favour forest seedlings as forage. In addition, elephants in Venetia-Limpopo Nature Reserve, South Africa, used riparian species of Acacia less than woodland Acacia spp. (MacGregor and O'Connor 2004). When presented with broad-leaved tree species similar to those in Serengeti forests, elephants avoid mature stands of trees and prefer fast growing pioneer species in Shimba Hills, Kenya (Hoft and Hoft 1995). The Asian elephant (Elephas maximus) avoids riparian vegetation entirely in Sri Lanka (Afolayan and Amubode 1985). At current damage rates, elephant populations would have to climb to 3-4 times the current population in Serengeti before they cause forests to decline by removing large trees.

Trees damaged by elephants account for a substantial proportion of the adult tree population in riparian (8-11%), and hilltop forests (30-49%). Approximately 10% per year of Acacia trees were damaged by elephants in Serengeti (Dublin 1986), similar or lower than the attack rates found in this study. However, most elephant damage occurs on Croton dichogamus and Teclea trichocarpa bushes, and involved the removal of only one branch from a multi-stemmed plant. This pattern may account for the high survival rates of these two species after attack by elephants.

Trees that are pushed-down have a much lower survival rate than those damaged by broken branches. The main stem of pushed-down trees is often broken, which effectively ring-barks the tree. Trees that survive push down attack, tended to be in the smaller and largest size class. Small trees are supple and these trees merely bend, and large trees became uprooted but do not break. Fewer trees were pushed-down than had branches broken, but push-down damage accounted for more tree deaths since survival was poor after push-down damage.

The total mortality induced by elephants on large trees was low in the riparian forests (~1% per annum), and higher in hilltop forests (~3.5% per annum). These rates were much lower than Dublin (1986) found for Acacia trees damaged by elephants. In this study, most damage by elephants occurred in short bursts, with damage to 5% of trees in a particular location in a single feeding bout and then no further damage for over a year. This result was consistent with Dublin's (1986) findings that damage by elephants on trees was highly variable and episodic.
Interactions between herbivores and fire

There was no significant interaction term between fire and herbivory damage in either seedlings or adult trees. Analysis of seedling survival is limited to the interactions between impala and fire, because elephant mortality was either very small or difficult to detect. There was no interaction effect for large trees (>0.75 m) in each of the combinations of fire + elephant browsing, fire + elephant push-down, and fire + antelope browsing. Thus, the effects of fire and elephants on large trees are additive. Impala herbivory did not appear to have a significant effect on large trees (>0.75m).

Conclusion

The impacts of elephants and antelope browsing were measured in Grumeti riparian, Mara riparian and Mara hilltop forests in Serengeti NP, Tanzania. Elephant damage accounted for a small proportion of seedling mortality (0.01 -0.6%) and large tree mortality (1-7%). Antelope damage accounted for most seedling mortality (28%) but little mortality of large trees (0.7-9%). Fire accounted for less total mortality (seedlings: 13-16%, large trees: 6-8%) than antelopes, but more than elephants. The effect of fire was limited to the forest periphery, while antelope and elephant damage occurred throughout the forest.

Antelopes, largely impala, were the dominant herbivore of seedlings within forest blocks. Elephants could attack larger size classes where their effect was similar to that of antelopes and fire, but their total effect on survival of seedlings was 45 times less than the effect of antelopes. By limiting growth of seedlings, antelope effectively preventing the forest from recruiting new canopy trees, and may also limit the ability to colonize new areas during periods of low fire. Thus, any conservation efforts directed at expanding or protecting forests must be adapted to make use of periods of low antelope population size.
References


Chapter 4 Germination and early seedling survival in riparian and hilltop forests of the Serengeti Ecosystem; the effects of grass, flooding, recent fires, and browsing.

Introduction

Isolated forest patches exist throughout tropical savannas as closed canopy stands on hilltops and in riparian areas. These forests are composed of continuous forest tree species, and are refugia for flora and fauna not otherwise found in savannas. In some parts of Africa, the removal of grassland fires has allowed the colonization of grasslands by Acacia and other woodland trees, a process known as bush encroachment (Bredenkamp 1986; Ben-Shahar 1991; Moleele et al. 2002). However, the removal of fire has not promoted expansion of closed-canopy forests into grasslands in Uganda (Chapman and Chapman 1999), Brazil (Hoffmann et al. 2004), Costa Rica (Holl et al. 2000), Australia (Setterfield 2002), Gabon (King et al. 1997), and Venezuela (Biddulph and Kellman 1998). This suggests that additional processes are limiting seedling recruitment of closed-canopy forests into grassland areas.

Riparian and hilltop forests in the Serengeti ecosystem have declined 30-85% in the last 30 years (Chapter 2). Tree seedlings did not establish into Serengeti grasslands when fire was removed for three years (G. Sharam pers obs.). Chapman (1999) proposed that forest distribution in savannas is controlled by two separate processes: fire controls the conversion rate of forest to grassland, and seedling recruitment into the grassland controls forest expansion.

Tropical tree species in continuous forest often establish in pulses to form even-aged cohorts. Thus, recruitment limitation is the norm for many tropical species and can occur in both the germination rate of seeds and early survival of seedlings. The factors that influence forest tree recruitment in grassland can be divided into three groups: (i) dispersal of seeds into the grassland; (ii) physiological limitations of seedlings to environmental conditions in the grassland; and (iii) processes such as granivory and fire that occur in the grassland. Seeds of tropical forest trees are largely dispersed by birds, with few wind and animal dispersed species (Duncan and Duncan 2000), and without perches in the grassland seed rain is low (Holl et al. 2000; Setterfield 2002). Once in the grassland, seeds may be unable to germinate and may survive poorly due to physiological constraints to high irradiance (Holl et al. 2000), low nutrient availability (Kellman and Miyanishi 1982; Bowman and Panton 1993; Holl 2002), and water stress (Bowman et al. 1993; Hoffmann et al. 2004). Finally, processes in the grassland may
remove seeds and seedlings. These include: seed predation by rodents (Chapman et al. 1999); fire (Unwin et al. 1985; Uhl and Kauffman 1990; Bowman et al. 1993; Bond and Van Wilgen 1996); competition with grass (Holl 1998; Cabin et al. 2000; Duncan et al. 2000; Setterfield 2002); and browsing by antelope (Chapter 3). In addition, other processes may increase seedling recruitment rate. Medley (1992) noted that seedling density increased dramatically in the year following flooding of forested areas of the Tana River delta, Kenya. If it occurs at low frequency, fire may also promote seedling establishment by removing competitive dicots and grass (Kellman and Meave 1997). The relative importance of these processes is poorly understood.

Each of these processes varies through time in Serengeti, and thus conditions may arise when seedlings can establish into grassland areas and forests expand. Fire frequency in Serengeti is reduced due to grazing by wildebeest (Connochaetes taurinus) (Packer et al. 2005), and during periods of higher rains (Sinclair et al. 2005), and is increased by poaching in riparian areas (G. Sharam pers obs.). Buffalo (Syncerus caffer) are currently scarce in Serengeti, but the population was high in the 1950s and 1960s (Campbell and Borner 1995). Buffalo may have reduced the biomass of grass which may subsequently have reduced fire in riparian and hilltop forests (A.R.E. Sinclair pers obs.). Antelope numbers were reduced in Manyara National Park, Tanzania, due to an outbreak of anthrax that likely allowed a pulse of recruitment in several savanna Acacia spp. (Prins and van der Jeugd 1993). Finally, floods occur in both the Grumeti and Mara tributary rivers during years of high rainfall (G. Sharam pers obs.).

In this chapter I examine the conditions under which seedlings can establish in forest and grassland areas, specifically the relative influence of (i) fire, (ii) grass competition, (iii) browsing, and (iv) flooding on germination rate and (v) grass competition, and the combination of (vi) grass competition and antelope removal on subsequent survival of forest tree seedlings. The influence of fire and browsers on seedling survival was addressed in Chapters 2 and 3.

I first examine the distribution of naturally occurring seedlings with respect to grass densities, recent fires and flooding. Seedling microhabitat is characterized by the variables of percent grass, percent ground cover, percent canopy cover, and distance to the nearest canopy tree. I observed high densities of seedlings in areas with low grass cover which suggests that competition with grass is taking place, and high seedling density close to the trunk (< 1 m) of canopy trees suggests that protection from herbivore trampling and browsing may be important. In Serengeti and elsewhere, higher densities
of seedlings have been found in canopy gaps, where higher sunlight leads to seedling establishment and higher growth rates (Otsamo 2000), and high ground cover can increase soil moisture (Bendfeldt et al. 2001).

I also examine the germination rate of seeds and survival of seedlings under experimentally manipulated conditions of (i) with grass, (ii) without grass, and combinations of (iii) with grass and protected from browsers, and (iv) without grass and protected from herbivores, inside forests and in the grasslands adjacent to forests.

Methods

Study site

The Serengeti Ecosystem is a mosaic of open grasslands and woodlands covering 25 000 km² of north western Tanzania and south western Kenya (Figure 4-1). Riparian forests within Serengeti National Park (NP) occur on the broad floodplain created by the Grumeti River in the west, and in the steeper valleys of the Mara River tributaries on the south side of the Mara River. Dense thickets occur on hilltops to the south of the Mara River.

The climate of Serengeti is semi-arid with mean maximum temperatures of 27-28°C in Seronera. Minimum temperatures vary from 16°C in the wet season (November-April), to 13°C in the dry season (May-September). Rainfall occurs bimodally with the “short rains” occurring in November-December and the “long rains” occurring in February-April. A rainfall gradient follows the altitude gradient across the park, with the highest altitude and annual rains in the north of the park (1950m, 1200 mm/year), and lowest in the south (1800m, 500 mm/year) (Sinclair 1995).

The most common herbivore in the ecosystem is the wildebeest (Connochaetes taurinus) with a population of approximately 1.4 million (Mduma et al. 1999). Other grazers include zebra (200,000) and Thompson’s gazelles (440,000) (Sinclair 1995). Browsers are also common, particularly in riparian forests, including impala (74,000) (Aepyceros melampus) (Campbell et al. 1995), and smaller numbers of bushbuck (Tragelaphus scriptus), steinbuck (Paphicerus campestris), and dikdik (Madoqua kirkii).

Fires in Serengeti are common, lit by park rangers and managers who attempt to light “early burns” at the beginning of each dry season in an effort to prevent large scale fires latter in the dry season, and by poachers and cattle thieves. Rangers report that many riparian areas burn every 2-4 years; however, some burn every year due to
Figure 4-1. Location of riparian and hilltop forests within the Serengeti ecosystem.
poaching and proximity to roads from which early burns are lit (G. Sharam *pers obs.* 2000).

**Grumeti riparian forests**

The Grumeti River riparian forests grow as patches and strips along the Grumeti River in the western corridor of Serengeti NP. Forests typically extend 100-150m from the river into the grassland, and 200-400m along the river. The canopy of the forest is made up largely of *Lecaniodiscus fraxinifolius* (Baker), *Elaeodendron buchananii* (Loes), and *Ziziphus pubescens* (Oliv.), and is closed with very low light levels. The forest edge is a "hard" boundary, with a dense row of bushes, and tree branches of *Ziziphus pubescens*, and *Grewia bicolar* (Juss.). This boundary is thick enough to reduce light levels to as low or lower than the forest canopy in the centre of the forest patch. Soils are sandy, and typical of floodplain levee forest soils (Medley and Hughes 1996).

**Mara riparian forests**

The Mara riparian forests grow as patches in the confluences of streams along the southern tributaries of the Mara River, and range from 50X50 m to 200X600 m. These forests are different from the Grumeti forests in that they are composed of two distinct belts of vegetation. The first belt is immediately adjacent to the river and is similar to the Grumeti riparian forests in patch density and low light levels. It is composed chiefly of *Diospyros abyssinica* (Hiern) F. White, *Drypetes gerrardii* (Hutch.), *Ekebergia capensis* (Sparrm.), *Olea africana* (Mill.), and *Ficus* spp. canopy trees.

The second band or outer band is 20-40 m thick and is unlike Grumeti forests in its open canopy structure of *Euclea divinorum* (Hiern) subsp. *keniensis* (R.E. Fries) de Wit. *and Olea africana* (Mill.), higher grass content and higher proportion of bushes such as *Croton dichogamus* (Pax), *Teclea trichocarpa* (Engl.) Engl., and *Strychnos sp.* The outer band dominant trees has an open canopy structure, small leaves, and little ability to block sunlight from reaching the ground. Topography is steeper (3-6%) and soils are deep and less sandy than the Grumeti riparian forests.

**Mara hilltop forests**

Hilltops and ridges south of the Mara river have thickets of *Croton dichogamus* and *Techlia trichocarpa* with emergent canopy trees of *Diospyros abyssinica*, *Euclea divinorum*, and *Drypetes abyssinica*. Dense hilltop thickets resemble the outer band of
Mara riparian forests with fewer canopy trees (Figure 2-2). Soils are thin, and rocky/gravely in these forests, and grass occurs throughout at low densities. Fires occur often in these hilltop forests, as roads run along ridge tops from which rangers light fires. Fires lit by poachers in riparian areas burn up to hilltop areas, and expose the hilltops to a higher than average burn frequency, reaching every 1-2 years in some areas (G. Sharam *pers obs.* 1998-2001).

*Observations*

*Seedling density*

For each forest type, three forest patches to be the focus of investigation were selected where all measurements and manipulations were carried out, for a total of nine study forest patches (Figure 4-2).

Tree density in forests was measured using belt transects through forest patches from grassland to river. Trees were divided into six size classes based on height: 1) 0.05-0.75 m (seedlings), 2) 0.75-1.5 m, 3) 1.5-3 m, 4) 3-5 m, 5) 5-8 m, and 6) >8 m. Transects were 1 m wide for the seedling size class, 2 m wide for all larger size classes, and 80-140 m long. Measurements in the three forest types were made in November 1998 (Mara riparian), July 1999 (Grumeti riparian), and June 2000 (Mara hilltops). Transect measurements were conducted until the variation (S.D.) in density per tree size class was less than 20%, generally with 9-13 transects per patch.

*Seedling habitat conditions*

In each of the nine focal patches, 250 seedlings were tagged to monitor survival and growth. For each seedling, I recorded the percent ground surface cover, percent grass cover, percent canopy cover, the distance and species of the nearest canopy tree, and the distance and species of the nearest bush.

The percent ground surface cover (detritus, fresh leaves, etc.), bare soil, and grass cover were estimated in 0.25 X 0.25 m quadrats placed around each seedling. Ground and grass cover for each forest were estimated every 5 m along five transects stretching from river to grassland for a total of 100 measurements per focal forest patch.

Canopy cover was measured using a spherical densiometer at each location where a seedling was found. Forest mean canopy cover was measured every 5 m along the same transects used for ground and grass % cover for a total of 100 canopy cover measurements per focal forest patch.
Figure 4-2 Experimental setup of seedling monitoring transects and germination plots in riparian and hilltop forests.
Mean inter-tree distance was estimated by randomly choosing 100 canopy trees in each forest plot and for each canopy tree measuring the distance to the five closest canopy trees. The mean distance between bushes and small trees within the forest was measured in the same fashion as for canopy trees to a total of 300 samples.

Seedling density was compared between forest types and transects within forests using analysis of variance (ANOVA) and Tukey-Kramer Honestly Significant Difference (HSD) tests. Data were tested for equal variance and transformations were carried out as needed to ensure normality. The percent ground, grass, and canopy cover where seedlings were found were compared to the averages for each forest type using t-tests. The distance between seedlings and nearest trees and bushes were compared to the average inter-tree and inter-bush distance using t-tests.

**Germination plots**

The number of new germinating seedlings was counted in twelve 3 X 3 m plots arranged into four transects of three plots each: River, Central, Forest Edge, and Grassland transects (Figure 4-2). New seedlings were counted, tagged, identified, and revisited every two months for two years to monitor survival. The number of new germinants was compared between forest types, transects within forests, and between season using analysis of variance (ANOVA) and Tukey-Kramer HSD tests. The relationship between germination rate and distance from the forest core/river was examined using simple linear regression with distance as the independent variable and germination rate as the dependant.

**Grass removal experiments**

Twelve grass removal plots were chosen in tandem with germination monitoring plots (Figure 4-2). Grass was removed from the plots by spraying with a C4 herbicide (Ornamec, Pbi/Gordon Corp, 1217 West 12th Street, Kansas City, Missouri) the herbicide to a distance of one metre around each seedling. New seedlings in each plot were tagged and counted every two months for two years. No seedlings were found in the grassland plots, so seedlings were germinated artificially and transplanted into the grassland. Seeds of the two forest trees *Diospyros abyssinica* and *Lecaneodiscus fraxinifolius* were collected, scarified, immersed in hot and then ice water three times for 20 minutes each. Seeds were then placed in paper cups filled with forest soil and buried
flush with the forest floor. Half of the germinated seedlings were transplanted into the grass and no-grass plots in the grassland, and the other half were dug up and replaced within the forest as a treatment control. The number of seedlings germinating in flooded and grass removal plots were compared using t-tests.

**Antelope exclosures**

The impact of antelope herbivory on germination and seedling survival (< 0.75 m) was measured by comparing plots with and without antelopes. Antelope were excluded from plots by thorn fences 1.5m high around 3 X 3 m plots that were paired with each germination plot.

**Survival estimates**

Seedlings tagged in germination plots, antelope exclosures, and grass removal plots were monitored every two months for three years for health and survival, and any signs of browsing were recorded on the apical meristem, lateral branches or leaves. Transplanted seedlings were monitored for one and a half years, until all had died. The survival of seedlings in various treatments was compared using Kaplan-Meier survival curves and compared using Log-rank tests.
Results

The distribution of canopy trees in the three types of forest

Grumeti riparian forests had the highest canopy tree densities, 700-1400 stems per hectare (Figure 4-3). Mara riparian densities followed at 300-600 stems per hectare, and Mara hilltops had the lowest total densities of 100-400 stems per hectare. Grumeti riparian canopy tree density was low within 10 m of the forest-grassland edge. From 10 m to the river, tree densities were variable, but did not change systematically with distance from the river (Figure 4-3). Mara riparian forests occurred in two distinct bands: an Outer band of fire resistant species which extended from the grassland 55-75 m into the forest, and a Core band which made up the rest of the forest to the river at the centre (85-95 m). The forest Core was composed of less fire-resistant tree species, and was darker, had lower grass content and high numbers of seedlings, similar to Grumeti River forests. The density of the Outer band of trees was approximately 20% that of the Core band, and was largely composed of the tree *Euclea divinorum*, and the bush *Croton dichogamus*. Mara hilltop forests were very similar to the Outer band of Mara riparian forests, but with lower densities of *E. divinorum* trees. (Figure 4-3).

Seedling distribution

The distribution of seedlings closely followed that of canopy tree species in each forest type, with high density of seedlings throughout the Grumeti River forests and no spatial shift in species type (Figure 4-4). Seedlings in both Mara riparian and hilltop forests reflected the species in the Core and Outer bands, but Mara hilltop seedling densities differed from Mara and Grumeti riparian forests (Figure 4-4) (p=0.012, ANOVA, F_{0.05,3,1985}=6.25; Mara Hills:Mara River p=0.026, Tukey-Kramer HSD, q_{0.05,3,1251}=6.28; Mara River:Grumeti River p=0.001, Tukey-Kramer HSD, q_{0.05,12,1292}=6.28) with Mara hilltop densities being lowest and Mara riparian forests being highest. Since seedling survival was collected in different ways in the three forest types, some in plots and others individually, all seedlings were considered individuals and compared between forest types. Survival was also different between forest types when forest patches were considered replicates (p<0.05).
Figure 4-3 Density of Grumeti river, Mara river, and Mara hilltop forest canopy trees at increasing distance from the forest-grassland boundary (0 m) to the river or patch centre at 85-95 m. Arrow (†) indicates forest edge; the maximum extent of forest tree canopy. (Error bars ± SD)
Figure 4-4  Density of tree seedlings as a function of distance from the forest - grassland boundary; distance increases as one travels into the forest. Arrow (↑) indicates forest edge; the maximum extent of forest tree canopy. Shade areas contain high grass densities.
Seedlings were found at very low densities in the grassland. Two seedlings were found in 12 searched hectares of Grumeti riparian grassland, three seedlings in 9 hectares of Mara riparian grassland, and no seedlings were found in the grasslands adjacent to Mara hilltop forest patches. All seedlings found in the grassland were within 2 m of the forest canopy.

Individual seedlings tended to be found in areas with lower ground and grass cover than the forest mean (Table 4-1). The canopy cover at sites with seedlings was not different from the mean canopy cover of forests. In both Mara riparian and hilltop forests, seedlings grew closer than expected to canopy trees and bushes from the average inter-tree and inter-bush distance (Table 4-2).

Table 4-1 The percent ground and canopy cover (± SD) where naturally occurring seedlings were found and the mean forest ground, grass, and canopy cover (± SD) for Grumeti riparian, Mara riparian and Mara hilltop forests.

<table>
<thead>
<tr>
<th>Forest</th>
<th>% cover around seedling</th>
<th>Average % cover in forest</th>
<th>Test</th>
<th>p-value</th>
<th># of seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>ground</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grumeti</td>
<td>9.8±4.8</td>
<td>35±12</td>
<td>t=-140</td>
<td>&lt;0.001</td>
<td>732</td>
</tr>
<tr>
<td>Mara R.</td>
<td>47±32</td>
<td>89±9.0</td>
<td>t=-26.9</td>
<td>&lt;0.001</td>
<td>563</td>
</tr>
<tr>
<td>Mara Hills</td>
<td>55±16</td>
<td>95±17</td>
<td>t=-121</td>
<td>&lt;0.001</td>
<td>691</td>
</tr>
<tr>
<td>grass</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grumeti</td>
<td>2.0±6.0</td>
<td>22±14</td>
<td>t=-122</td>
<td>0.001</td>
<td>732</td>
</tr>
<tr>
<td>Mara R.</td>
<td>15±19</td>
<td>86±13</td>
<td>t=-106</td>
<td>&lt;0.001</td>
<td>563</td>
</tr>
<tr>
<td>Mara Hills</td>
<td>28±17</td>
<td>81±16</td>
<td>t=-89.5</td>
<td>&lt;0.001</td>
<td>691</td>
</tr>
<tr>
<td>canopy</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grumeti</td>
<td>86±4.9</td>
<td>85±14</td>
<td>t=2.30</td>
<td>0.32</td>
<td>732</td>
</tr>
<tr>
<td>Mara R.</td>
<td>68±18</td>
<td>72±12</td>
<td>t=6.57</td>
<td>0.12</td>
<td>563</td>
</tr>
<tr>
<td>Mara Hills</td>
<td>55±16</td>
<td>78±21</td>
<td>t=3.23</td>
<td>0.56</td>
<td>691</td>
</tr>
</tbody>
</table>

Table 4-2 The distance between naturally occurring seedlings and the nearest canopy tree and nearest bush (± SD), and the mean distance between canopy trees and bushes (± SD) for Grumeti riparian, Mara riparian and Mara hilltop forests.

<table>
<thead>
<tr>
<th>Forest</th>
<th>Average distance (m) Seedling to tree/bush</th>
<th>Average Inter-tree/bush distance (m)</th>
<th>Test</th>
<th>p-value</th>
<th># of seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>tree</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grumeti</td>
<td>1.3±0.6</td>
<td>3.2±1.1</td>
<td>t=-15.7</td>
<td>0.001</td>
<td>732</td>
</tr>
<tr>
<td>Mara R.</td>
<td>1.1±0.6</td>
<td>3.9±0.6</td>
<td>t=-26.0</td>
<td>&lt;0.001</td>
<td>563</td>
</tr>
<tr>
<td>Mara Hills</td>
<td>1.3±1.3</td>
<td>5.2±0.9</td>
<td>t=-83.2</td>
<td>&lt;0.001</td>
<td>691</td>
</tr>
<tr>
<td>bush</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grumeti</td>
<td>0.5±0.5</td>
<td>1.2±0.8</td>
<td>t=-1.8</td>
<td>0.21</td>
<td>732</td>
</tr>
<tr>
<td>Mara R.</td>
<td>0.24±0.4</td>
<td>2.1±0.3</td>
<td>t=-97.1</td>
<td>&lt;0.001</td>
<td>563</td>
</tr>
<tr>
<td>Mara Hills</td>
<td>0.34±0.6</td>
<td>3.5±1.3</td>
<td>t=-56.7</td>
<td>&lt;0.001</td>
<td>691</td>
</tr>
</tbody>
</table>
The effect of floods

Flood depth averaged 5-40 cm, sufficient to flatten grass in some areas and carry seeds away. However, occasional higher floods during the wet season of 1998 deposited material 1.5 metres up trees. The number of new seedlings at the end of the wet season in riparian forests was between 9X and 15X higher in years with floods (p=0.001, t-test, $t_{0.05(2)}=1.6$; where a total of 3 floods occurred in 3 forests observed for 3 years) (Table 4-3). Within plot variation was high both within and between study forests. Floods lasted for 2-3 days following high rainfall periods upstream.

Table 4-3 Number of seedlings per square metre at the end of the wet season in riparian forests with and without flooding during that wet seasons of 1998-2000. Standard deviations in brackets.

<table>
<thead>
<tr>
<th>Replicate</th>
<th>Flooded</th>
<th>Not Flooded</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Grumeti R</td>
<td>Mara R.</td>
</tr>
<tr>
<td>Forest Patch 1</td>
<td>16 (1.5)</td>
<td>28 (12)</td>
</tr>
<tr>
<td>Forest Patch 2</td>
<td>9.2 (3.4)</td>
<td>9.2 (5.1)</td>
</tr>
<tr>
<td>Forest Patch 3</td>
<td>17 (8.3)</td>
<td>11 (6.1)</td>
</tr>
</tbody>
</table>

Germination following fires

The number of new seedlings was higher in plots that had recently been burned than in plots that had not been burned in all three forest types (p=0.016, t-test, $t_{0.05(2)}=12.38$) (Table 4-4).

Table 4-4 The number of new seedlings per square metre in areas following fires and in areas without fires in Grumeti and Mara riparian forest, and Mara hilltop forest. Standard deviations in brackets.

<table>
<thead>
<tr>
<th></th>
<th>Grumeti R.</th>
<th>Mara R.</th>
<th>Mara Hilltops</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Fire</td>
<td>1.6 (0.68)</td>
<td>1.9 (1.6)</td>
<td>0.21 (0.56)</td>
</tr>
<tr>
<td>Fire</td>
<td>5.2 (2.4)</td>
<td>3.2 (3.4)</td>
<td>2.8 (3.5)</td>
</tr>
</tbody>
</table>

Distribution of germination in space and time

I examined the germination rate in the repeatedly sampled germination plots (Figure 4-2) at various distances from the forest core/river throughout the year, and the proportion of forest core:forest edge species germinating in core and edge areas of the forest. The number of germinating seedlings per plot was similar between riparian forest types (p=0.107, t-test, $t_{0.05(2)}=2.45$) (Figure 4-5), but fewer seeds germinated in Mara hilltop forests than in riparian forests (p=0.008, t-test, $t_{0.05(2)}=6.24$). No new seedlings
were found in any grassland plots, and so these plots were excluded from further analysis. The number of new seedlings in the three internal forest transects decreased with distance from the river in Mara riparian forests ($p=0.024$, Simple Linear Regression (SLR), $F_{0.05,3,563}=4.64$, $r^2=0.68$) and from the forest core in Mara hilltop forests ($p=0.005$, SLR, $F_{0.05,3,24}=13.4$, $r^2=0.74$), but not Grumeti riparian forests ($p=0.785$, SLR, $F_{0.05,3,24}=0.54$, $r^2=0.14$) (Figure 4-5) comparing plots within forest type. Germinations occurred throughout the year with a minimum in the early dry season (May-July) ($p=0.032$, ANOVA, $F_{0.05,4,23}=8.64$; Early dry season: wet season $p=0.018$, Tukey-Kramer HSD, $q_{0.05,4,23}=3.28$) (Figure 4-6) comparing plots within forest type.

The proportion of Core species seedlings was higher in the forest Core area than the Edge area of each forest type ($p=0.009$, t-test, $t_{0.05(3),16}=13.28$; comparing plots), and the proportion of Core species tended to decline in each forest type according to the homogeneity of the canopy cover (Table 4-5). In Mara riparian forests, where the forest changes gradually from Core to Edge species, the proportion of Core species seedlings in plots declined linearly from river to edge ($p=0.003$, SLR, $F_{0.05,3,24}=13.03$, $r^2=0.71$). Grumeti forests have a homogenous group of species in the canopy from river to forest edge and there was no difference in the ratio of Core to Outer band seedlings in plots within the forest ($p=0.64$, t-test, $t_{0.05(2),24}=0.54$), but a lower proportion of Core to Edge species in the forest edge transect ($p=0.009$, t-test, $t_{0.05(2),16}=5.32$). In Mara hilltop forests, where there is a Core area defined by a low density of Core riparian tree species, there was no difference in Core:Edge ratio in plots through the forest ($p=0.17$, ANOVA, $F_{0.05,3,24}=2.34$).

Table 4-5 Proportion of Core to Edge forest seedlings found in four forest transects; near river (except in hilltops), central forest, inside forest edge, and in grassland.

<table>
<thead>
<tr>
<th></th>
<th>Grumeti R.</th>
<th>Mara R.</th>
<th>Mara Hilltops</th>
</tr>
</thead>
<tbody>
<tr>
<td>Near river</td>
<td>0.65</td>
<td>0.43</td>
<td>N/A</td>
</tr>
<tr>
<td>Central forest</td>
<td>0.78</td>
<td>0.21</td>
<td>0.18</td>
</tr>
<tr>
<td>Inside forest edge</td>
<td>0.13</td>
<td>0.02</td>
<td>0.08</td>
</tr>
<tr>
<td>In grassland</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
</tbody>
</table>
Figure 4-5 The number of new seedlings per metre$^2$ per year in each River, Central, Inside Edge and Grassland transects of Grumeti riparian, Mara riparian, and Mara Hilltop forests. Arrow (†) indicates forest edge; the maximum extent of forest tree canopy. (Error bars ± SD)
Figure 4-6 The number of new seedlings per m² per three month season in the Mara riparian forests. Short Rains are November-January, Long Rains are February-April, Early Dry is May-July, Late Dry is August-October.
(Error Bars ± SD)
Seedling germination with and without grass and antelopes

Germination and survival of forest trees seedlings was monitored in control, grass removed, and grass and antelope removed plots in the forest and grassland. The number of new seedlings in germination plots without grass was higher than in plots with grass in Mara riparian and Mara hilltop forests, but not in Grumeti riparian forests (Mara R: p=0.002, t-test, $t_{0.05(25)}=-23$; Mara hills: p=0.03, t-test, $t_{0.05(25)}=-14$; Grumeti R: p=0.82, t-test, $t_{0.05(25)}=-5.6$) (Table 4-6) using plots pooled within forest type. When both antelopes and grass were removed, the germination rate did not increase compared to grass removal plots (p=0.51, t-test, $t_{0.05(25)}=2.53$). No new seedlings were found in any of the grassland plot treatments. In Mara riparian and hilltop forests the number of new seedlings in grass removed plots was similar to the number of new seedlings in germination plots after floods in Mara riparian forests (p=0.046, t-test, $t_{0.05(25)}=4.21$) (Tables 4-3 and 4-6).

The survival of seedlings within all three forest types did not change when grass was removed (p=0.56, Log-Rank, $\chi^2_{0.05,1}=2.91$, n=197 seedlings) (Figure 4-7). However, seedling survival was higher in grass removed than in control plots in the grassland (p=0.021, Log-Rank, $\chi^2_{0.05,1}=11.91$, n=122 seedlings), although the sample size in grass removed plots was low (n=6 surviving). In forest and grassland, seedlings in plots where both grass was removed and antelopes excluded had higher survival than seedlings in plots where grass was removed (p=0.006, Log-Rank, $\chi^2_{0.05,1}=21.67$, n=34 seedlings) (Figure 4-7). In some grass removal plots up to 100% of seedlings were browsed. When seedlings were transplanted into grassland and forest plots, no seedlings survived in the grassland plots with grass, 4% survived in grassland areas with grass removed and 78% of transplant control plants survived in the forest. Again, high levels of browsing by antelope were observed on seedlings in grass removed plots.

Table 4-6 Mean number of new seedlings per metre in forest plots at the end of the wet season with and without grass removed from the experimental plot. Averages are across 9 treatment plots in each of three focal study patches, of each forest type. (Standard deviations are in brackets).

<table>
<thead>
<tr>
<th></th>
<th>Grumeti R.</th>
<th>Mara R.</th>
<th>Mara Hilltops</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest + Grass</td>
<td>1.6 (0.68)</td>
<td>1.9 (1.6)</td>
<td>0.21 (0.56)</td>
</tr>
<tr>
<td>Forest - Grass</td>
<td>2.8 (1.4)</td>
<td>11 (5.4)</td>
<td>6.2 (4.7)</td>
</tr>
<tr>
<td>Forest – Grass - Antelope</td>
<td>2.4 (1.9)</td>
<td>9.6 (7.2)</td>
<td>10 (8.6)</td>
</tr>
</tbody>
</table>
Figure 4-7 Survival of forest canopy tree seedlings (%) with grass present, and removed, with grass removed and antelopes excluded inside forests and in the adjacent grassland. No seedlings survived in the Grassland + Grass present treatment. (Error Bars ± SD)
Discussion

Natural Seedlings

The distribution of naturally occurring seedlings is determined by the presence of forest canopy, grass, and distance to canopy trees, but not canopy gaps. Seedlings were found in forested areas, but not in the grassland. Within the forests, seedlings are found in areas with less grass, close to canopy trees and bushes, but less often in canopy gaps than expected. This distribution pattern may be due to competition with grass. Grass density is high in each of the areas where seedling density was low, particularly a greater distances from canopy trees and bushes, and in canopy gaps.

Germination

The distribution of germination is similar to that of naturally occurring seedlings. No germination was observed in the grassland. Within the forest, the presence of grass was the largest single variable affecting seedling germination. Twelve X more seedlings germinating in plots without grass than in plots with grass. More germination also occurred near the rivers and forest centres where less grass was present, except in Grumeti River forests where grass was absent throughout the forest. Inside forests recent fires and floods both also increased the germination rate (6X and 9X respectively) but did so to a smaller extent than grass removal.

Flooding has many effects on riparian forests including deposition of organic matter, moving seeds, and increasing soil moisture (Hughes 1990). In Serengeti riparian forests, flooding also flattens and kills much of the grass (G. Sharam pers obs.). Seedling competition with grass occurs via competition for water (Bendfeldt et al. 2001). Increased soil moisture and reduced grass competition from flooding may cause increased germination when riparian areas are flooded.

Despite removal of fire, grass, and antelope, no new seedlings germinated in the grassland. In contrast, other studies have found consistent, but low levels of germination despite the presence of grass. *Euclea divinorum*, one of the main canopy species in the Mara riparian Outer band, established in grasslands in dry areas of South Africa when fire was removed but grass was present (Smith and Goodman 1987; Ben-Shahar 1991). Hoffmann (2004) found germinating seedlings of forest trees in grassland areas of Brazil with similar rainfall levels. Chapman (1999) found germinating seedlings of similar species as in Mara riparian forests at a low rate of 0.54 /m²/year in Kibali, Uganda, with no fire, and similar amounts of grass (5.4 kg/m² compared to 2.8 - 8.9
In Hoffmann's (2004) study, seeds were hand sewn into grassland areas and scarified in some cases, thus removing potential seed dispersal and some degree of germination limitation. In Kibali, forest tree germination was halted in the grassland for two years by a population surge of rodents. Canopy tree seedling survival was also limited in Hawaii by rodents (Cabin et al. 2000), and in Costa Rica by rabbits (Holl et al. 2000). In studies of the germination of Acacia drepanolobium, invertebrates and rodents exhibited compensatory herbivory on newly germinated seedlings when browsers were removed (Shaw et al. 2002). This may explain the lack of increase in germination in this study when antelopes were excluded from germination plots. Clearly, one or more further factors is limiting seedling germination of forest trees into grassland sites in Serengeti.

The low numbers of seedlings and germinats may also be due to frequent fires in Serengeti that kill forest seeds in the seed bank (Williams 2000). Fires near riparian and hilltop forests in Serengeti have a return time of 2-5 years (Chapter 2), which is higher than in areas where other studies were carried out. A 12-15 year return time was reported in savannas of Belize (Kellman et al. 1997), or abandoned agricultural land in Uganda which remained unburned (Chapman et al. 1999).

In addition, the germination rate in the grassland may be limited by poor seed dispersal. The seeds of most forest canopy tree species in Serengeti are bird dispersed, with small brightly coloured seeds. None of the study species are wind dispersed (Beentje 1994, G. Sharam pers obs.). In Costa Rica, seed rain of bird dispersed species was higher under roosts and small trees in the grassland (Holl 2002). Thus, birds may be good vectors for seed dispersal between forested areas, but poor dispersers into areas without roosts. Mammalian seed dispersers may also have little effect in this system, as tree species do not have seeds with hooks or barbs (G. Sharam pers obs.), and seeds consumed by antelope have low survival rates due to antelope’s small bite size (Mucunguzi 1995).

The proposition that African buffalo facilitate seedling establishment into grasslands by removing grass appears to be false. Within forests, the germination response to grass removal was different. Germination there increased when grass was removed. The effects of buffalo in the grassland may not be limited to grass removal. Buffalo scarify the soil, deposit dung, and may provide suitable microsites for seedling germination. In Gabon, plowing savanna areas adjacent to forests decreased fire and
increased forest seedling abundance in areas where fire removal alone did not increase seedling density (King et al. 1997).

**Seedling survival**

My results suggest that three processes - grass competition, flooding, and recent fires - affect germination rate, while only one - antelope browsing - acts on survival of seedlings. Germination rate increased in forests when grass was removed, but did not increase further when antelopes were excluded. Seedling survival rate did not increase when grass was removed in the forest, but did increase when antelopes were removed.

Low survival in the first months after germination is common in other forest types. In Kibali, Uganda, seedling survival was low for the first 6 months (20%) but higher thereafter (80-90%), suggesting that grass suppresses either germination or the development of young seedlings (Duncan et al. 2000). In Serengeti, when canopy trees were removed at the forest edge, subsequent ingrowth of grass did not reduce the survival of tree seedlings (Chapter 2). This specific effect on the seedling stage was not apparent in grassland sites, where grass removal and grass and antelope removal both increased seedling survival. It may be a consequence of the higher grass biomass adjacent to forest patches than inside them.

The survival of individual seedlings in plots without grass is more variable than in plots with grass, and may be due to increased browsing. Seedlings in grass-removed plots appear more vigorous than seedlings in grass plots (G. Sharam pers obs.), and experience higher rates of antelope browsing, up to 100% in some plots. Cabin (2000) reported that seedlings in areas with grass had lower growth rates, but higher survival rates if goats were present, and proposed that grass serves to hide seedlings from herbivores. Moreover, seedlings without grass competition may have higher growth rates and thus be preferred by antelope browsers (Almeida-Cortez et al. 2004).
Conclusion

In this chapter, I examined the natural distribution, germination rate and survival rate of seedlings to determine the relative effect of grass, floods and fire in riparian and hilltop forests. Grass competition caused the greatest decline in germination, while recent fires and flooding increased germination. Grass competition, recent fires, and flooding acted principally upon germination rate, while antelope browsing acted largely on the survival of seedlings. Despite removing grass competition and antelope browsers, no new seedlings germinated into the grassland during this study. Thus, an additional factor must be limiting seedling germination rate in Serengeti grassland. It could be limited seed dispersal, rodent herbivory, or poor seed dispersal. Other studies in similar habitats found germination did occur in the grassland, and poor germination may be contributing to the current decline in Serengeti riparian and hilltop forests, as forests then cannot reclaim area lost to grassland fires.
References


Chapter 5 Nurse trees facilitate the establishment of riparian forests in Serengeti National Park, Tanzania.

Introduction

Natural and human-produced forest fragments occur in grasslands throughout the tropics. Natural fragments are typically composed of tree species from continuous forests and occur in refuges from fire, such as riparian and hilltop areas (Kellman and Tackaberry 1993; Medley and Hughes 1996; Geldenhuys 2005). Human-produced fragments are surrounded by deforested and abandoned agricultural land which is often overtaken by grass (Chapman and Chapman 1999a; Chapman et al. 1999b). The maintenance of natural forests, and restoration of degraded areas depend on forest trees establishing in grassland areas. Despite fire suppression, direct forest expansion into grasslands is poor (Kellman 1985; Hoffmann 1996; Chapman et al. 1999b; Hoffmann et al. 2004). Natural forests may expand via “nurse” trees in the grassland (Holl 2002), and this process may provide insights for the restoration of degraded landscapes.

Naturally fragmented forests occur across East Africa in river drainages and on hilltops (Medley et al. 1996). Forests are composed of Central African and West African continuous forest species and montane species common in the highlands surrounding Lake Victoria (Medley et al. 1996). Individual forest fragments are likely remnants of Central African and montane forest expansions during a warm wet period 10 000 – 8 000 BP and a cooler period 8 000 - 6 000 BP (Livingstone 1982; Jolly et al. 1997).

Within the Serengeti ecosystem, riparian and hilltop forests have declined rapidly since the early 1970s (Chapter 2). Fires have eroded the forest edges, removing both canopy trees and seedlings (Chapter 2). When fires were excluded, seedlings of forest trees did not establish into grassland areas (Chapter 2). Similar riparian forests exhibit poor seedling establishment in Venezuela (Biddulph and Kellman 1998), Belize (Kellman and Miyanishi 1982), and Australia (Unwin et al. 1985; Bowman and Panton 1993; Setterfield 2002). Human-produced forest fragments of montane species have been studied in Uganda, where seedlings established at low rates in grassland areas and deforested areas have remained that way for up to 100 years (Chapman and Chapman 1996; Chapman et al. 1999b).

The establishment of tree seedlings in grasslands is often low because of fire (Goldammer and Siebert 1990; Hoffmann 1996; Bachelet et al. 2000), poor seed
dispersal (Meave and Kellman 1994; Chapman et al. 1999a; Holl 2002), seed predation (Duncan and Duncan 2000; Holl et al. 2000), competition from grasses (Chapman et al. 1999a; Williams 2000), browsing (Holl et al. 2000; Roques et al. 2001; Shaw et al. 2002; Husheer et al. 2003), poor soil nutrients (Kellman 1984; Kellman 1985; Hoffmann et al. 2004), and harsh physical conditions (high sunlight and temperature) (Bowman et al. 1993; Chapman et al. 1999a; Duncan et al. 2000). Moreover, factors such as fire (Chapter 2), browsing (Chapter 3), and grass competition (Chapter 4) can individually halt tree seedling establishment in Serengeti.

Despite the eroding effects of fire, and poor seedling establishment in the grassland, riparian and hilltop forests have remained extant in East Africa, presumably for the last 8,000 years (Livingstone 1982; Jolly et al. 1997; DeBrusk 1998). Forests must therefore have a means to recover area lost to fires and to expand into grasslands.

**The nurse species hypothesis**

Kellman (1985) proposed that trees and shrubs in savannas facilitated the establishment of riparian forest seedlings in Venezuela. Savanna trees can provide perches for birds which increases seed rain (Holl et al. 2000); while shading increases soil moisture (Van Wilgen et al. 1990; Biddulph et al. 1998; Bendfeldt et al. 2001); and reduces grass density (Biddulph et al. 1998; Holl 2002); which may together exclude fire (Biddulph et al. 1998). Chapman (1999) proposed that succession of grassland areas in Uganda was hampered by the lack of such aggressive, pioneer species. Forest seedlings can establish when not associated with conspecifics. Seedlings established in stands of fast growing plantation trees in Indonesia (Otsamo 2000a; Otsamo 2000b), and similar plantations facilitated forest expansion in Africa (Leju et al. 2001; Senbeta et al. 2002). Thus, macro-conditions such as light, browsing, or competition are likely important for seedling establishment, rather than conditions that only conspecific trees can create.

The establishment of potential nurse tree species such as *Acacia* in savanna appears to be limited largely by fire. In many parts of Africa overgrazing by livestock has led to an increase in woody plants in range lands, a process referred to as “bush encroachment” (Moleele et al. 2002). Livestock reduced the grass fuel load and thus fire frequency which allowed seedlings of savanna trees such as *Acacia* to establish (Roques et al. 2001). *Acacia* species also underwent a pulse of establishment in the Serengeti ecosystem in the late 1970s and early 1980s due to a reduction in fire (Packer
During the late 1970’s, the rapidly increasing wildebeest population in Serengeti reduced grass biomass and thus fire, which allowed several *Acacia* species to establish across large areas of Serengeti (Sinclair 1995a). Other factors, however, may also reduce nurse tree recruitment. Seedling survival and growth rate of *Acacia* and forest tree species are reduced by antelope browsing (Belsky 1984; Prins and van der Jeugd 1993), and grass competition (Smit and Van Romburgh 1993).

Single nurse trees, however, may not be sufficient to facilitate establishment of a forest canopy. Bowman (1993) found poor regeneration under single eucalyptus trees in northern Australia and proposed that a dense matrix of canopy trees and bushes were required to sufficiently alter site conditions for seedlings to establish. Moreover, most solitary *Acacia* savanna trees are not replaced by other species in a successional process. However, in dense bush stands the initial colonizing species were replaced by less fire tolerant species on dry sites in South Africa (Ben-Shahar 1991).

Within the Serengeti ecosystem, two tree species could act as nurse tree species: *Acacia polyacantha* (Willd.), and *Euclea divinorum* (Hiern). Stands of *A. polyacantha* are found adjacent to riparian forests along the Grumeti, Mbalageti, and Orangi Rivers (G. Sharam, pers obs.) (Figure 5-1). *Acacia polyacantha* is a locally rare but widely occurring tree found in riparian areas from Ethiopia to South Africa (Coates Palgrave 1983). Large *A. polyacantha* trees are also found at low density within the Grumeti riparian forests (G. Sharam, pers obs.). Along the tributaries of the Mara River in northern Serengeti, seedlings and stunted rootstocks of *Euclea divinorum* are found adjacent to riparian forests (G. Sharam, pers obs.). This species is known as a bush encroachment species in South Africa (Tobler et al. 2003).

In this chapter, I examine (i) whether riparian forest tree seedlings can establish under the canopies of savanna “nurse”trees, and (ii) under what conditions nurse trees are able to establish in riparian grassland. I studied existing stands of *A. polyacantha* along the Grumeti River to test the following predictions: (1) nurse trees exclude grass and therefore fire; and (2) soil moisture is higher under nurse trees than in the grassland. I also test the predictions for the establishment of nurse species into grassland areas. I prevented fires, and removed grass and herbivores around *E. divinorum* trees along the tributaries of the Mara River to test the predictions that establishment of nurse species is controlled by (3) fire, (4) grass competition, and (5) browsing.
Figure 5-1  *Acacia polyacantha* stand on the Kimarishi River (tributary of the Grumeti River): (A) *Acacia polyacantha* stand canopy trees, (B) edge of riparian forest, (C) understory of dense bushes in *A. polyacantha* stand.
**Pioneer Species**

*Acacia polyacantha* (Willd.) subsp. *campylacantha* (Hochst. Es. A. Rich.) Brenan

*Acacia polyacantha* is a tall deciduous tree, from 20-25m tall, with a long, straight bole that holds 4-5 cm thorns. It is found in sub-saharan Africa from South Africa to the Somali horn on the east coast and in disjunct patches on the west coast of Africa. The species is widespread in Africa, and is generally found near water courses or in areas of high water table. It also occurs in some rocky soils, and rarely in open woodlands. It can be gregarious, or found in pure stands (Hutchinson *et al.* 1954; Dale and Greenway 1961; Coates Palgrave 1983).

It has a high growth rate, reaching 3.5-6.8 m in height and 8.0-14.3 cm basal diameter only 28 months after seeding, and seedlings generally have a high survival rate (Kamara and Maghembe 1994). Due to this high growth rate and nitrogen-fixing ability, it has been used as an inter-cropping species with wheat and grass in agricultural areas and is grown on fallow fields in long rotation schemes (Harmand *et al.* 2004). See Appendix for more information on alternative names.

*Euclea divinorum* Hiern subsp. *keniensis* (R.E. Fries) de Wit

This species is common in thorn scrub, riparian areas, and termite mounds in south and south-east Africa (Coates Palgrave 1983). It also occurs on rocky areas and hilltops in Kenya and Tanzania (Dale *et al.* 1961). It is common in riparian forests where it reaches 8-10 m, and in areas of the hills south of the Mara river in Serengeti (G. Sharam Pers Obs.) as individual seedlings in the grassland (often at points of relief, rocks or old termite mounds), and as stunted root stocks.

**Methods**

**Study Site**

The Serengeti Ecosystem is a mosaic of open grasslands and woodlands covering 25 000 km² of north western Tanzania and south western Kenya (Figure 5-2). Riparian forests within Serengeti National Park (NP) occur on the broad floodplain created by the Grumeti River in the west, and in the steeper valleys of the Mara River tributaries on the south side of the Mara River. Dense thickets occur on hilltops to the south of the Mara River.
Figure 5-2 Location of riparian and hilltop forests within the Serengeti ecosystem.
The climate of Serengeti is semi-arid with mean maximum temperatures of 27-28°C in Seronera. Minimum temperatures vary from 16°C in the wet season (November-April), to 13°C in the dry season (May-September). Rainfall occurs bimodally with the “short rains” occurring in November-December and the “long rains” occurring in February-April. A rainfall gradient follows an altitudinal gradient across the park, with the highest altitude and annual rains in the north of the park (1950m, 1200 mm/year), and lowest in the south (1800m, 500 mm/year) (Sinclair 1995b).

The most common herbivore in the ecosystem is the wildebeest (*Connochaetes taurinus*) with a population of approximately 1.4 million (Mduma *et al.* 1999). Other grazers include zebra (200,000) and Thompson’s gazelles (440,000) (Sinclair 1995b). Browsers are also common, particularly in riparian forests, including impala (74,000) (*Aepyceros melampus*) (Campbell and Borner 1995), and smaller numbers of bushbuck (*Tragelaphus scriptus*), steinbuck (*Paphicerus campestris*), and dikdik (*Rynchotragus* (*Madoqua*) *kirkii*).

Fires in Serengeti are common, being lit by park rangers and managers who attempt to light “early burns” at the beginning of each dry season in an effort to prevent large scale fires latter in the dry season, and by poachers and cattle thieves. Rangers report that many riparian areas burn every 2-4 years, however some burn every year due to poaching and proximity to roads from which early burns are lit (G. Sharam *pers obs.* 2000).

**Grumeti riparian forests**

The Grumeti River riparian forests grow as patches and strips along the Grumeti River in the western corridor of Serengeti NP. Forests typically extend 100-150m from the river into the grassland, and 200-400m along the river. The canopy of the forest is made up largely of *Lecaniodiscus fraxinifolius* (Baker), *Elaeodendron buchananii* (Loes), and *Ziziphus pubescens* (Oliv.), and is closed with very low light levels. The forest edge is a “hard” boundary, with a dense row of bushes, and tree branches of *Ziziphus pubescens*, and *Grewia bicolor* (Juss.). This boundary is thick enough to reduce light levels to as low or lower than the forest canopy in the centre of the forest patch. Soils are sandy, and typical of floodplain levee forest soils (Medley *et al.* 1996).
Mara riparian forests

The Mara riparian forests grow as patches in the confluences of streams along the southern tributaries of the Mara River, and range from 50X50 m to 200X600 m. These forests are different from the Grumeti forests in that they are composed of two distinct belts of vegetation. The first belt is immediately adjacent to the river and is similar to the Grumeti riparian forests in patch density and low light levels. It is composed chiefly of Diospyros abyssinica (Hiern) F. White, Drypetes gerrardii (Hutch.), Ekebergia capensis (Sparrm.), Olea africana (Mill.), and Ficus spp. canopy trees.

The second band or outer band is 20-40 m wide and is unlike Grumeti forests in its open canopy structure of Euclea divinorum (Hiern) subsp. keniensis (R.E. Fries) de Wit. and Olea africana (Mill.), higher grass content and higher proportion of bushes such as Croton dichogamus (Pax), Teclea trichocarpa (Engl.) Engl., and Strychnos sp. The outer band dominant trees have an open canopy structure, small leaves, and little ability to block sunlight from reaching the ground. Topography is steeper (3-6%) soils are deep and less sandy than the Grumeti riparian forests.

Photographic analysis of A. polyacantha establishment

Photographs were taken of the Orangi River from Kimerishi Hill approx. 500-750 m south of the Orangi River in 1980 by A.R.E. Sinclair (Prof. Zoology Department, University of British Columbia, Vancouver, BC). I repeated these photographs in 2001 from the same positions, and visually compared the photos to determine the distribution of A. polyacantha stands at the two time periods.

Riparian seedling distribution under A. polyacantha thickets

Seventy five Acacia polyacantha stands of various sizes, from individual trees to 25 X 35 m patches were surveyed for riparian forest tree seedlings by searching one 5 X 5 m quadrat per stand and a single 3.5 m radius area under single canopy trees. For each tree seedling found in the search plot, I recorded the species of the seedling, height, grass height, distance to nearest bush, distance to the trunk of the nearest A. polyacantha canopy tree, mean percent canopy cover, the existence of elephant or buffalo trails at the site, and whether the site had been burned. Seedlings were tagged and monitored annually for two years for survival estimates. Percent canopy cover was estimated using a spherical densiometer. The percent cover of understory vegetation in each A. polyacantha stand was estimated visually into ranks of abundance for grasses,
herbs, and bushes in the search plot. The mean distance between canopy trees and between bushes was estimated by taking the mean of 25 measurements between canopy trees and between bushes in each *A. polyacantha* plot.

The relationship between the size of *A. polyacantha* stands and seedling density was evaluated using simple linear regression of seedling density on patch size, and 1-way ANOVA on patch size. The distance between seedlings and *A. polyacantha* trees and bushes was compared to the average inter-tree or inter-bush distance using t-tests. The densities of seedlings, herbs and bushes was each compared across patch sizes using analysis of variance (ANOVA) and Tukey-Kramer Honestly Significant Different (HSD) tests. All data were first tested for equal variance and transformed when necessary to ensure normality.

**Fire in *A. polyacantha* stands**

To test whether fire would penetrate into *A. polyacantha* stands, I lit fires during the mid-dry season (July) in the adjacent grassland and monitored the distance that fire penetrated into stands. Fires lit in the grassland burned areas from 1-200 hectares. In some cases, they burned to the edge of several *A. polyacantha* stands. Fires were also lit adjacent to 16 large stands (>25 X 25 m) and 21 single *A. polyacantha* trees of the same height as canopy trees in stands. To test if *A. polyacantha* trees were excluding grasses in large stands, I created 10 canopy gaps by cutting down 10 (8-10 m tall) trees on the periphery of the stand and monitored the time until grass invaded by returning to the sites each month. To determine whether the grass in canopy gaps would burn, I then burned these areas during the following dry season (July, 2001). Tree seedlings found in these sites before the canopy trees were removed were monitored every two months for two years for survival. Seedling survival in burned and unburned areas was compared using Kaplan-Meier survival curves and Log-Rank tests.

**Soil moisture measurements**

Bulk soil moisture in *A. polyacantha* stands was measured by collecting soil during the wet season (March 15, 1999 and 2000) and the dry season (June 15, 1999 and 2000) inside 10 *A. polyacantha* stands and in the adjacent grassland. Soils were collected in ten 2.5 cm diameter cores to a depth of 20 cm, bagged, weighed, spread to air dry and weighed again. The difference in percent soil moisture between inside and outside of *A. polyacantha* stands, and season was compared using t-tests.
Influence of grasses on *E. divinorum* seedling survival

Forty *E. divinorum* seedlings were chosen at each of three riparian sites in the hills to the south of the Mara River. Each seedling was tagged, flagged, measured for height, and its initial condition (scorched, clipped by browsers, attacked by insects, etc) was recorded in March 2000. I then removed the grass from around half of the seedlings at each site using the C4 herbicide (Ornamec, Pbi/Gordon Corp, 1217 West 12th Street, Kansas City, Missouri). A plastic shield was placed around each seedling to prevent the herbicide from contacting the plant during spraying. Seedling survival, growth, and condition were then monitored every two months for two years. Seedling survival was compared between with and without grass treatments using Kaplan-Meier survival curves and Log-Rank tests.

The effect of herbivores and fire on *E. divinorum* seedling survival

One hundred and fifty *E. divinorum* seedlings were tagged and measured at each grass experiment site, in the hills south of the Mara River in Sept 2000. For half of these seedlings, protective thorn fences were built around and above them to exclude herbivores. I burned the grass surrounding half of both protected and unprotected seedlings each year for two years during the mid dry season (June, 2000 and 2001). Survival and growth were measured every four months for two years. Each study site was searched exhaustively in the final sampling period. An ANOVA was used to compare the numbers of seedlings between initial and final sampling periods instead of a Cox regression on survival times, due to poor re-sighting of seedlings in tall grass, and resulting uncertainty in survival times.

Results

*Forest seedlings in A. polyacantha stands*

No seedlings of forest trees were found in the grasslands surrounding either riparian forests or *A. polyacantha* stands, but seedlings were abundant under stands of *A. polyacantha*. Seedling density varied from 0 to 0.5 seedlings per m$^2$ and increased with the size of *A. polyacantha* stands. There were few seedlings under solitary trees, and the highest densities were in larger stands (Figure 5-3) ($r^2 = 0.64$, Seedling #/ m$^2 = -0.008 + 0.0002$ X Stand area (m$^2$), $p=0.01$, $F_{0.05(2),1.73}=129$). An exponential curve also fit the data when transformed (0.5 added to each value to remove zeros), with a slightly
higher $r^2 = 0.66$ (Seedling #/ m$^2 = -0.703 + 0.0003 \times \log$ Stand area (m$^2), p<0.001, F_{0.05(2), 1.73}=146.2$), but both models were similar (Figure 5-3).

The densities of grasses, herbs, and bushes were also related to the area of *A. polyacantha* stands. Stand area was divided into three classes: (i) single canopy trees, (ii) medium size patches of approximately 100 m$^2$, and (iii) large patches of $> 650$ m$^2$. Single canopy patches had an understory of grass, medium patches had an understory of herbs, while large patches had an understory of bushes, herbs, and tree seedlings (Figure 5-4). As patch size increased, the density of grass declined rapidly from single *A. polyacantha* trees to medium sized stands (Figure 5-4) ($p=0.001$, ANOVA, $F_{0.05(2), 2.72}=26.2$; $p=0.001$, Tukey-Kramer HSD, $q_{0.05, 1.72}=3.28$). Herb density increased from single trees to medium sized stands ($p=0.011$, ANOVA, $F_{0.05(2), 2.72}=17.3$; $p=0.009$, Tukey-Kramer HSD, $q_{0.05, 1.72}=2.48$). The density of bushes increased between medium sized and large stands ($p=0.001$, ANOVA, $F_{0.05(2), 2.72}=22.5$; $p=0.001$, Tukey-Kramer HSD, $q_{0.05, 1.72}=6.25$), as did riparian forest tree seedling density ($p<0.001$, ANOVA, $F_{0.05(2), 2.72}=34.2$; $p<0.001$, Tukey-Kramer HSD, $q_{0.05, 1.72}=8.98$).

Within *A. polyacantha* stands, riparian seedlings were found closer to canopy trees and bushes than expected if distributed randomly between canopy trees (Figure 5-5) (average inter-tree distance = 3.4 m; $p=<0.001$, $t_{0.05(2), 73}=-24.36$, n=362 seedlings; average inter-bush distance = 1.6 m; $p=<0.001$, $t_{0.05(2), 73}=-21.63$, n=362 seedlings). Seventy six percent of seedlings were located within 1 m of canopy *A. polyacantha* trees, and 68% were within 0.5 m of the main stem of bushes. Ninety three percent of all seedlings were found growing under or within bushes. Of 362 seedlings examined, only 4% had evidence of browsing by antelopes.

*Acacia polyacantha* trees excluded grass and thus fire, the exclusion of which increased forest seedling survival. Of sixteen experimentally set fires, none penetrated more than 1 m into intact *A. polyacantha* stands, while fires burned under nine of 22 lone individuals of *A. polyacantha*. When *A. polyacantha* trees were removed on the periphery of larger stands (10 individual trees), the average time until the herbaceous and bush ground cover was replaced by grass was 1.5 yrs, and seven of the 10 canopy tree removal areas burned.
Figure 5-3 The relationship between density of forest seedlings and area of *Acacia polyacantha* stands along the Grumeti River, Serengeti National Park. (n=75 stands)
Figure 5-4 The mean density of forest seedlings, and mean understory percent cover of grasses, herbs, and bushes in *Acacia polyacantha* stands. Medium sized patches were approximately 100 m$^2$, and large patches > 650 m$^2$. (n=75 stands) (Error bars = ±SD seedling density)
Figure 5-5 Distance between seedlings of riparian forest trees and the nearest *A. polyacantha* trees and nearest bushes within *A. polyacantha* stands. (n=327 seedlings)
Mean seedling survival in unburned plots with herbaceous and bush cover was higher (0.87/yr) than unburned plots (0.21/yr) (p=0.021, Log-Rank, \( \chi^2_{0.05,1}=22.31, n=39 \) seedlings pooled between the 10 canopy removal plots).

Elephants appeared to avoid contact with *A. polyacantha* trees, though they rubbed against other tree species nearby, damaging bark and covering tree trunks with mud. *Acacia polyacantha* trees were probably protected from elephants by the large, broad-based spines on their trunks.

**Soil Moisture**

During the dry season, bulk soil moisture was higher inside large *A. polyacantha* stands (19 ± 8.4%) than in the adjacent grassland (7 ± 5.2%) (p=0.021, \( t_{0.05(14)}=11.2, n=16 \)). The soil moisture during the wet season was high, and similar inside (28 ± 2.8%) and outside (27 ± 5.6%) of stands (p=0.54, \( t_{0.05(14)}=2.3, n=16 \)). Soil moisture in the dry season was reduced to 70% inside stands and 25% in grasslands of the respective wet season maxima.

**Acacia polyacantha establishment**

I compared photographs taken of the Orangi River in 1980 (Figure 5-6) with the distribution of *A. polyacantha* stands in 2001. *Acacia polyacantha* had undergone a pulse of recruitment in the late 1970's in these sites. In each of the available 1980 photographs, dense thickets of juvenile thorn trees 0.75-1.0 m tall were found on the same locations as canopy *A. polyacantha* stands in 2001. Since 1980, however, recruitment has been poor. No *A. polyacantha* trees were found smaller than canopy trees, and no seedlings were found either in grassland or *A. polyacantha* stands. *Acacia polyacantha* establishment in the late 1970's and early 1980's coincided with a pulse of recruitment of several *Acacia* species across Serengeti due to low fire frequency at that time.
Figure 5-6 Current position (July 2001) of *Acacia polyacantha* stands superimposed on photo taken from Kimerishi Hill of the riparian forests along the Orangi River, June 1980.
Survival and growth of *Euclea divinorum*

Removal of both fire and herbivores increased the survival of *E. divinorum* seedlings in the Mara riparian grassland (Figure 5-7) (fire: p=0.039, ANOVA, $F_{0.05(2),4,8}=6.02$; herbivory: p=0.022, ANOVA, $F_{0.05(2),4,8}=7.98$; comparing proportion surviving in 12 replicates of 7-15 seedlings each), but there was no interaction effect (p=0.93, ANOVA, $F_{0.05(2),4,8}=0.009$). Seedling growth rate was reduced by burning (p=0.019, ANOVA, $F_{0.05(2),4,8}=2.92$), but not by herbivory (p=0.931, ANOVA, $F_{0.05(2),4,8}=0.09$), and again, there was no interaction effect (p=0.145, ANOVA, $F_{0.05(2),4,8}=1.61$). The removal of grass increased survival of *E. divinorum* seedlings (Figure 5-7) (p=0.047, t-test, $t_{0.05(2),10}=8.00$), and increased their growth compared both with fire treatment and herbivores removed treatment, and those in the grassland treatment (p=0.0378, t-test, $t_{0.05(2),20}=3.06$).

Discussion

*Forest tree seedlings in stands of nurse trees*

The hypothesis here is that nurse trees facilitate the establishment of forest trees by providing locally suitable environmental conditions. The hypothesis predicts that: (1) nurse trees exclude grass and therefore fire; and (2) soil moisture is higher under nurse trees than in the grassland. The results showed that *A. polyacantha* nurse trees excluded both grass and fire, and that soil moisture was significantly higher inside stands than in the grassland during the dry season, thus supporting both predictions. However, the effects of *A. polyacantha* on grass, fire, and soil moisture depended on stand size. Larger stands excluded grass and therefore fire than single trees and grassland areas.

The high proportion of tree seedlings growing beneath bushes was unexpected. Ninety five percent of seedlings occurred within a dense matrix of thorn bushes and lianas where light levels were low. Only 4% of seedlings had evidence of antelope browsing, much lower than the 84% damage rate found in riparian forests (Chapter 3). This difference suggests that thorn bushes acted as natural antelope exclosures, and it may also account for the higher density of seedlings found in large *A. polyacantha* stands where bushes were abundant. Unprotected seedlings in riparian forests had both low survival rates and close to zero growth rates due to antelope browsing (Chapter 3).
Figure 5-7 Survival of *Euclea divinorum* seedlings in riparian areas of the Mara River; with and without fire and browsing, and with and without grass present. The grass present treatment is equivalent to the unburned, with browsers treatment. (Error bars ± SD) (average survival of 214 seedlings in 12 plots)
Figure 5-8 Growth rate of *Euclea divinorum* seedlings in riparian areas of the Mara River with and without fire and browsing, and with and without grass present. The grass present treatment is equivalent to the unburned, with browsers treatment. (Error bars ±SD)
These results were similar to those of Bowman (1993) who found that a canopy of *Eucalyptus* trees was insufficient to promote seedling success. He proposed that old *Eucalyptus* stands with an understory of bushes improved site conditions by increasing shading and soil moisture. Holl (2002) reported that perches for birds in grassland areas of Costa Rica increased seed rain, but not seedling establishment because perches did not exclude grasses and thus change local conditions.

I also found forest seedlings under single trees in the grassland, but single trees were unable to exclude grass and thus fire. Single trees may, therefore, be insufficient to promote forest re-establishment. Likewise, medium-sized *A. polyacantha* stands did not contain bushes, which appeared to act as herbivore exclosures. Thus, I propose that there is a minimum stand size where nurse trees can act to protect forest seedlings depending on the level of disturbance. In areas without fire and browsers, single trees provide sufficient protection. In areas with fire but without antelope browsers, medium sized patches (100 m$^2$) can exclude grass and provide sufficient protection. In areas with browsers, large stands (> 650 m$^2$) are required with thorn bushes to limit browsing. Thus, forest restoration may occur in dense stands of exotic plantation species, as suggested by Otsamo (2000a & b), but not via perches in the grassland or singly-planted nurse trees (Holl *et al.* 2000; Holl 2002). In addition, larger stands may be more attractive to the birds that disperse forest trees, which would increase the seed rain of forest tree seeds in larger *A. polyacantha* stands.

Kellman (1984) proposed that riparian forest seedlings could not establish in grasslands due to a combination of frequent fires and low soil nutrients. In Belize, woody plants accumulated mineral nutrients in grasslands (Kellman 1989). Hoffmann (2004) reported that low mineral nutrients in grassland areas decreased forest seedling success. Nitrogen-fixing trees such as *Acacia* spp. sequester nitrogen, some of which leaches into the surrounding soil and is available for other plants (Harmand *et al.* 2004). *Acacia polyacantha* is a nitrogen fixing species (Beentje 1994), and is inter-cropped with corn and used as a nitrogen fixing fallow species in parts of Africa (Owino 1989; Kamara *et al.* 1994; Nyadzi *et al.* 2003; Harmand *et al.* 2004). I did not test soil fertility in *A. polyacantha* stands in this study, but I assume that this mechanism applied.
Establishment of nurse trees

The establishment of the two potential nurse species in Serengeti appears to be controlled by fire, and to a lesser degree by browsing and grass competition. Both *Acacia polyacantha* and *Euclea divinorum* occur in the grassland adjacent to riparian forests and as large, old, canopy trees in the riparian forests themselves. Current riparian forests are likely the result of previous pulsed recruitment of nurse species and subsequent establishment of forest trees.

In order for these two species to act as nurse trees, they must be able to establish in grasslands when forest trees cannot. This is certainly the case for *A. polyacantha*, which established in the late 1970s probably due to a reduction in fire, while forest trees did not establish at that time. *Euclea divinorum* has also established itself into grassland areas. However, subsequent growth from seedlings to canopy trees has not occurred, largely due to fire.

The recruitment of *A. polyacantha* with other *Acacia* spp. in the late 1970s suggests that exclusion of fire alone allowed seedlings to establish (Packer et al. 2005), thus supporting my prediction (3) that fire reduces influences seedling survival. *Acacia polyacantha* established along the Grumeti River but not in riparian areas of the Mara River. This result may be due to seed availability, soil type, altitude and other environmental conditions. This species will establish in a variety of habitats when hand sown (Owino 1989; Kamara et al. 1994; Nyadzi et al. 2003), and seed sources for *A. polyacantha* were present within Grumeti riparian forests, but not along the Mara River. In addition, *A. polyacantha* is most often found on clayey, waterlogged floodplain soils (Beentje 1994) such as the Grumeti riparian area. Mara riparian areas are steeper and may be too well drained for this species.

Experiments with *E. divinorum* showed that in addition to fire (prediction 3), grass competition and browsing strongly reduced growth and survival, thus supporting predictions (3), (4), and (5). Stunted *E. divinorum* root stocks were found in riparian grassland areas, and large trees are common in riparian forests along the Mara River, confirming that this species can persist in grasslands and attain canopy tree size in Serengeti. In dry areas of South Africa, *E. divinorum* is able to establish when fire is removed (Smith and Goodman 1987; Ben-Shahar 1991). However, it did not establish (unlike the *Acacia* spp.) in Serengeti in the late 1970s.

There are several possibilities as to why *E. divinorum* has not established along the Mara River. First, fire frequency may have remained too high in northern Serengeti,
despite the reduction in fire elsewhere during the late 1970s. Political unrest along the north west border of Serengeti may have led to more fires being lit by poachers. During the late 1970s and 1980s, virtually all of the African buffalo (*Cyncerus caffer*) were removed from northern Serengeti by poaching (Campbell et al. 1995), and poachers lit fires preferentially in riparian areas to attract animals to their snares (G. Sharam *pers obs.*). However, *Acacia robusta* underwent a pulse of establishment in northern Serengeti concurrent with the rest of the ecosystem, from which I infer that fire frequencies must have fallen in grassland areas of northern Serengeti.

Second, browsing and grass competition may be more severe in riparian areas of Serengeti, than in dry areas of South Africa. Third, *E. divinorum* may have a lower tolerance to fire than *Acacia* spp., and the period of low fires in Serengeti was insufficient to allow it to establish. *Euclea divinorum* may establish when fires are removed (Ben-Shahar 1991), but it is not considered an aggressive pioneer species in South Africa (Bredenkamp 1986). Smith (1987) described *E. divinorum* as a second sere species; seedlings were shade tolerant, established below *Acacia nilotica* trees in savanna, and subsequently formed dense thickets in South Africa. In Serengeti, *E. divinorum* may have historically established via other nurse species for shade and soil nitrogen, or is able to establish directly in grassland, but not under the current conditions of frequent fire and abundant browsers.

Despite the evidence that both *A. polyacantha* and *E. divinorum* recruitment is limited by fire, neither species established in grassland areas when fire was experimentally excluded for four years. This lack of establishment implies that either fire was not removed for long enough, or a second factor also limited establishment, such as seed limitation, grass competition, browsing, or rainfall. Both species fruited each year of the fire manipulation (G. Sharam *pers obs.*) and thus, seeds were likely not limiting. *Acacia polyacantha* seedlings are not shade tolerant and establishment is limited by strong intra-specific competition for light in Tanzania and Kenya (Owino 1989; Nyadzi et al. 2003), and perhaps by grass in Serengeti. *Euclea divinorum* success was reduced by both grass competition and browsing in this study, which may have been sufficient to limit regeneration. In addition, Higgins (2000) proposed that establishment of *Acacia* spp. in grassland relied on both removal of fire and frequent rains in the dry season (at least every 30 days). Increased dry season rains occurred in Serengeti in the late 1970s, thus, the two study species may require both fire removal and increased dry season rains in order to establish successfully. In addition, a history of fire in a site may
be sufficient to reduce the seed bank, and thus limit recruitment when fires are excluded (Williams 2000). Despite poor regeneration in fire exclusion plots, each of the study species had high growth and survival rates when seeded by hand in areas without fire (Smith et al. 1987; Owino 1989; Bell and Van Staden 1993; Kamara et al. 1994; Nyadzi et al. 2003). It may, therefore, be useful to use these species to facilitate forest establishment into grassland and degraded agricultural sites.

Conclusion

I hypothesized that some savanna tree species act both as nurse trees for riparian forest trees by excluding grass and fires, and by maintaining high soil moisture and shade. In addition, these trees should establish into grasslands when other species cannot, but recruitment may be limited by fire, browsing, or grass competition. My results indicated that pioneer nurse species facilitate the establishment of riparian forest trees into savanna, although stand sizes must be large in areas of high fire and browsing disturbance. These stands occur naturally and establish in pulses, likely with periods of low fire, and perhaps low browser numbers. Thus, riparian forests in East Africa can expand via nurse trees and colonize new areas.
References


Chapter 6 Decline and establishment in closed canopy forests of Serengeti: the cumulative effects of fires, elephants, antelope browsing, floods, and grass competition.

Introduction

Little is known about the long term dynamics of riparian and hilltop forests in East Africa. Most riparian forests are thought to be remnants of an expansion of Central African forests 10 000 BP during a warm, wet period (Livingstone 1982; Jolly et al. 1997). Forests may have remained extant since isolation, or expanded periodically and colonized new areas when conditions were suitable (Medley and Hughes 1996). In addition to grassland fires, which erode the forest edge (Chapter 2), forests suffer from frequent browsing of seedlings by antelopes (Chapter 3), creeping ground fires, and damage to large trees by elephants (Chapter 3); each of these reduces the growth rate and survival of trees, particularly of seedlings. Few seedlings and small trees are found within forest patches (Chapter 4), and the cumulative effect of reduced seedling survival and growth may result in forests that cannot replace canopy trees lost to disturbance or senescence. The relative impact of these factors must be understood to determine if forests are self-replacing, and to predict under what conditions new forest stands can establish.

Three types of forests occur in Serengeti National Park, Tanzania: (i) closed canopy riparian forests along the Grumeti River in the west of the park, (ii) closed canopy riparian forests with a dense outer band of Croton thicket along the tributaries of the Mara River, and (iii) Croton thickets on the hilltops in the north of the Serengeti. The Grumeti riparian forest is largely composed of Central African tree species (Beentje 1994). The Mara River and Mara hilltop thickets are composed of montane species from the Loita, Ngoro, and Mau mountains to the north and east of Lake Victoria (Beentje 1994), which underwent an expansion in range 6 000 BP during a cool period (Jolly et al. 1997). Based on structural similarities, growth rates, and survival of trees, these forests can be grouped into: Closed canopy riparian forests, and Croton thickets.

In earlier chapters I have shown that seed germination of forest canopy trees occurred at a low rate inside Croton thickets, riparian forests and in the adjacent grasslands (Chapter 4). Germination rate was increased by flooding in riparian forests and by removal of the dense grass which occurred along the edge of riparian forests and sparse grass throughout hilltop Croton thickets (Chapter 4). Grassland fires entered forest edges, which increased germination rate, but decreased survival of existing
seedlings (Chapters 2 & 4). Antelope browsing decreased both survival and growth rate of seedlings and small trees in both forest types (Chapter 3). Elephants are found in all forest types, where they damaged and pushed down large trees (Chapter 3).

In this chapter, I used a Leslie matrix model to synthesize the observed demography of forest trees. I estimate the population growth rate of canopy trees in response to flooding, grass removal, fires, antelope browsing, and elephant damage in intact forest stands. Seedling survival and growth rates are often higher in canopy gaps due to greater sunlight. Population growth rates of forest trees, are thus density dependent, with low recruitment under canopy trees and high recruitment in gaps. I also examine the population growth rate in canopy gaps and on the forest edge.

Methods

Study site

The Serengeti Ecosystem is a mosaic of open grasslands and woodlands covering 25 000 km$^2$ of north western Tanzania and south western Kenya. Riparian forests within Serengeti National Park (NP) occur on the broad floodplain created by the Grumeti River in the west, and in the steeper valleys of the Mara River tributaries on the south side of the Mara River. Dense thickets occur on hilltops to the south of the Mara River.

The climate of Serengeti is semi-arid with mean maximum temperatures of 27-28°C in Seronera. Minimum temperatures vary from 16°C in the wet season (November-April), to 13°C in the dry season (May-September). Rainfall occurs bimodally with the “short rains” occurring in November-December and the “long rains” occurring in February-April. A rainfall gradient follows an altitudinal gradient across the park, with the highest altitude and annual rains in the north of the park (1950 m, 1200 mm/year), and lowest in the south (1800 m, 500 mm/year) (Sinclair 1995b).

The most common herbivore in the ecosystem is the wildebeest (*Connochaetes taurinus*) with a population of approximately 1.4 million (Mduma et al. 1999). Other grazers include zebra (200,000) and Thompson’s gazelles (440,000) (Sinclair 1995b). Browsers are also common, particularly in riparian forests, including impala (74,000) (*Aepyceros melampus*) (Campbell and Borner 1995), and smaller numbers of bushbuck (*Tragelaphus scriptus*), steinbuck (*Paphicerus campestris*), and dikdik (*Rynchotragus (Madoqua) kirkii)*.
Fires in Serengeti are common, being lit by park rangers and managers who attempt to light “early burns” at the beginning of each dry season in an effort to prevent large scale fires latter in the dry season, and by poachers and cattle thieves. Rangers report that many riparian areas burn every 2-4 years, however some burn every year due to poaching and proximity to roads from which early burns are lit (G. Sharam pers obs. 2000).

*Leslie matrix model assumptions and experimental manipulations*

This model calculates the number of trees surviving to the largest size class in a given area with and without the effects of (i) fire, (ii) antelope browsing, (iii) elephant damage, (iv) grass competition, (v) flooding, (vi) canopy gaps, and combinations of (vii) antelope browsing and grass competition, and (viii) antelope browsing and fire on germination rate, seedling growth and survival, and survival of large trees. All measurements were carried out in three focal forest patches along each of the Grumeti River, Mara River tributaries and Mara hilltops. Germination plots were arranged in groups of three 3X3 m plots with three groups of plots in the forest at increasing distance from the river, and one group in the grassland adjacent to the forest (Chapter 4). Three hundred un-manipulated tree seedlings (0.05-0.75 m) were tagged, and 1000 larger trees were tagged and monitored every two months along three transects in each focal forest patch (Chapter 3).

*Fire:* Fire reduced survival of tree seedlings and large trees (Chapter 2) and increased germination rates in the year following fire (Chapter 4). Seedlings and trees in forest areas adjacent to the grassland were burned every fourth year and the survival and growth of tagged seedlings and survival of larger tagged trees were recorded. The germination rate after fires was also measured in 3X3 m plots in burned areas for two years following fires.

*Antelope browsing:* Antelope browsing reduced the growth rate and survival of tree seedlings (0.05-0.75 m) and survival of the next larger size class (0.75-1.5 m) (Chapter 3), but did not affect germination rate (Chapter 4). Antelope were excluded from tagged seedlings using 3X3 m thorn fences and the growth and survival of seedlings were recorded and compared to those of unprotected seedlings. The germination rate was
measured inside protected areas in 3X3 m plots, and in adjacent unprotected 3X3 m plots.

*Elephant damage:* Elephants consumed tree seedlings, and removed branches, and pushed down large trees (Chapter 3). The number of seedlings consumed by elephants was estimated using seedlings tagged near ground level and looking for characteristic signs of elephant feeding to the seedling stem. The percent of tagged large trees damaged by elephants, and the survival rates of damaged and undamaged trees were also recorded.

*Grass competition:* Competition with grass reduced the growth rate of tree seedlings and survival (Chapter 4) and germination rate (Chapter 5). Tagged seedlings were assigned to treatments of with and without grass, and grass was removed using the C4 herbicide (Ornamec, Pbi/Gordon Corp, 1217 West 12th Street, Kansas City, Missouri). Germination rate was measured as above in areas with and without grass removed.

*Flooding:* Flooding increased germination rate (Chapter 4) and was measured as above in riparian areas during flooded and non flooded years.

*Canopy gaps:* The germination rate, and seedling growth rate and survival were measured on 30 seedlings in twenty canopy gaps as above, with seedling treatments being protected and unprotected from antelope browsers.

*Antelope browsing and grass competition:* This combination of factors increased germination rate (Chapter 4), which was measured as above inside areas of antelope fencing and grass removal.

*Antelope browsing and fire:* This combination decreased growth and survival rate of tree seedlings in hilltop thickets (Chapter 3), where tagged seedlings were protected from browsers using thorn fences and then half of each study plot was burned every second year.
The model

Population growth rate \( r \): the increase or decrease in the number of individuals, was estimated using a Leslie Matrix model which combined germination, survival and growth rates to calculate the density of trees surviving to the largest size class (>8 m) and the model compared that number of trees with the measured density of trees in 2000 where:

\[
 r = \ln \left( \frac{\text{pop size}_{t+1}}{\text{pop size}_t} \right)
\]

A Leslie Matrix model uses the number of new individuals in a population (germination rate) and the survival per year or size/age class to calculate the number of individuals that will occur in each size class in the future. Germination rates were measured in plots with and without grass and browsers in forests, in the adjacent grassland, and in canopy gaps. A yearly number of new germinating plants/ hectare was added to the population, and this number multiplied by the number of years that the seedlings spend in the first size class to give a “per time period” germination rate (Chapter 4). Survival rates were monitored in six size classes in the field: 1) 0.05-0.75 m (Seedlings), 2) 0.75-1.5 m, 3) 1.5-3 m, 4) 3-5 m, 5) 5-8m, and 6) >8 m (Chapter 2).

The survival rates of trees from one size class to the next was calculated by multiplying the number of years that an average tree spent in a size class by the survival in that size class. The number of years in a size class is the quotient of the height in m of the size class divided by the growth rate. Growth rates were measured directly on seedling and size class 2) trees. For larger trees, the number of years spent in each size class was estimated from a yield curve where:

\[
 \text{Height}_{(t)} = \exp (A + B \times (1/t))
\]

Where

- \( \text{Height}_{(t)} \) = the height of the tree (m) at time \( t \) (years)
- \( A \) & \( B \) = fitted parameters
- \( t \) = the age in years

No growth curves were found published for the species in this study, but the shape of the growth curve equation and the fitted parameter \( B \) were verified against age-size data for \textit{Croton megalocarpus} (Thijssen 1996), a species closely related to \textit{Croton dichogamus}, that occurs in montane areas near Serengeti (G. Sharam, \textit{pers obs.}). Two species of trees were used as focal species in this model: \textit{Croton dichogamus}, the main constituent of \textit{Croton} hilltop thickets with a maximum height of 4 m, and \textit{Diospyros}...
*Abyssinia*, a fast growing riparian forest tree found in both Mara and Grumeti riparian forests with a maximum height of 9 m. The B parameter of the yield curve was used from *C. megalocarpus* (*B* = -2.1), and the A parameter varied such that the maximum height of *C. dichogamus* was 4 m (*A* = 1.39), and the max height of *D. abyssinica* was 9 m (*A* = 2.23). Using these two yield curves, I calculated the average number of years that trees spent in each size class. Only the population growth rate of canopy trees was used to calculate r. For *C. dichogamus*, I compared the measured (in 2000) and calculated number of trees per hectare in the fourth size class. For *D. abyssinica*, I used the measured and calculated number per hectare in the fifth size class. The growth rate of fire and elephant damaged trees was not measured, but was probably lower than for undamaged trees. Thus, estimates of the effects of elephants and fire should be considered conservative.

Results

The instantaneous rate of growth (r) was calculated for the population of forest canopy trees under conditions of: (i) fire, (ii) antelope browsing, (iii) elephant damage, (iv) grass competition, (v) flooding, (vi) canopy gaps, and combinations of (vii) antelope browsing and grass competition, and (viii) antelope browsing and fire (Figure 6-1 and Table 6-1).

Under the current conditions of severe browsing by antelope (largely impala), both *Croton* thickets and closed canopy riparian forests have negative population growth rates (Figure 6-1, Table 6-1). At the current population size and associated damage rate, elephants were unable to remove sufficient large trees for the tree population to decline. However, at 6 X the current population sizes, elephants could cause the decline of closed forests by removing larger trees. Ground fires on the forest edges removed sufficient seedlings to cause the population to decline. Thus, despite limited damage to canopy trees with one year of burning out of four, sufficient seedlings were removed to limit replacement of the canopy, and thus erode the forest edge. Flooding and removal of grass competition increased the germination rate of seedlings, which in turn increased the population growth rate. However, this effect was insufficient to counteract the effects of antelope browsing.

The germination rate, and seedling growth rate (height) were higher in canopy gaps, and thus, the population growth rate was higher (Table 6-1). After a canopy gap
Figure 6-1 Population growth rate ($r$) of canopy trees in *Croton* thickets and closed canopy riparian forests under conditions of (i) no elephants, antelope, or fire, (ii) with elephant, (iii) with antelope, and (iv) with fire.
Table 6-1 The effects of antelopes, elephants, fire, floods, grass removal, and canopy gaps on the population growth rate (r) of *Croton* thickets and closed riparian forests via changes in germination rate, seedling growth and survival, and large tree survival. Each treatment was conducted in the absence of other effects: thus antelope are assumed to be removed when the effects of elephants are varied, unless otherwise stated.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Treatment</th>
<th>Croton thicket (r)</th>
<th>Closed forest (r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antelope</td>
<td>No Antelope</td>
<td>0.150</td>
<td>0.776</td>
</tr>
<tr>
<td></td>
<td>The effect of antelope on germination</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>The effect of antelope on seedling growth rate</td>
<td>-0.203</td>
<td>-0.010</td>
</tr>
<tr>
<td></td>
<td>The effect of antelope on seedling survival</td>
<td>-0.145</td>
<td>-0.061</td>
</tr>
<tr>
<td></td>
<td>Cumulative effects of antelope</td>
<td>-0.497</td>
<td>-0.694</td>
</tr>
<tr>
<td></td>
<td>Antelope with 20% seedling escapement</td>
<td>-0.259</td>
<td>-0.563</td>
</tr>
<tr>
<td>Elephant</td>
<td>No elephant</td>
<td>0.150</td>
<td>0.776</td>
</tr>
<tr>
<td></td>
<td>The effect of elephants on germination</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>The effect of elephants on seedling growth rate</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>The effect of elephants on seedling survival</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>The effect of elephants on larger trees</td>
<td>0.141</td>
<td>0.654</td>
</tr>
<tr>
<td></td>
<td>Cumulative effects of elephants</td>
<td>0.141</td>
<td>0.654</td>
</tr>
<tr>
<td></td>
<td>Effects of elephants at 2X density</td>
<td>0.132</td>
<td>0.522</td>
</tr>
<tr>
<td></td>
<td>Effects of elephants at 3X density</td>
<td>0.124</td>
<td>0.380</td>
</tr>
<tr>
<td></td>
<td>Effects of elephants at 4X density</td>
<td>0.115</td>
<td>0.224</td>
</tr>
<tr>
<td></td>
<td>Effects of elephants at 5X density</td>
<td>0.106</td>
<td>0.053</td>
</tr>
<tr>
<td></td>
<td>Effects of elephants at 6X density</td>
<td>0.096</td>
<td>-0.137</td>
</tr>
<tr>
<td>Fire</td>
<td>No fire</td>
<td>0.150</td>
<td>0.776</td>
</tr>
<tr>
<td></td>
<td>The effect of fire on germination</td>
<td>0.393</td>
<td>0.940</td>
</tr>
<tr>
<td></td>
<td>The effect of fire on seedling growth rate</td>
<td>-0.189</td>
<td>0.109</td>
</tr>
<tr>
<td></td>
<td>The effect of fire on seedling survival</td>
<td>-0.290</td>
<td>-0.576</td>
</tr>
<tr>
<td></td>
<td>The effect of fire on larger trees</td>
<td>0.100</td>
<td>0.481</td>
</tr>
<tr>
<td></td>
<td>Cumulative effects of fire</td>
<td>-0.632</td>
<td>-0.962</td>
</tr>
<tr>
<td>Germination</td>
<td>Without floods, with grass</td>
<td>0.150</td>
<td>0.776</td>
</tr>
<tr>
<td></td>
<td>Without grass (increase germination)</td>
<td>0.559</td>
<td>1.208</td>
</tr>
<tr>
<td></td>
<td>With floods (increase germination)</td>
<td>N/A</td>
<td>1.564</td>
</tr>
<tr>
<td>Antelope &amp;</td>
<td>The effect of antelope on growth rate and survival</td>
<td>-0.497</td>
<td>-0.694</td>
</tr>
<tr>
<td>Germination</td>
<td>Antelope - Grass (increased germination)</td>
<td>-0.480</td>
<td>-0.683</td>
</tr>
<tr>
<td></td>
<td>Antelope + Flooding (increased germination)</td>
<td>N/A</td>
<td>-0.679</td>
</tr>
<tr>
<td>Canopy gaps</td>
<td>Closed forest - Antelope</td>
<td>0.150</td>
<td>0.457</td>
</tr>
<tr>
<td></td>
<td>Gap (increased germination) - Antelope</td>
<td>0.711</td>
<td>1.453</td>
</tr>
<tr>
<td></td>
<td>Gap + Antelope (decrease growth &amp; survival)</td>
<td>-0.274</td>
<td>-0.449</td>
</tr>
<tr>
<td></td>
<td>Gap - Antelope, + Grass (decrease germination)</td>
<td>-0.356</td>
<td>-0.464</td>
</tr>
</tbody>
</table>
was produced, grass filled the site with an average lag of 2.5 years (Chapter 4). Higher growth rates allowed seedlings to reach a height where they were not affected by competition from invading grass species in new canopy gaps. However, when antelope were present, growth rates were lower, allowing time for grass to invade. Once grass was present, germination rates and seedling survival fell such that the canopy could not be replaced.

Discussion

Destabilizing processes

Under the current conditions of frequent fires and heavy antelope (impala) browsing, forests in Serengeti grassland are not self replacing due to recruitment limitation. At a low fire frequency, where canopy trees and bushes are undamaged, fire can erode the forest edge by removing seedlings. Moreover, antelope reduce seedling growth rate and survival so much that forests can not replace canopy trees in dense stands or in canopy gaps. As forests decline, grass competition, fire, and antelope browsing may reduce forest cover further.

A destabilizing process is one that increases its impact as forest cover declines. When canopy trees are removed by fire, elephants, or senescence, grass rapidly fills the canopy gap, and burns the following dry season. Grassland fires can jump into these canopy gaps if the gaps are adjacent to the forest edge and kill the intervening trees. As the size of patches declines and the relative size of grass canopy gaps increase, the damage rate to surrounding trees also increases, hastening the forest decline. Antelope also act as a destabilizing influence as they browse on the high density of seedlings and bushes in the forests, but their primary food source is browse and forbs in the grassland. As forest size declines, the rate of antelope browsing on forest seedlings likely increases, further decreasing tree recruitment.

Despite the visually dramatic damage caused by elephants, their effects on forest dynamics are minor compared to those of fire and browsers. Elephants have often been blamed for declining tree populations in savannas, particularly in areas where seedling recruitment is poor (Laws 1970; Croze 1974; Dunham 1989; MacGregor and O'Connor 2004). Elephants can remove woodland vegetation when their population is supported by alternative food sources during the dry season (Sinclair 1995a), as in Uganda where rainfall is high and grass and forbs are abundant in the dry season (Lock 1993). In savannas, the rate of elephant damage to trees often ranges between 8-15% in
populations that are declining (Dublin 1986), although damage rates can reach 35% (Dunham 1989). The damage rates found in Serengeti Croton thickets and riparian forests were lower and range between 1-5% (Chapter 3). The low rates of elephant damage, and even lower rates of elephant-based mortality (1-2%) (Chapter 3) may be due to low elephant numbers in Serengeti, or differences in elephant diet preference. Elephants in Venetia-Limpopo Nature Reserve, South Africa, used riparian species of Acacia less than woodland Acacia spp. (MacGregor et al. 2004). When presented with broad-leaved tree species similar to those in Serengeti forests, elephants avoid mature stands of trees and prefer fast growing pioneer species in Shimba Hills, Kenya (Hoht and Hoft 1995). The Asian elephant (Elephas maximus) avoids riparian vegetation entirely in Sri Lanka (Afolayan and Amubode 1985). At current damage rates, elephant populations would have to climb 6 X in Serengeti before they would cause forests to decline.

Grassland fires once every four years reduce seedling survival at the forest edge such that the forest canopy can not be replaced, despite the increased growth rate in canopy gaps. Thus, recruitment limitation is eroding the forest edge at a fire frequency lower than the one required to visibly damage canopy trees and edge bushes (Chapter 2). If forests are to persist, fire frequency must be less than level at which seedlings are removed by edge fires, not at which damage is visible to canopy trees.

At greater fire intervals of 12-16 years, fires may have a positive effect on forest dynamics. In Belize, fires opened the forest canopy and removed competitive herbaceous plants, increasing spatial heterogeneity and tree species richness in riparian forests (Kellman and Meave 1997). The high fire frequencies found in Serengeti may also be affecting forests indirectly. Frequent fires may reduce the soil nutrient supply (Hoffmann et al. 2004), remove the seed bank of forest trees (Williams 2000), and limit recruitment of “nurse” tree species (Chapter 5), thus reducing the likelihood of forest establishment in the grasslands even when a longer fire-free period occurs.

Forest establishment

The key to conserving forests in riparian and hilltop areas in Serengeti and elsewhere is in the understanding of the processes that allow new forests to establish. My model and observations in the field suggest that there are four ways in which the forests may have established: (i) all forests are remnants of Central African and Montane forest expansion 10 000 and 6 000 BP (the Null hypothesis), (ii) pioneer nurse trees
established in the grassland and facilitated the establishment of forest trees, (iii) exclusion of fire and antelope allowed forests to establish directly into grassland areas, and (iv) long term removal of fire allowed sufficient seedlings to germinate and escape the effects of antelope browsing.

Observations of species composition in Serengeti riparian forests suggest that these forests have established recently. Forests along the Grumeti River contain a low density of very large *Acacia polyacantha* trees, and seedlings of forest trees were observed in stands of *A. polyacantha* adjacent to the riparian forests (Chapter 5). These *A. polyacantha* stands established in the late 1970's due to reduction in fire (A.R.E. Sinclair pers obs., Chapter 5). Thus, it appears that forests along the Grumeti river are currently undergoing a pulse of establishment under *A. polyacantha* nurse trees in the grassland, and that intact forest patches are a product of a previous establishment pulse as evidenced by remnant mature *A. polyacantha* within the current forests. Moreover, *Acacia polyacantha* seedlings died when planted in riparian forest and protected from browsers, further suggesting that large *A. polyacantha* trees in the riparian forests were the result of an earlier successional stage (Chapter 5). These data support the hypothesis that forests establish via pioneer nurse species on the Grumeti River.

The process of nurse tree establishment and facilitation of riparian tree establishment was not observed on the tributaries of the Mara River, nor in Mara hilltops. Experiments at these sites showed that fire and antelope browsing reduce seedling growth rate and survival. Results from my model show that when fire and antelope are excluded, sufficient numbers of seedlings could survive to produce a forest canopy. Mara area forests also appear to have undergone a recent pulse of expansion; small islands within tributaries of the Mara River had higher species diversity and much larger trees of the same species as riparian forests (G. Sharam pers obs.), suggesting that these islands had been forested for longer than the surrounding area. Moreover, the canopy of individual forest patches was often composed of one or two similar species and these species varied from patch to patch, suggesting a founder effect from a seedling establishment pulse (G. Sharam pers obs.).

Fire was absent in Serengeti for prolonged periods twice in the last century. The most recent period was in the late 1970s and early 1980s, when the increasing wildebeest population caused reduced grass fuel load and subsequent reduction in fire (Packer et al. 2005). The second period of fire removal is thought to have been in 1890-1920s when the cattle disease rinderpest killed most of the wildebeest and buffalo from
Serengeti, and cattle from the surrounding areas (Sandford 1919; Sinclair 1979). The loss of cattle caused famine and emigration by the local peoples, which in turn reduced the frequency of set fires (Ford 1971). Both of these periods of reduced fire allowed a pulse of woodland *Acacia* spp. to establish (Sinclair 1995a). *Acacia polyacantha* established along the Grumeti River during the 1970s-80s period, and the cohort of large and old *A. polyacantha* trees within the forest may be the result of the 1890-1920s period of low fire. No such establishment pulse occurred in Mara forests during the 1970s-80s period, although establishment may have occurred during the 1890s-1920s period if rinderpest also removed antelope; recent evidence indicates that antelope are not susceptible to rinderpest. However, buffalo in 1982-1986 were less susceptible to rinderpest than in the period prior to 1964 (Dublin *et al.* 1990), suggesting that the virulence of rinderpest may have fallen in these wildlife populations. Hence, rinderpest may have removed antelope during the 1890-1920s period, and Mara riparian and hilltop forests may have expanded at that time. Small scale tests where antelope and fire were removed (Chapter 3) showed that sufficient growth and survival occurred and the forest canopy could be replaced. What is now required is a large scale experiment with both fires and antelope removed from a large area of forest and grassland.

Finally, there is evidence that antelope browsers can limit recruitment at the current germination rates. There are examples of browsers limiting recruitment of forests and woodlands in temperate (Potvin *et al.* 2003; Tsujino and Yumoto 2004), and tropical areas (Prins and van der Jeugd 1993; Barnes 2001). Prins (1993) found that periodic reductions in antelope population in Manyara NP, Tanzania, were coincident with recruitment pulses of *Acacia tortilis*. Browsers were also found to limit recruitment of *Acacia* spp in savanna areas of Masai Mara and Serengeti, where the height of seedlings exposed to antelope declined through time, likely due to repeated removal of the apical meristem (Belsky 1984; Dublin 1986).

Despite the evidence that antelope can limit recruitment, there is also evidence from *Acacia* woodlands that the effects of browsers can be overwhelmed by high seedling establishment rates. *Acacia* spp. underwent a recruitment pulse in Serengeti during the late 1970s and early 1980s (Sinclair 1995a), likely due to a reduction in fire frequency (Packer *et al.* 2005) and despite the presence of antelope. Moreover, germination may be controlled by greater dry season rainfall (Higgins *et al.* 2000), and seed dispersal (Chapman and Chapman 1999; Duncan and Duncan 2000; Holl *et al.* 2000). I propose that, if fires were removed for long enough with a constant seed rain
into the grassland, a year or two of high dry season rainfall may be sufficient to promote a large pulse of establishment that would dilute the effects of antelope and allow the establishment of new forests. An experiment to test this hypothesis would require exclusion of fire, but not antelope, for a long period from riparian and hilltop areas.

Conclusion

In this chapter, I examined the conditions under which riparian and hilltop forests in Serengeti are stable using a Leslie matrix analysis. Under the current conditions of frequent fires and browsing by antelope (largely impala), forests are unable to replace lost canopy trees even when germination and growth are increased by flooding, grass removal, and canopy openings. Fires removed sufficient seedlings to stop canopy replacement at a fire frequency that did not damage canopy trees and bushes. Elephants did not play a significant role in forest removal, but may do so if their population increases 6 X. Forests can establish under nurse trees where fire and browsers are excluded, as is occurring on the Grumeti River. Many of the forest stands in Serengeti are likely the product of a period between 1890-1920s when both fire and antelope were removed by the disease rinderpest. The long term history of these forests is likely one of repeated establishments followed by long declines. My research illustrates that reducing fire frequency will halt erosion of the forest edges. Given the appropriate conditions, high diversity forests can establish and be maintained in savanna systems.
References


Chapter 7 General Conclusions

Overview of the thesis

Riparian and hilltop forest dynamics in Serengeti National Park, Tanzania, are controlled by separate processes at three distinct phases in the growth of forest trees: (i) germination, (ii) seedling growth and survival, and (iii) canopy tree survival. Germination in forests is increased 9-12 X by recent fires, flooding and grass removal, but remains poor in grasslands despite removal of grass and fire (Chapter 4). However, both germination and seedling survival are high under nurse trees in the savanna, which can establish during periods of infrequent fires (Chapter 5). Seedling growth and survival are limited throughout the forest by browsing antelope, and at the forest-grassland boundary by burning at least one year out of four (Chapters 3 and 6). Despite damage by elephants inside forests, elephants do not remove sufficient seedlings or canopy trees to limit the number of canopy trees (Chapter 3). Canopy tree survival is reduced by fires at the forest periphery, but only when areas are burned three or more years out of four (Chapter 2).

(i) Germination

Research on germination in tropical forest fragments has focused on two questions: what processes control the patterns of species distribution in forests (MacDougall and Kellman 1992) and what limits the germination in grasslands adjacent to forests (Kellman 1985; Chapman et al. 1999b)? Within forests, many species recruit in pulses, implying that seed safe sites or seedling survival is limited by factors such as shade, competition with grass, and poor nutrients (MacDougall et al. 1992). Thus, canopy gaps could have reduced competition and hence increased seedling success in continuous forests (Brown 1993). I found that competition with grass controls the germination success and thus the distribution of seedlings, while browsers did not alter germination rate. Processes such as fire and floods remove grass competition and increase the germination rate. Even in areas without grass, germination increases following floods, implying that floods have additional effects on seeds, such as increasing soil moisture. The timing of floods, thus, could lead to pulses of germination and recruitment.

Patchy forests in East African savannas are remnants of Central African forests which spread to the Indian Ocean during a warm wet period 10 000 BP and which retreated as the climate cooled (Jolly et al. 1997). Forest patches are also produced currently by timber cutting and farming (Chapman 2003). Establishment of forest trees
is poor in grassland, despite the exclusion of fire, which has led to concerns that conversion of forest to grassland is irreversible (Kellman 1985; Chapman and Chapman 1999a; Hoffmann et al. 2004). Research on germination and seedling survival in grasslands has focused on the mechanisms of inhibition in grasslands (Hoffmann 1996; Hoffmann et al. 2004). Agroforestry plantations have been proposed to facilitate forest establishment in grasslands (Otsamo 2000a; Otsamo 2000b; Leju et al. 2001).

Germination in grassland areas is reduced by poor seed dispersal (Holl et al. 2000), high irradiance (Bowman and Panton 1993), granivory (Duncan and Duncan 2000), and competition with grass (Loik and Holl 2001). My research indicated that germination rate is very low, despite the removal of fire, grass, and browsers. Low seed dispersal has been blamed for poor germination in grasslands in Costa Rica (Holl et al. 2000; Holl 2002), but in Uganda, seed rain remained unchanged to 25 m, i.e. further from the forest than did the treatment plots in my study (Duncan et al. 2000). In West Africa, plowing adjacent to riparian forests dramatically increased germination (King et al. 1997), although it was concluded that reduced grass competition allowed greater germination. I propose that germination is limited by a suite of factors: competition with grass, and soil conditions, principally moisture.

(ii) Seedling growth and survival

The main determinants of seedling growth and survival are grassland conditions, fires, and browsing by antelope. Seedlings transplanted into grassland areas did not survive, and survival remained poor when grass and browsers were removed in Serengeti. This suggests that abiotic conditions such as low soil moisture, low nutrients, or high irradiance are reducing seedling survival. At the forest periphery, fires remove grass and increase the germination rate, but also remove most seedlings in burned areas, and kill all seedlings that are directly exposed to fire. Seedlings that survive in burned areas have 5-11 X slower growth rates, despite the removal of grass. The key to interpreting interactions between fire and seedlings is to understand that because germination and seedling success in grassland areas is poor and seedling density is very low, most seedlings being burned are within the forest-grassland edge. Open, advancing forest edges allow grass and therefore fire to enter the forest, whereas closed, dripline edges exclude fire. Replacement of the forest edge is limited by seedling mortality due to fire in advancing forest edges when burned only one year out of four, as fires must first remove the protective layer of bushes in dripline edges and so replacement is not limited until burning occurs in three of four years. My data imply that
managers should use caution when estimating the fire tolerance of forest patches. The effects of fire are not consistent between edge types and erosion of the forest edge does not depend on death of canopy trees.

Antelope browsing of seedling apical meristems may limit *Acacia* recruitment in savannas in Tanzania (Belsky 1984) and Botswana (Barnes 2001). In Manyara National Park, Tanzania, *Acacia* trees recruited in a pulse during a two year period where impala populations were reduced by anthrax (Prins and van der Jeugd 1993). My results are the first evidence that antelope can limit the growth and reduce the survival of broad-leaved forest seedlings. Moreover, as forest area declines, antelope populations in forested areas may increase and further limit recruitment. However, antelope suffer disease outbreaks which reduce population sizes and may allow seedlings to escape from browsing above a threshold size (Boshe and Malima 1986; Bengis et al. 1994). Any management actions taken to facilitate forest establishment should consider antelope browsing. Managers should either exclude antelope from managed areas or conduct treatments during periods of low antelope abundance.

The special case of nurse trees

Limited recruitment by forest trees into grassland areas has been attributed to few aggressive pioneer species in Africa (Chapman et al. 1999b) and has led to research on using agroforestry stands (Otsamo 2000b) and artificial bird roosts in grasslands (Holl et al. 2000) to facilitate seedling establishment. A wide variety of seedlings successfully establish in agroforestry stands (Senbeta et al. 2002), but artificial perches and single planted nurse trees in savannas have met with poor success (Holl et al. 2000). I found evidence of two nurse trees in Serengeti, *Acacia polyacantha* and *Euclea divinorum*. *Acacia polyacantha* established in a pulse in the late 1970s along the Grumeti River, and has facilitated the establishment of riparian forest seedlings. Stands of *A. polyacantha* exclude grass and therefore fire, and contain a dense understory of thorn bushes that exclude antelope. When canopy *A. polyacantha* trees were removed, grass grew into the canopy gaps within 1.5 years and allowed fire to enter the stand, which killed tree seedlings. Removal of bushes allowed antelope to feed on seedlings and reduced seedling survival. Grass and browser exclusion effects, however, depended on stand size. Stands of 100 m² were able to exclude grass, but did not contain bushes. Only stands over 650 m² (30-60 trees) excluded both grass and browsers. The establishment of *A. polyacantha* and *E. divinorum* is reduced by fire, grass competition and browsing (for *E. divinorum*), and *A. polyacantha* established in the
late 1970s during a period of infrequent fires in Serengeti (Sinclair et al. 2005). *Acacia polyacantha* grows on a variety of sites, is currently inter-cropped as a nitrogen-fixing species in agriculture (Harmand et al. 2004), and may be a good management tool for facilitating forest regeneration on degraded sites.

(iii) **Canopy tree survival**

Canopy tree survival was reduced by frequent fires, but not by elephants in all forest types. Most interactions between fire and trees took place at the forest edge, as fires did not penetrate into forest patches. Mortality rate due to fire depended on the type of forest-grassland edge. Open, advancing edges allowed grass to grow as an understory, thus allowed fire to directly access the trunks of trees, and increased the mortality rate. Advancing edges were composed largely of *Croton dichogamus* and *Euclea divinorum*, species that have a sparse canopy and so allow grass to grow even when the canopy is closed. These trees have thick, fissured bark, presumably as a defense against fire. At fire frequencies of one year or greater out of four, seedlings, intermediate sized, and canopy trees are removed by fire. Thus, fire frequencies must be reduced below this level if forests are to persist. Closed canopy, dripline edges, such as the Grumeti riparian forests are composed of a dense tangle of bushes and branches that overhang the grassland and reduce grass density near the trunks of the trees. Several years of repeated burning are required to remove these branches before bush and tree mortality occur. My study followed advancing and dripline forest edges over only four years, and there is little information about the previous burning history of these forests. Thus, the example of dripline forests having low mortality despite being burned three years out of four should be considered a preliminary estimate of the forest's resistance to fire. Repeated burns are likely cumulative over a time scale longer than my study. Thus, the long term effects of burning at this frequency are likely more severe than this study would suggest.

*The Ecology of closed canopy forests*

A picture of forest dynamics has emerged from my research in which forests establish and decline depending on disturbance regimes. During periods of infrequent fires, nurse species such as *Acacia polyacantha* and *Euclea divinorum* establish in dense patches in riparian areas. Nurse stands increased dry season soil moisture, reduced grass cover (and therefore fire) and support an understory of thorny bushes that exclude browsing antelopes (principally impala, *Aepyceros melampus*). Physical
characteristics of nurse stands also likely exclude elephants; *Acacia polyacantha* trees have large thorns on the bole. They also provide roosts for seed dispersing birds, which increases the seed rain in these areas. Forest tree seeds germinate and seedlings survive well in these stands, eventually replacing the nurse stand altogether by dense riparian forest with a few large nurse trees remaining in the canopy. Forests can then persist with infrequent fires and low impala numbers.

However, at a fire frequency of one burn every four years, seedling mortality at the forest edge increases such that canopy trees cannot be replaced and the forest edge will erode as canopy trees are removed by chance and new trees do not replace them. At higher fire frequencies of two burns in four years large tree mortality occurs in advancing edges and with burns every year tree mortality occurs in dense, dripline edges. The differential erosion rates of forest edges has led to bushy hilltop forests (Mara hilltops) declining faster than riparian forests, and riparian forests with open edge (Mara Riparian) declining faster than dripline-edge forests (Grumeti). Browsing antelopes exacerbate the decline of forests by reducing seedling growth rate to zero, such that forests cannot replace lost canopy trees.

The current pattern of Serengeti riparian forest distribution likely dates from an establishment pulse of *Acacia polyacantha* and *E. divinorum* in 1890. I infer this from the species composition of current stands and recent examples of nurse trees establishment. This pulse was indirectly caused by the cattle disease rinderpest, which decimated the surrounding pastoralist population and reduced fire frequency (Sandford 1919; Mallet 1923). A more recent pulse of *A. polyacantha* recruitment occurred along the Grumeti river during a period of infrequent fires in the 1970s. Trees that established during that period are now in turn facilitating the current establishment pulse, suggesting that riparian forests in these areas are the products of earlier establishment pulses. Similar establishment was not observed in the Mara riparian areas in the late 1970s possibly due to higher frequencies of fires there, or larger populations of browsing antelope.

**Future research**

The three main question in the ecology and management of riparian and hilltop forests are: (i) at what fire-return frequency are forests stable? (ii) how do *Croton* thickets establish into grasslands? and (iii) does fire control the establishment of nurse species? My study followed forests over a short period of four years and concluded that the existing canopy trees at the forest periphery showed no increase in mortality when
burned at one and three years out of four, depending on the forest type. Given that I do not know the history of fire at my study sites, these fire return rates may be overestimates of the resistance of forest edges to fire. Forests may not show an effect when burned three years out of four if they have not been burned before, but will likely decline if burned consistently at this rate. I found evidence that riparian forests likely establish via nurse trees in the grassland, but did not find any evidence of a similar nurse species for hilltop *Croton* thickets. *Croton dichogamus* trees may establish directly into the grassland, although no seedlings were found in areas where fire was excluded for four years, suggesting that a much longer interval between fires is required for *Croton* establishment. Finally, *Acacia* species established in a pulse across Serengeti during the late 1970s during a period of infrequent fires due to an increased wildebeest population which removed grass. Fires were also reduced during the late 1970s due to a redistribution of rainfall within years such that dry seasons had more rain, and grass did not dry as in other years. In addition to fire, dry season rainfall may be essential for *Acacia* establishment (Higgins *et al.* 2000), which implies that *Acacia polyacantha*, and other nurse species may not establish if fire is reduced by managers.

**General implications**

My research provides several new insights into the ecology of riparian and hilltop forests, and it underlines the pulsed nature of forest establishment. I comment on the importance of antelope, fires, grass competition, flooding, and elephants in forest dynamics. The process of natural nurse tree establishment and subsequent forest succession implies that forests are very dynamic. Previous research on natural forest fragment refugia and human-produced fragments has concluded that seedling establishment into grassland is effectively limited by grass competition, abiotic conditions and herbivory. Establishment must therefore be facilitated by humans in order for forests to expand (Otsamo 2000b). The influence of elephants has been overestimated in riparian forests, largely due to visible damage to large trees and high rates of browsing on *Acacia* woodland trees (Dublin 1986). The effect of elephants on riparian and hilltop forests in Serengeti is small, and attack rates by elephants can rise by six times or greater before they limit tree population growth rates. Flooding in riparian forests increases the germination rate by 10 – 12 times, which may lead to pulsed establishment of forest trees, and may effect forest dynamics downstream from dams where floods are less frequent. Finally, antelope have previously been implicated in limiting seedling growth rates of *Acacia* species, but I provide the first evidence that they
limit the growth and survival of broad-leaved species. This suggests that establishment of natural and managed forests are, and must be, timed to coincide with periods of low antelope numbers.

References


Appendix: Nurse species taxonomy and alternate names

*Acacia polyacantha* (Willd.) subsp. *campylacantha* (Hochst. Es. A. Rich.) Brenan
(Family: Fabaceae/Leguminosae, Subfamily: Mimosoideae)

*Acacia polyacantha* is a tall deciduous tree, from 20-25m tall, with a long, straight bowl. The bark is grey, peeling or flaking when young and appears yellow-grey and fissured when older. Some trees (as in Serengeti) have large (2cm), broad-based thorns on the trunk and branches. In addition, there are pairs of hooked barbs below each node of leaf-bearing branches. Flowers are white, and held in spikes 8-12cm long (Hutchinson *et al.* 1954; Dale *et al.* 1961; Coates Palgrave 1983).

Opinions vary on whether this tree is indigenous or introduced from India pre-European settlement. All African trees of this species are classed into subspecies *Acacia polyacantha* (Willd.) subsp. *campylacantha* (Hochst. Es. A. Rich.) Brenan. (Hutchinson *et al.* 1954). *Acacia polyacantha* subsp. *polyacantha* (the typical subspecies) is only found in India and possibly in Sri Lanka (Coates Palgrave 1983).

*Acacia polyacantha* is also known as *Acacia campylacantha* (Hochst.), *Acacia caffra* (Willd.) var. *campylacantha* (Hochst. Ex A. Rich). Other true synonyms are *Acacia suma* (Roxb.) J.Voigt, *Mimosa suma* Roxb., *Senegalia suma* (Roxb.) Britton & Rose (Dale *et al.* 1961). The species has been missapplied to *Acacia catechu* (Willd.) var. *campylacantha*, although the common name in North America for *Acacia polyacantha* is “the catechu” tree. It is also misapplied to *Gagnebina tamariscina* sensu Bojer (Dale *et al.* 1961). This tree is also known as Mkengewa in Tanzania and Kenya (Swahili) and “Falcon’s Claw Acacia” (Dale *et al.* 1961).

*Euclea divinorum* Hiern subsp. *keniensis* (R.E. Fries) de Wit
(Family: Ebenaceae)

Often a shrub or small tree, *E. divinorum* can reach 8-10m in height with grey, smooth or fissured (as in Serengeti) bark, single or multiple stems (as in Serengeti), and a thin canopy of sub-opposite or opposite 5 X 2cm leaves, with tapering base and tip and distinctly wavy edges. Leaves often have a reddish or cream-coloured (as in Serengeti) scales on the underside. Trees are dioecious, with males and females on the same tree. Flowers are cream coloured and organized on short racemes 1-2 inches long (Dale *et al.* 1961).

This species is also known as *Euclea keniensis* (R.E. Fries) and is very similar to *Euclea schimperi* (A.DC.)Dandy, with poor division between the species. Common names include “Magic guarri” and “Diamond-leaved Euclea” in S. Africa and Zimbabwe (Coates Palgrave 1983), and “Lolorien” in Masaii (G. Sharam Pers. Obs.).