DRIVERS OF TREE COMMUNITY COMPOSITION AND SEED DEMOGRAPHY IN
SERENGETI NATIONAL PARK - TANZANIA

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Master of Arts

by

DEUSDEDITH RUGEMALILA
Dr. Ricardo M. Holdo, Thesis Supervisor
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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

DRIVERS OF TREE COMMUNITY COMPOSITION AND SEED DEMOGRAPHY IN SERENGETI NATIONAL PARK - TANZANIA

Presented by Deusdedith Rugemalila,
a candidate for the degree of master of arts,
and hereby certify that, in their opinion, it is worthy of acceptance.

Professor Ricardo M. Holdo

Professor Raymond Semlitsch

Professor Grant P. Elliott
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LIST OF ABBREVIATIONS

BD  Basal Diameter
C   Carbon
C: N Carbon to Nitrogen ratio
DBH Diameter at Breast Height
DEM Digital Elevation Models
GIS Geographic Information Systems
GPS Geographical Positioning System
MAP Mean Annual Precipitation
MODIS Moderate Resolution Imaging Spectroradiometer
N   Nitrogen
NMDS Non-Metric Multidimensional Scaling
PCA Principle Component Analysis
SEM Structural Equation Modeling
SNP Serengeti National Park
STRM Shuttle Radar Topographical Mission
TANAPA Tanzania National Parks Authority
TAWIRI Tanzania Wildlife Research Institute
CHAPTER 1:
ECOLOGICAL DRIVERS OF TREE COMMUNITY COMPOSITION IN SERENGETI

1.1. INTRODUCTION

Savannas differ from grassland and forest ecosystems in that trees and grasses tend to be co-dominant vegetation components (Scholes and Walker 1993). Much of the research on savanna vegetation has tended to focus on the factors that allow trees and grasses to coexist (House et al. 2003, Sankaran et al. 2004, Bond 2008). Many savannas are also prone to high rates of disturbance (notably fire), and the ability of trees to survive or escape disturbance events is strongly size-dependent (Pellew 1983, Holdo 2005). There has therefore also been a significant amount of interest on tree population dynamics in relation to disturbance regimes (Baxter and Getz 2008, Holdo et al. 2009a, Wakeling et al. 2011). Less effort has been devoted to understanding the processes that drive tree community composition in these systems, despite the fact that savanna tree communities can be highly diverse and variable across space (Higgins et al. 2012, Scholtz et al. 2014).

An ongoing debate in the savanna literature concerns the relative importance of bottom-up drivers (water and nutrients) vs. top-down factors (fire and herbivory) for vegetation structure, e.g., the amount of tree cover and tree size distributions (Higgins et al. 2000, Sankaran et al. 2004, Bond et al. 2005, Lehmann et al. 2009). Of equal interest is to understand how these two groups of variables influence tree community composition. In a recent study, Scholtz et al. (2014) found that variation in the tree community across Kruger National Park was primarily related to edaphic and climatic factors rather than to disturbance (although the importance of top-down and bottom-up
factors varied across tree size classes). It remains unclear, however, to what extent this pattern can be generalized to other savanna systems.

Here I use tree species composition data collected across woodland habitats in the Serengeti ecosystem of East Africa to identify the key environmental factors driving variation in tree composition in savanna. This study spans widespread variation in mean annual precipitation, fire frequency, mega-herbivore population density and soil properties. Serengeti is an iconic savanna that has been the subject of extensive study because it is a relatively intact ecosystem, providing a wide degree of variation in abiotic and biotic drivers within a single study system, without introducing potentially confounding effects of heterogeneous land use or management history. I asked the following specific question: is savanna tree community composition primarily a function of bottom-up factors (e.g., resource availability and the factors that modify it, such as precipitation, soil nutrients and soil texture), or of the disturbance regime (fire and elephant herbivory)?

1.2. MATERIALS AND METHODS

1.2.1. STUDY SYSTEM AND DATA COLLECTION.

The study was conducted in Serengeti National Park (SNP hereafter, fig. 1), which is located in northern Tanzania. SNP lies within a broader ecosystem extending over ~30,000 km², between 1350 and 1800 m asl. Two dominant environmental features of the ecosystem are opposing gradients of mean annual precipitation (which varies between ~600 and 1000 mm/y, increasing from SE to NW, fig. 1a) and soil fertility (Sinclair 1979, Holdo et al. 2009b). About two thirds of SNP can be categorized as true savanna, with the remainder being an edaphic grassland on shallow volcanic soils. The present study
took place in the former, in sites conducive to tree establishment. Much of the savanna portion of the ecosystem is dominated by trees in the *Acacia* genus, with two dominant species, *Acacia tortilis* and *A. robusta*. Sub-dominant species include *A. drepanolobium*, *A. senegal*, *Commiphora trothae* and *Balanites aegyptica*. The system is subjected to frequent fire and a diverse herbivore community dominated by grazers such as wildebeest (*Connochaetes taurinus*) and zebra (*Equus burcheli*), as well browsers such as elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis*).

**Figure 1.1** (a) Mean annual precipitation, (b) fire frequency, (c) elephant population density, and (d) soil N values across 38 Serengeti NP (shown in outline) vegetation plots.

I used a system of 38 plots clustered within 10 randomly selected sites spanning the SNP mean annual precipitation (MAP) gradient. The plots are 20 x 50 m (0.1-ha) in size.
and were initially established in 2009 (Holdo et al. 2014, Anderson et al. 2015). Within every plot, each individual woody stem > 0.5 m in height was identified to species and measured for basal diameter (BD) and diameter at breast height (DBH) annually. The driest site in the network was only established in 2013, so to maximize the MAP range available for this analysis I conducted my analysis only on 2013 data. I used species-specific total basal area (based on basal diameter) for each plot as my raw variable for the community composition analysis. In addition to my field data, I collected two soil samples at opposing corners (along the long axis) of each plot to a depth of 20 cm with a soil auger. I weighed the soil after drying in an oven at 65°C for at least 48 hours at the Serengeti Wildlife Research Centre and calculated bulk density (BD) by dividing the volume collected by the dry mass. I obtained total N, total C, and soil texture (clay, silt and sand fractions) from the World Agroforestry Centre Soil-Plant Diagnostic laboratory in Nairobi, Kenya. C and N were determined by combustion while soil texture was determined via laser diffraction. To minimize the number of variables in my community-environment analysis, I reduced the set of soil variables by means of a principal component analysis conducted on the correlation matrix of four variables: BD, clay fraction (CLAY), total N (N) and C:N ratio (CN). I first verified that pairs of variables were approximately bivariate-normal distributed. I conducted the analysis with the prcomp function in R (R Development Core Team 2011). The first two components of the PCA accounted for 78.8 percent of the total variance in the dataset, with CLAY and N loading positively and CN and BD loading negatively on the first component (SOIL PC1), respectively (Table 1). The second component (SOIL PC2) identified a soil organic matter quality vs. bulk density tradeoff, with C: N and BD loading positively and
negatively on this axis, respectively (Table 1). I retained these two components in my subsequent analysis.

Table 1. Original variable loading on the first (SOIL1) and second (SOIL2) axes of a PCA conducted on four soil variables across 36 plots in Serengeti NP (variance explained by each axis shown in parentheses).

<table>
<thead>
<tr>
<th>Variable</th>
<th>SOIL1 (53%)</th>
<th>SOIL2 (26%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>0.57</td>
<td>0.00</td>
</tr>
<tr>
<td>Clay</td>
<td>0.61</td>
<td>0.02</td>
</tr>
<tr>
<td>BD</td>
<td>-0.29</td>
<td>-0.84</td>
</tr>
<tr>
<td>CN</td>
<td>-0.47</td>
<td>0.55</td>
</tr>
</tbody>
</table>

I used a number of GIS layers to extract additional environmental covariates for my plots using ArcMAP 10.2.1 (ESRI 2013). I used a digital elevation model (DEM) based on Shuttle Radar Topography Mission (STRM) data to produce a slope layer at 90-m resolution. I considered slope (variable SLOPE) as a potentially important modifier of MAP effects on soil moisture availability. I used a river layer from my GIS database for SNP to calculate the distance (DIST) to major rivers (rivers of class 1 or 2) for each of my plots. I used this metric as one of my potential herbivory indices, given the water-dependence of many of the major ungulate herbivores in the system (especially elephants). I obtained a mean annual precipitation (MAP) layer through interpolation of monthly rain gauge data for SNP for the period 1960-2006 (Anderson et al. 2015). I used a MODIS-based analysis of fire occurrence across SNP for the period 2000-06 (Dempewolf et al. 2007) to calculate fire frequency (FIRE) by dividing the number fires recorded by the number of years in the dataset. Finally, I used 2008 aerial census data
provided by Frankfurt Zoological Society to generate a map of elephant population
density for the park. The census data included GPS locations for all elephant herds
sighted in the park during the dry season. I used the elephant counts to calculate elephant
population densities (variable ELE) within circular neighborhoods with two radii (5 and
10 km) centered on each plot, but discarded the smallest of these because of the large
number of zero values generated.

1.3. DATA ANALYSIS

1.3.1. TREE COMMUNITY COMPOSITION

To characterize tree community composition across plots, I performed a Non-Metric
Multidimensional Scaling (NMDS) analysis on species-specific basal area (m² ha⁻¹) per
plot for all species with a basal diameter > 2 cm. To avoid excessive influence by rare
species, I only included those species that were present in three or more of the 38 plots (N
= 10 species). I used the metaMDS function in the R package vegan (Oksanen et al. 2013)
to perform for the NMDS analysis. Although basal diameter has been suggested to
overestimate tree size in savanna ecosystem due to frequent top-kill and other
disturbances (Holdo 2006), I considered this metric to represent a more realistic estimate
of species relative dominance or cover than e.g., density. I converted basal area values to
percent of total woody cover prior to the analysis. I tested two-axis and three-axis models
and assessed overall fit with the stress statistic. I then used the plot scores on the NMDS
axes as dependent variables in my subsequent analysis.

I developed a set of 13 a priori candidate models relating community composition
based on the NMDS analysis to different combinations of my plot-level environmental
covariates (Table 2). I largely restricted my analysis to main effects, except for a MAP x
SLOPE interaction, which I included under the assumption that slope effects are most likely to be manifested via their modulation of soil moisture availability (Table 2). I used linear mixed models implemented with the *lme* function in the *nlme* package (Pinheiro and Bates 2000) in R. I treated my environmental variables as fixed effects and SITE as a random effect, given the spatial clustering of plots within sites (fig. 1). I compared model fits with the Akaike Information Criterion corrected for small sample size (AICc) independently for MDS1 and MDS2.

1.3.2. Structural Equation Modeling

To explore the causal determinates of tree community composition, such as whether tree species composition drives elephant population density patterns or *vice versa*, I conducted an additional analysis using structural equation modeling (SEM), a technique with its roots in path analysis, in which several potential causal networks are evaluated for goodness of fit between the model and the observed data. As a pre-requisite for this analysis, I needed to identify potentially independent drivers of elephant population density across the system. Because my elephant density estimates were based on 10-km circular kernels centered on my plots, I required variables that were relevant at that scale. I focused on two types of metrics: distance from water sources (the existing variable DIST) and topographic measures. The former is based on the known water-dependence of elephants and the role of permanent water sources on elephant habitat use. For the latter I calculated two metrics: topographical roughness (TOPO), equal to the standard deviation of elevation within the elephant density kernel, and mean slope (MSLOPE) within the kernel.
I conducted the SEM in R using the package ‘piecewise SEM’, which combines multiple complex linear regressions (i.e., hierarchical linear regression estimated with \textit{lme}) into a single model structure, allowing for evaluation of model fit for the entire causal network. I fit two alternative models, both composed of two linear mixed effects models: (i) one with elephant kernel density (ELE) as a response, TOPO and MSLOPE as fixed effects and SITE as a random effect and (ii) one with tree community composition (MDS) as a response, MAP as a fixed effect and SITE as a random effect. Due to the spatial autocorrelation of elephant densities among adjacent sites, I included a correlation structure of the form ‘\texttt{corr=corSpher(form=~X+Y)}’ in the \textit{lme} estimating elephant density. The models differed with respect to the directionality of the path between elephants and tree community composition. In the first model, I included ELE as a fixed effect in the \textit{lme} predicting MDS; in the second model I included MSD in the \textit{lme} predicting ELE. Evaluation of model fit in a piecewise SEM is done via a two-stage process: first, a test of directional separation (d-sep) identifies whether any paths are missing from the model (Shipley 2009); an associated test statistic, Fisher’s C statistic, is produced in which smaller statistics and larger \textit{P}-values indicate better model fit. Subsequently, the best final model is selected using AICc for small sample sizes, in which the likelihood term is estimated for the entire SE model, and lower AICc values represent superior models.
1.4. RESULTS

1.4.1. Tree Community Composition

The NMDS analysis yielded an acceptable stress value (0.09) with two axes, so I restricted my analysis to a two-dimensional model. A visual examination of environmental variable associations with the NMDS axes suggested positive relationship between MDS 1 and MAP and elephant population density (ELE) and a potentially negative relationship between MDS1 and SOIL PC1 (fig. 1.2). This tracks the well-known inverse relationship between precipitation and soil fertility in Serengeti (Ruess and Seagle 1994, Holdo et al. 2009b). The two dominant tree species in the community segregated clearly along these axes: *Acacia tortilis* is associated with dry, fertile sites, and *A. robusta* with wetter environments (Fig. 1.2).

**Figure 1.2.** (a) Plot and species scores on axes 1 and 2 of the tree community NMDS analysis, with a subset of environmental variables shown as vectors (correlations with NMDS axes across plots, shown × 3 for legibility). Labels identify species (Key: Aceg = *Acacia gerrardi*, Acro = *A. robusta*, Acsi = *A. sieberiana*, Acse = *A. senegal*, Acto = *A. tortilis*, Baae = *Balanites aegyptica*, Coaf = *Commiphora africana*, Dici = *Dichrostachys cinerea*, Ortr = *Ormocarpum trothae*). (b) Tree community axis 1 (MDS1) as a function of mean annual precipitation (MAP) across 38 Serengeti NP vegetation plots.
My model selection exercise supported clear relationships between the first community axis (MDS1) and MAP and ELE (Table 1). None of the other covariates, including fire frequency (FIRE) and soil variables, improved model fit (Table 1). None of the candidate models improved over the null (intercept) model in the analysis of MDS2, suggesting that most of the community variation of interested was captured by MDS1.

My results suggested that the primary drivers of variation in tree community composition across Serengeti are soil moisture, as related to mean annual rainfall, and possibly elephant herbivory. The fact that adding elephant density to a MAP-only model improved model fit suggests an association between tree community composition and elephant density, but does not resolve the direction of causality in the relationship.
Table 2. Model fits (AICc, the Akaike Information criterion corrected for small sample sizes) for tree community structure (axis 1 of an NMDS analysis) to alternative combinations of environmental covariates.

<table>
<thead>
<tr>
<th>Model†</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTERCEPT</td>
<td>3</td>
<td>95.9</td>
<td>19.0</td>
</tr>
<tr>
<td>MAP</td>
<td>4</td>
<td>79.4</td>
<td>2.4</td>
</tr>
<tr>
<td>MAP + SLOPE</td>
<td>5</td>
<td>81.8</td>
<td>4.9</td>
</tr>
<tr>
<td>MAP + SOIL PC1</td>
<td>5</td>
<td>80.6</td>
<td>3.6</td>
</tr>
<tr>
<td>MAP + FIRE</td>
<td>5</td>
<td>80.3</td>
<td>3.3</td>
</tr>
<tr>
<td>MAP + ELE</td>
<td>5</td>
<td>77.0</td>
<td>0.0</td>
</tr>
<tr>
<td>MAP + ELE + SOIL PC1</td>
<td>6</td>
<td>79.3</td>
<td>2.3</td>
</tr>
<tr>
<td>MAP + ELE + SOIL PC1 + SOIL PC2</td>
<td>7</td>
<td>79.1</td>
<td>2.1</td>
</tr>
<tr>
<td>SLOPE + MAP + FIRE</td>
<td>6</td>
<td>82.5</td>
<td>5.6</td>
</tr>
<tr>
<td>SLOPE × MAP</td>
<td>6</td>
<td>84.7</td>
<td>7.7</td>
</tr>
<tr>
<td>MAP + DIST + ELE</td>
<td>6</td>
<td>78.3</td>
<td>1.3</td>
</tr>
<tr>
<td>MAP + DIST + ELE + SOIL PC1</td>
<td>7</td>
<td>81.3</td>
<td>4.3</td>
</tr>
<tr>
<td>MAP + DIST</td>
<td>5</td>
<td>81.3</td>
<td>4.4</td>
</tr>
<tr>
<td>MAP + DIST + FIRE + ELE</td>
<td>7</td>
<td>80.8</td>
<td>3.8</td>
</tr>
</tbody>
</table>

†See text for variable descriptions; in all cases SITE was treated as a random effect

1.4.2. Structural Equation Modeling results.

Because regression analysis could not resolve the direction of causality between ELE and MDS1, one of the primary goals of the SEM analysis was to discriminate between the two possible causal models, one in which ELE affects MDS1 and the other in which MDS1 affects ELE. Soil variables (PC1) and FIRE proved to be insignificant predictors.
of MDS or ELE so they were removed from subsequent SE modelling procedures. Of the two candidate SE models (Fig. 1.3) the model in which ELE predicted MDS1 had a superior model fit (Fisher’s C = 0.98, \( P = 0.61 \); AICc = 29.13) compared to the alternative version in which MDS predicted ELE (Fisher’s C = 5.37, \( P = 0.25 \); AICc = 33.52). Here the better fitting model is associated with a lower Fisher’s C and AICc and larger P-value (less difference between observed and expected model).

In addition, after accounting for the rest of the model interactions, the individual causal path from MDS1 to ELE had very little support (\( P = 0.52 \); fig 1.3B) compared to the causal path from MDS1 to ELE (\( P = 0.08 \); fig. 1.3A). In the final accepted model (fig. 1.3A) MSLOPE was a significant predictor of ELE (\( R^2 = 0.39 \), path coefficient = 0.37), while MAP (0.62) and ELE (0.23) had positive effects on MDS1 (\( R^2 = 0.59 \)). Thus, in terms of drivers of dominant species, \textit{A. tortilis} and \textit{Balanites aegyptiaca} were negatively associated with MAP and ELE, while species such as \textit{A. gerardii}, \textit{A. sieberiana}, \textit{A. senegal} and \textit{A. robusta} were positively associated with MAP and ELE.
1.5 DISCUSSION AND CONCLUSION

These results suggest that tree community composition in Serengeti is largely driven by resource availability (mainly as represented by rainfall), and to a lesser extent by elephant herbivory. Strikingly, although fire has been shown to play an important role regulating vegetation structure in the Serengeti over the past few decades (Dublin 1995, Holdo et al. 2009d), these results suggest that it plays a negligible role in terms of regulating tree community composition. In general, these results support the pattern encountered in Kruger National Park by Scholtz et al. (2014), i.e., tree community composition is largely a function of bottom-up drivers.
Fire regulates woody structure by constraining tree recruitment from seedling to adult stages (Peterson and Reich 2001, Smit et al. 2010) and by causing topkill (Pellew 1983, Higgins et al. 2000). I contrast my findings with those of Staver et al. (2012), who found a tradeoff between the ability to survive herbivore and the ability to survive fire in South African acacias, a tradeoff that was associated with acacia species turnover along negatively correlated fire frequency and elephant population density gradients. Given the long history of fire (Sinclair et al. 2007) and fire effects on vegetation structure in Serengeti (Pellew 1983, Holdo et al. 2009d), one interpretation for the lack of a fire signal in my study may be that fire-susceptible species may have largely been filtered out of the savanna portions of this system (and are currently confined to riverine forests) and those that remain exhibit similar tolerances to this form of disturbance.

Prolonged herbivory has also long been an evolutionary force in African savannas, and some tree species are uniquely adapted to withstand browsing (e.g., Staver et al. 2012). Elephants, however, the largest and most destructive of the megaherbivores (Laws 1970), have occurred at relatively low densities over ecologically relevant time scales in Serengeti (Sinclair 1995), and may only recently have become strong filters in this system. The most recent herbivore census results from Serengeti (Mduma et al. 2014) suggest that elephant numbers have increased dramatically over the past few years (a process that is likely to be arrested and/or reversed by the current wave of elephant poaching). In conjunction with strong selective feeding by elephants in this system (Morrison et al., in review), this can lead to changes in tree community composition over time, particularly in the larger size classes favored by elephants as food sources. I propose that soil moisture availability acts primarily by influencing the assembly process
(i.e., it is a filter on recruitment) while elephants are primarily agents of mortality: their recent population increases in Serengeti mean that they have only recently become a pervasive factor, and their role is primarily one of selective removal rather than recruitment limitation (Morrison et al., in review).

Including soil as a covariate in my models did not improve fit over simpler models. This is consistent with studies of herbaceous vegetation in Serengeti, in which factors such as rainfall and herbivory are the primary drivers of vegetation turnover (Anderson et al. 2007, Anderson 2008). Another (global meta-analysis) study on 236 sites of different types of vegetation spanning from deserts, grasslands to forests found no relationship between change in species composition and soil nutrients (Milchunas and Lauenroth 1993). Therefore my findings are consistent with other previously reported trends on the key role of soils.

The SE model results suggest that elephant density may directly cause changes in tree community composition, rather than the other way around. These effects are likely the result of selectivity by elephants or the differential survival of tree that are damaged by elephants. For example in South Africa’s Kruger National Park, Shannon et al. (2008) found active elephant selectivity for Sclerocarya birrea compared to other species. Likewise, another study in Serengeti showed that Acacia robusta seem to have higher tolerance to elephant damage than other species such as Acacia senegal (Morrison et al. In Review). I expect that variation in tolerance to elephant damage among species may be linked to other traits through tradeoffs, such as between fecundity and recruitment rates, thus stabilizing species coexistence across the ecosystem, as has been demonstrated elsewhere (Staver et al. 2012).
In addition, my model suggests that topographic heterogeneity may have an indirect effect on tree community composition by modulating elephant habitat selection. In previous studies of Serengeti vegetation both rainfall and topography were identified as significant contributors to the spatial distribution of woodland patches across the environmental gradient (Anderson et al. 2007, Reed et al. 2009). In their study Reed et al (2009) suggested a unimodal relationship with woodland patch area and MAP, while TOPO has a negative relationship with woodland patch area. Ostensibly, these effects are linked to the way TOPO modifies soil moisture, although their study made no attempt to analyze species composition and no metrics of elephant damage or habitat preference were included. The results of my study suggest that TOPO may also influence composition by mediating the density and distribution of herbivores.

Generally, my findings show that woody species composition varies across the key Serengeti environmental gradient and that rainfall and elephant density are the most likely drivers of this variation. Further, topography may provide further predictive information by modifying how elephants select habitat. Consequently, the aftermath of the latter is impacting the way elephants disperse (De Beer et al. 2006). Fire plays an important role in shaping woody cover, but its role seems not to be significant in influencing species composition. Here I recommend that in addition to understanding the “savanna problem” (Sarmiento 1984), focus should also be directed towards understanding vegetation turn-over as a function of environmental factors.
CHAPTER 2:

SEED PRODUCTION, DISPERSAL, VIABILITY, INFESTATION AND
PREDATION IN SERENGETI NATIONAL PARK

2.1. INTRODUCTION

The Chapter 1 results suggest that mean annual precipitation (MAP) plays a major role in determining species composition turnover in Serengeti; I observed a clear transition from *Acacia tortilis-* (hereafter referred as *A. tortilis*) to *Acacia robusta-* (hereafter *A. robusta*) dominated savanna from the dry to the mesic end of the MAP gradient. In this chapter I assessed whether these patterns can be partly attributed to demographic processes occurring at the seed stage. In other words: is the replacement of *A. tortilis* by *A. robusta* with increasing precipitation explained by pre-germination mechanisms? If so, studies conducted at the seed stage should be prioritized for understanding savanna composition.

Most empirical studies examining the drivers of savanna vegetation structure tend to focus almost exclusively on recruitment and survival processes at the post-germination stages (Goheen et al. 2004, Sankaran et al. 2004, February et al. 2013), while far less emphasis has been placed on the seed stage.

Tree recruitment, defined as the entry of new individual trees into a community (Ribbens et al. 1994), occurs in a series of stages (Fig. 2.1), from production of seeds to germination, seedling establishment and finally sapling growth to maturity (Harcombe 1987, Midgley and Bond 2001). Each recruitment stage in a tree’s life cycle is susceptible to demographic bottlenecks (Nathan and Muller-Landau 2000). While some of the mechanisms determining seed production and viability in savannas are quite well studied (Witkowski and Garner 2000, Walters and Milton 2003), the role of rainfall and other
processes in limiting or encouraging species turnover is less understood as few studies have looked at the seed stage across rainfall or disturbance gradients. For instance, in many African acacias, seed germination is greatly impacted by bruchid beetle (*Bruchidius spadiceus*) infestation, with infestation rates as high as 80% reported in some studies (Okello and Young 2000). However, the extent to which infestation is related to moisture or other environmental gradients, or whether it influences species turnover, is still unclear.

Seed limitation at any given site occurs when the addition of viable seed above ambient levels leads to enhanced seedling recruitment (Eriksson and Ehrlén 1992, Nathan and Muller-Landau 2000). It has the potential to affect species distribution at local and regional scales (Münzbergová and Herben 2005). The trajectory of seeds from adult tree to seedling (fig. 2.1) is subject to bottlenecks that can, in aggregate, lead to seed limitation and reduced recruitment. These bottlenecks include (1) low seed production and pre-dispersal predation (Greene and Johnson 1994, Ashman et al. 2004); (2) infestation by beetle larvae or other parasites (Lamprey et al. 1974, Miller 1996, Rodríguez-Pérez et al. 2011), leading to reduced viability and germination rates; (3) dispersal limitation (Nathan and Muller-Landau 2000, Salazar et al. 2011) and (4) post-dispersal predation by baboons, velvet monkeys (Barnes 2001), rodents (Goheen et al. 2004), birds (Linzey and Washok 2000) and/or invertebrates (Hulme 1998, Shaw et al. 2002). In general, seed limitation has been well studied in a number of biomes (Luo et al. 2013), but its role in tree recruitment has received relatively little attention in the savanna literature (Midgley and Bond 2001, Svenning and Wright 2005).
Figure 2.1. Simplified tree life history showing stages of tree recruitment, with added emphasis on processes that affect seeds.

The primary objective of this study was to examine whether the replacement of *A. tortilis* with *A. robusta* along a MAP gradient in Serengeti, as observed in the previous study (Chapter 1), is associated with constraints operating at the seed stage. I quantified seed production, infestation, germination and primary dispersal in these two species at 10 sites spanning MAP gradient ranging between 600 and 900 mm y\(^{-1}\) in the Serengeti ecosystem. I hypothesized that *A. robusta* and *A. tortilis* would show contrasting responses to MAP, with production, infestation, and germination rates showing negative, positive, and negative relationships with MAP in *A. tortilis*, respectively, and the opposite relationships with *A. robusta*. A second objective of the study was to generate parameter estimates (e.g., seed production as a function of tree size, rates of seed predation) for insertion into a general model of Serengeti tree demography, currently under development. The model will ultimately put this work into a broader context by explicitly reciting the strength of seed limitation.
2.2. MATERIALS AND METHODS

2.2.1. STUDY SYSTEM AND SPECIES

The study was conducted in Serengeti National Park (hereafter Serengeti) in northern Tanzania – East Africa (fig 2.2). Serengeti has a total area of 14,760 km² and is part of a larger 30,000 km² ecosystem. Serengeti lies between 1–2° S, 34–26° E and is buffered by protected areas and game reserves in both Tanzania and Kenya. Mean annual precipitation (MAP) ranges between ≥500 mm.yr⁻¹ in the SE to ~1100 mm.yr⁻¹ in the NW near Lake Victoria. Woody vegetation in Serengeti is dominated by *Acacia robusta*, *Acacia tortilis* and other species (Anderson et al. 2015). More details about Serengeti vegetation and rainfall can be found elsewhere (Dempewolf et al. 2007, Anderson et al. 2015).

The two species that are the focus of this study were identified as target species by a broader investigation of tree cover dynamics in Serengeti (Holdo et al. 2014, Anderson et al. 2015).

*A. tortilis*, also known as umbrella acacia, is a small to large-sized evergreen tree with a spreading umbrella-shaped canopy. It produces pods that are variable in size and indehiscent (ICRAF 2010). In Serengeti, *A. tortilis* seed production peaks between October and December (Loth et al. 2005). This species has a broad geographic range, being widespread in Serengeti and occurring in many other African savanna systems (Diouf and Grouzis 1996).

*A. robusta* is a single-stemmed, fairly high-branching tree. The higher branches are almost upright, but the lower ones are more horizontal, forming a semi-circular canopy. The larger branches are clearly visible in the canopy, giving the tree a robust appearance.
The tree has dark brown pods rounded at the tip. They are dehiscent, bursting open on the tree when ripe (Gordon-Gray 1965, Mduma et al. 2007), and may be seen on the tree for long periods. These two species were originally targeted because, *a priori*, they appeared to fall into two categories in terms of their population dynamics, with *A. tortilis* appearing to be in decline, and *A. robusta*, to be increasing (Anderson et al. 2015). In Chapter 1, it was shown that the two species also fall at two extremes of the Serengeti MAP gradient.

2.2.2. **DATA COLLECTION**

*Collection sites*

This study took advantage of a network of the pre-existing permanent plots established along the MAP gradient across the Serengeti ecosystem (Holdo et al. 2014). There are 10 sites (variable SITE in my analysis) with four 20 × 50 m plots (variable PLOT) per site (except the Ngorongoro Conservation Authority [NCA] site, which has two plots, giving a total of 38 plots) distributed across the Serengeti landscape (Appendix 1). The sites were originally selected to span the rainfall gradient and to represent the major woodland savanna habitat dominated by *A. tortilis* and *A. robusta* throughout the ecosystem (Holdo et al. 2014). Half of the plots have been protected from fire, while the remaining half subjected to annual burn treatments although this study utilized the 19 plots (2 plots in each of nine sites plus one NCA plot) that are protected from fire. Each plot was visited at least once a month for data collection on phenology (flowering and pod production) between January 2013 and July 2014 (19 months). On each visit, every individual tree > 2 m in height was scored as having pods or not. Trees that had any pod production during the survey period were scored with a value of 1 and with a value of 0 otherwise. I used
annual tree survey data conducted at each plot to obtain height and basal diameter data for each tree.

In general, seed production is patchy, and the timing of pod production varies across the system, and A. robusta and A. tortilis in Serengeti have different flowering and fruiting regimes (Lamprey et al. 1974, Mduma et al. 2007). Therefore, to conduct assessments of infestation and germination potential across sites, fruiting trees located beyond the plot boundaries were required. To secure a suitable sample of trees during periods of field collection, I identified sets of five mature trees per species per site for pod and seed collection during two separate periods between February 2013 and August 2014. Trees were tagged and mapped with GPS, and height and basal diameter were measured. Pods were collected by shaking and/or by hitting branches with a light PVC pipe onto a tarpaulin placed on the ground. Pods were sun-dried for about 3-5 days before manual seed removal at the Serengeti Wildlife Research Center. After sun-drying and cleaning for debris and litter, a subset of seeds was taken for sorting. Seeds were sorted into infested and non-infested pools to obtain an infestation proportion per tree. Seeds were classified as infested when they had entry or exit holes made by bruchid beetles on their seed coat. The sorted seeds were stored at room temperature for 2 to 4 weeks and then checked again for any new infestation not detected at the first sorting. Seeds were also weighed in batches to obtain mean seed mass per tree.

**Seed rain**

To quantify primary (i.e., non-animal) seed dispersal I quantified seed rain using seed traps (Salazar et al. 2011) deployed inside the fire-protected study plots. My initial goal was to quantify both primary and secondary (animal-induced) dispersal, but I omitted
animal dispersal from the current study due to logistical and time constraints. To quantify seed rain, 10 seed traps were buried within each of the 20 x 50 m plots. The traps were made with 5-gallon buckets (with a cross-sectional area of 0.69m$^2$) arranged in two parallel lines spaced at 5-m intervals along the 50-m axis of the plot. A total of 160 traps were deployed at all sites except for NCA which had no traps due to logistic difficulties. To protect the falling seeds from possible predation and seed removal, the traps were covered by a thick wire mesh. The traps were checked at least once a month, and during each visit all seeds and pods were identified, counted, and removed. The ratio of trap area to plot area were used to estimate seed rain in seeds plot$^{-1}$ y$^{-1}$ for each of the two species.

**Seed viability**

I conducted two separate studies to assess germination rates. To investigate how germination potential varies as a function of site conditions, laboratory germination trials were conducted. Separately, actual germination rates were quantified on planted seeds at the permanent plots (see below). For the laboratory germination trials, trays were used to plant both infested and non-infested seeds. The objective was to quantify germination potential as a function of species, infestation status and site long term rainfall (MAP). For each species, a known number (usually 100, fewer if sample sizes were insufficient) of infested and non-infested seeds were randomly selected for each site. The non-infested seeds were scarified slightly by cutting the seed-coat using a razor blade or gently scratching on sand paper to enhance overall germination. It must be noted that although germination rates following scarification may not capture those expected under field conditions, natural germination rates are known to be low and would provide low power for making inferences (Danthu et al. 1992, Mucunguzi and Oryem-Origa 1996, Danthu et
Infested seeds were not scarified as the bruchid exit holes allow water uptake by the seed (Lamprey et al. 1974). Seeds were planted into plastic germination trays filled with soil from the field.

Figure 2.2. Map of Serengeti National Park showing permanent plots, *A. robusta* and *A. tortilis* trees locations. The map also shows Mean Annual Precipitation isohyets and identifies game reserves buffering the park.
To improve soil porosity, sand was added in a well-mixed 50:50 ratio with soil. Each seed was covered with soil about one seed length deep and watered daily. The experiment was monitored every day for 35 days, and seed emergence date and number were recorded.

**Germination experiment**

To quantify seed germination under natural conditions, seed emergence was tracked within 1-m² sub-plots distributed across the 19 plots used for the phenology data. Unlike the laboratory germination trials, the experiment was designed to quantify germination rates under natural environmental conditions (soil moisture, temperature and predation rates). Within each plot, eight 1-m² subplots were randomly located in open areas (*i.e.*, not under tree canopies) and marked with rebar poles. The plots were randomly assigned to have a caged (Cage +) or uncaged (Cage -) treatment (Fig 2.3), resulting in four replicates of each treatment per plot. The cages consisted of four pieces of rebar held together with wire in a pyramid and secured to the ground with U-shaped rebar fasteners (Fig. 2.3). Chicken wire was wrapped around the pyramid to avoid disturbance from large animals and fine-grained wire mesh was wrapped around the lower ~15 cm of the pyramid, extending ~20 cm beyond the exclosure boundary to deter digging. Over the course of the experiment (until October 2014), evidence of small mammals entering the cages was detected on only a few occasions (<5), suggesting that the cages were effective. Within each subplot, eight *A. robusta* and eight *A. tortilis* seeds were planted in an alternating grid pattern prior to the long rainy season (February and March) in 2014. Each seed species and planting location were tracked so that subplots could be revisited
to assess germination status. Therefore, at each plot there were 4 seed predator exclusion and 4 seed predator inclusion treatment subplots. Seed germination was monitored in each subplot every 1-2 months following planting, until the end of the experiment in October 2014. During each visit, volumetric water content (VWC) values were obtained at the center of each plot using a Campbell Scientific (Logan, UT) HS2 portable soil moisture meter.

**Figure 2.3** Design for seed transplantation experiment. The dark squares represent herbivore exclusion (Cage +) subplots and open squares represent control (Cage -) subplots.

2.2.3. **Data Analysis**

Most of the analyses included regressions testing seed variable responses to MAP. A MAP layer containing interpolated rain gauge data for Serengeti for the period of 1960 –
2006 was used in all analyses (Anderson et al. 2015). MAP values were extracted for every individual tree and plot location using ArcMAP 10.2.2 (ESRI, Redlands, CA). The general approach to the analysis was the use of generalized linear mixed models (GLMMs) using the \texttt{glmer} function from the R package (Burnham and Anderson 2002, Bates et al. 2007). In several analyses, year of collection was included as a covariate. Normally this variable would be treated as random effect, but it was treated as a fixed effect to simplify the analysis, given that N = 2 for this variable and that many of the models already estimated two random effects. All analyses were conducted in R.

For the phenology analysis, I first computed site-level proportions of pod production and plotted production as a function of MAP. The clear lack of a relationship between production and MAP led us to omit this variable from further analysis. I developed a set of five candidate models containing combinations of tree height, basal area and species as fixed effects, and used the \texttt{glmer} function with a binomial distribution to fit the models. For the infestation analysis, I used a set of seven candidate models, including an intercept (null) model plus six others combining effects of MAP, species and year (plus some interactions of interest). I initially used a GLMM approach (with binomial error), but the results suggested serious overdispersion, indicating that infestation counts at the tree level were not binomially distributed. Rather than include a third random effect for the individual tree level, I opted for a simpler linear mixed model approach. A logit transformation was applied to the proportion data (Warton and Hui 2011) and the model selection exercise was conducted with the \texttt{lme} function in the \texttt{nlme} package in R (Pinheiro et al. 2011) using SITE as a random effect.
For the laboratory seed germination trials, the cumulative numbers of germinated \((N_c)\) and ungerminated \((N_{initial} - N_c)\) seeds at the end of the 35-day trial period were used as the response variables in a binomial regression. The data were first categorized by site, species, year and infestation status (infested or not). An R script was used to generate plots of daily cumulative proportion of seeds germinated. The plots suggested non-saturation for a subset of the curves (particularly in 2013). To test whether non-saturation might affect the analysis results, a second dataset was generated using the asymptote of a Michaelis-Menten function as the estimated maximum germination proportion. This proportion was back-transformed into the asymptotic cumulative number of germinated seeds \((N_{asym})\), to be used with \((N_{initial} - N_{asym})\) as the binomial response variables in a second analysis. Seven candidate models were compared in each case, separately for each year, in four separate analyses. The candidate models included an intercept model plus six explanatory models that included main effects of MAP, species and/or infestation status plus some targeted interaction effects, and were fitted using `glmer` with a binomial error. To better understand the mechanistic basis of any variation in germination potential, I tested for a relationship between seed mass and MAP. I tested for effects of MAP, year of collection and species on seed mass using five candidate models fitted with linear mixed-effects models implemented with the `lme` function.

The seed rain study was initially intended to develop seed production and dispersal kernels for *A. tortilis* and *A. robusta* using an inverse modeling framework (Ribbens et al. 1994), but the limited amount of seed accumulated over the duration of the study precluded this option. Seeds were consolidated by plot and species, and used to estimate mean annual seed rain at the plot level. The site-level means of this metric are reported. A
visual examination of seed rain as a function of site-level MAP suggested no relationship between rainfall and seed production probability.

For the field germination experiment, a GLMM with a binomial distribution was used to test for effects of caging, species, and MAP on the cumulative number of seeds germinated by the end of the study (~ 10 months after planting). A separate analysis was conducted with mean subplot VWC as a covariate instead of MAP. This allowed testing of both current soil moisture effects as well as long-term climatic effects on germination rates across the system. For these analyses, subplot was observation unit and PLOT and SITE were random effects.

2.3. Results

2.3.1. Seed Production

Over the two-year period of the study, 585 individual trees (260 of the two focal species) were visited between 5 and 10 times for the determination of pod production. There was clearly no relationship between pod production proportion and MAP for either species (Fig. 2.4). Model selection results showed that a model containing species and height effects provided the best fit to the data. The species effect alone did not improve model fit over a null model (ΔAIC < 2), but the addition of height (a positive effect) improved fit over the species-only model (Table 2.1).
Figure 2.4. Pod production in a) *A. robusta* (acarob) and b) *A. tortilis* (acator) as a function of MAP.

### 2.3.2. INFESTATION

Bivariate scatterplots suggested that infestation rates differed between species within years, with *A. tortilis* seeds showing high infestation rates in 2013 relative to *A. robusta*, but with the pattern reversing in 2014 (Fig 2.5). Model selection results suggested that only species and collection year (and their interaction) explained differences in infestation among sites. The model with species effects only did not improve over the intercept model (Table 2.1), but the species × year model did, suggesting that variation in infestation among species is not consistent. MAP did not improve model fit either alone or in combination with any of the other covariates (Table 2.1).
Figure 2.5. Infestation proportions for *A. robusta* (acarob) and *A. tortilis* (acator) in **a)** 2013 and **b)** 2014.

Table 2.1. Model fits (AIC, the Akaike Information criterion) for the effect of MAP, species, year and their interaction on infestation proportion using generalized linear mixed-effects models

<table>
<thead>
<tr>
<th>Model fixed effects</th>
<th>df</th>
<th>AIC</th>
<th>ΔAIC†</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTERCEPT</td>
<td>3</td>
<td>435.1</td>
<td>95.4</td>
</tr>
<tr>
<td>MAP</td>
<td>4</td>
<td>448.0</td>
<td>108.3</td>
</tr>
<tr>
<td>MAP + SPECIES</td>
<td>5</td>
<td>450.8</td>
<td>111.1</td>
</tr>
<tr>
<td>MAP + SPECIES + YEAR</td>
<td>6</td>
<td>381.8</td>
<td>42.1</td>
</tr>
<tr>
<td>MAP × SPECIES</td>
<td>6</td>
<td>458.8</td>
<td>119.1</td>
</tr>
<tr>
<td>SPECIES × YEAR</td>
<td>6</td>
<td><strong>339.7</strong></td>
<td><strong>0.0</strong></td>
</tr>
<tr>
<td>MAP + SPECIES + YEAR + MAP × SPECIES + YEAR × SPECIES</td>
<td>8</td>
<td>362.3</td>
<td>22.6</td>
</tr>
</tbody>
</table>

† Lowest ΔAIC is the AIC value of the best model
2.3.4. **Seed viability**

Under laboratory conditions, as expected, non-infested seed for both species showed higher germination compared to infested seeds. *A. tortilis* seeds had a maximum germination proportion of about 70% while *A. robusta* seldom exceeded 25%, suggesting that, *A. tortilis* has a higher germination potential than *A. robusta* (Appendix 2). Against expectations, infestation did not completely inhibit germination. The model selection exercise revealed two things; first, the rate of germination was affected mainly by the interaction between infestation rate and species differences for 2013, and second, germination rates in *A. robusta* were positively related to MAP at collection site (Fig 2.6). In 2013, model selection results suggested that only species and infestation status explained differences in germination among sites. The model with species effects only did not improve over the intercept model (Table 2.2), but the interaction (species × infestation status) model did, suggesting that variation in germination among species is not determined by species. MAP did not improve model fit either alone or in combination with any of the other covariates (Table 2.2), suggesting that long term site condition is not a factor for germination difference. In 2014, model selection results suggest that the interaction between MAP, species and infestation status explain the difference in germination rates. Again, the model containing species or MAP only did not improve over intercept model, suggesting that these covariates are independently explaining differences in germination rates.
Table 2.2. Model fits for the effect of MAP, species, infestation and their interaction on seed viability using generalized linear mixed-effects models

<table>
<thead>
<tr>
<th>Fixed effects model</th>
<th>2013</th>
<th>2014</th>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>AIC</td>
<td>Δ AIC</td>
<td>df</td>
<td>AIC</td>
<td>Δ AIC†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>INTERCEPT</td>
<td>2</td>
<td>1011.5</td>
<td>771.4</td>
<td>2</td>
<td>509.1</td>
<td>392.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAP</td>
<td>3</td>
<td>1011.6</td>
<td>771.4</td>
<td>3</td>
<td>511.0</td>
<td>394.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SPECIES</td>
<td>3</td>
<td>732.7</td>
<td>492.6</td>
<td>3</td>
<td>477.0</td>
<td>360.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SPECIES + INFESTED</td>
<td>4</td>
<td>290.4</td>
<td>50.2</td>
<td>4</td>
<td>143.1</td>
<td>26.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAP + SPECIES + INFESTED</td>
<td>5</td>
<td>292.0</td>
<td>51.8</td>
<td>5</td>
<td>143.1</td>
<td>26.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAP * SPECIES + INFESTED</td>
<td>6</td>
<td>290.3</td>
<td>50.1</td>
<td>6</td>
<td><strong>116.6</strong></td>
<td><strong>0</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SPECIES * INFESTED</td>
<td>5</td>
<td><strong>240.1</strong></td>
<td><strong>0</strong></td>
<td>5</td>
<td>140.3</td>
<td>23.7</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

† Lowest ΔAIC is the AIC value of the best model

The model fits results for the germination proportion as a function of rainfall for both species showed that in both years infested seeds had lower germination rates compared to non-infested rates. Also germination rates showed no relationship with long term rainfall except for 2014 where *A. robusta* was positively related with MAP at collection sites, suggesting inconsistent pattern between years.
Figure 2.6. Maximum laboratory germination proportion as a function of MAP and infestation for *A. robusta* (acarob) and *A. tortilis* (acator) in a) 2013 and b) 2014.

2.3.3. Seed Rain

Over the course of the study, a total of 137 seeds were collected from the 180 seed traps, with *A. robusta* and *A. tortilis* seeds being present in 4 and 3 of the 18 plots, respectively (Fig. 2.7). There was no relationship between seed rain and MAP for either species.
Figure 2.7 Seed rain for *A. robusta* and *A. tortilis* seeds across plots. (Refer appendix 1 for plot information)

2.3.5. GERMINATION

Field germination rates were low, yielding 16 seedlings from 1216 (0.013%) planted *A. tortilis* seeds and 52 seedlings from 1216 (0.043%) planted *A. robusta* seeds. A Generalized linear mixed model fit by maximum likelihood suggested that field germination rates were significantly different between species (*P* < 0.05) but were not explained by either predation treatment or MAP (*P* > 0.05).

Table 2.3. Model fits for the effect of MAP, species, soil moisture and predation on seed germination using generalized linear mixed-effects models

<table>
<thead>
<tr>
<th>Fixed Effect</th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>PREDATION</td>
<td>0.906</td>
<td>0.601</td>
<td>1.508</td>
<td>0.132</td>
</tr>
<tr>
<td>SPECIES</td>
<td>-1.418</td>
<td>0.651</td>
<td>-2.178</td>
<td><strong>0.029</strong></td>
</tr>
<tr>
<td>SOIL MOISTURE</td>
<td>-0.068</td>
<td>0.070</td>
<td>-0.977</td>
<td>0.329</td>
</tr>
<tr>
<td>MAP</td>
<td>0.142</td>
<td>0.380</td>
<td>0.374</td>
<td>0.708</td>
</tr>
</tbody>
</table>

Even the analysis that included plot moisture condition at the time of planting showed the same results, *i.e.* germination rates were explained by species differences but not
moisture or seed predation treatment, suggesting that neither soil moisture values during the study nor long term MAP values affected germination.

2.3.6. Seed mass

The model selection analysis for seed mass suggested strong interactions between species, infestation and MAP on seed mass (Appendix 2). To tease apart these complex interactions, I subset the data by species and fit a single model in each case, with main effects for MAP and infestation (plus their interaction) and a main effect for year of collection. For both species, there were clear negative effects of infestation on seed mass (P <0.0001), and a negative effect of MAP on seed mass in *A. tortilis* (P<0.02), but not *A. robusta* (P=0.4) (Fig. 2.8).

![Figure 2.8. Seed mass response to MAP gradient for a) A. robusta (acarob) and b) A. tortilis (acator).](image)

2.4. DISCUSSION

In this study the overall hypothesis was that the patterns regulating species compositional change over time and across space are partly attributed to demographic processes
occurring at the seed stage. Also I hypothesized that these demographic processes can be influenced by long term rainfall regime. My results suggest that demographic processes (seed limitation) differ in intensity between species and time and that in most part are not influenced by MAP.

In the course of study I observed that *A. tortilis* seed mass declined with MAP, however this does not appear to affect germination rate. Mixed effect modeling showed that infestation was negatively correlated with seedmass. This observation may be attributed to tradeoff in *A. tortilis*. I hypothesize that *A. tortilis* does not perform well in wet sites because either wet sites have small seeds, hence low energy reserves which may rise their vulnerability to infestation; or seeds in wet sites fewer resources are needed for germination. The tradeoffs between seed mass and seed survival strategies has been suggested to be a case in woody species in which large seeded species tend to show higher germination and survival rates (Westoby et al. 2002); in this case *A. tortilis* seeds found in dry sites have higher chances of survival.

Germination rates under laboratory conditions were higher in *A. tortilis* than in *A. robusta* and strongly reduced by insect infestation, although infestation did not completely inhibit germination. While these findings on the contrary contradict with a study on *A. tortilis* which reported no germination of infested seeds (Ahmed 2008), they correspond to a study by (Mucunguzi 1995) on germination of infested seeds which found that beetles reduced the germination but promoted early germination. My hypothesis for these contradicting results is that seed mass and intensity of predation may play a role where larger seeds have more cotyledons compared to smaller seeds (Leishman 2001, Shaw et al. 2002). This may lead to some seeds managing to have larger
quantity of food reserve than the beetles can exhaust and hence increasing the chances of germination. Field germination trials showed surprisingly lower germination for both species compared to laboratory germination trials. This low level of germination has been observed in other Acacia species in African savannas. One of the suggested reason is that Acacia species require constant water supply during the first few days of planting (Wilson and Witkowski 1998, Barnes 2001) which may be intermittent in savanna ecosystems. For example Wilson and Witkowski, (1998) studied water requirements for four Acacia species. In their study they found that each species had a different level of retaining water level enough for germination. In some species such as Acacia karoo and Acacia tortilis they found that prolonged seed exposure to high temperatures soon after being hydrated, severely jeopardize their viability. I believe this might be the case in Serengeti where anecdotal observation suggest high local variability in rainfall regime among sites.

Model selection results showed that the proportion of trees producing seeds increased with tree height, but did not differ between species. While my study results suggest non-significant relationship between proportion of trees producing seeds and MAP in both species, I observed a positive relationship with tree height for A. robusta but not in A. tortilis. This suggests that, seed production can be explained by species morphological traits rather than environmental variables. I originally predicted the proportion of seed producing trees to increase with MAP but my results did not support the prediction. These results differ from other previous hypothesis which suggest that increase in moisture leads to successful seed production and growth of seedlings (Greene and Johnson 1994). It has been previously suggested that plant growth is water limited in
savannas, so greater soil moisture availability may lead to higher production of seeds (Greene and Johnson 1994, Salazar et al. 2011). While this study did not focus on the suitability of the microsite where these seeds land, long term MAP was the main covariate for inference and I think this scenario may respond differently if analysis involved rainfall data of seed production year were used.

Seed rain study revealed patchy low amount of seed collected in traps. These findings are relatively similar to the findings by (Salazar et al. 2011) although with relatively different seed density. Salazar et.al, (2011) estimated seed rain for Neotropical savanna trees for 23 species where they collected more seeds per unit area (ca.19 seeds m$^{-2}$) than what I report here (ca. 0.14 seeds m$^{-2}$ or 20 seeds per plot). I find it difficult to pinpoint with certainty the reason for low seed rain but I think many factors may contribute to this. First, the seed production study focused on phenology observation to quantify the number of trees producing pods vs non-seed producing trees in the plots. I did not explore plant pollination biology or total seed production per tree within a plot, hence, I think data on the overall levels of pollination success and seed production per tree are important to tease apart the real cause. I hypothesize that pollination limitation could be one of the reason for low seeds output as suggested by (Brown et al. 2003).

These results also suggest that infestation rates differed between species within years, but A. tortilis seeds were highly infested in the first year of study relative to A. robusta, but with the trend reversing in the subsequent year. This inconsistent trend suggests that species type and collection year explain differences in infestation among sites. Seed infestation has been reported in several ecosystems as a factor for reduced tree recruitment (Rohner and Ward 1999). In this study I predicted higher infestation in mesic
sites than dry sites assuming favorable conditions for pests in those sites. The findings did not support the suggestion that infestation is not explained by long term MAP.

In conclusion, my study revealed species variation in stages of seed limitation and no clear effect of long term MAP suggesting that tree community patterns are not generated at the seed stage. Also my study suggest that seed limitation is likely important and probably depends on current rainfall regime rather than long term rainfall. Laboratory germination trials tested for revealed higher germination potential in seeds compared to intrinsic germination in field experiment. Constant supply of moisture is probably necessary for maximum germination. I think the results of this experiment are helpful in restoration ecology as they show how different bottlenecks in savanna affect tree recruitment. In general, the relationships with MAP are weak or non-existent, suggesting that the landscape-level relationships are probably not due to factors at the seed stage. It should be noted though that these relationships were tested in terms of long-term MAP, and not rainfall at the time of the study suggesting that may be the trends may change if rainfall at study period were to be used. In future, I suggest that seed demographic dynamics should also be related to current environmental (weather) conditions so that ecologists can be able to predict species dynamics in relation to projected climate changes.

Literature Cited


Appendices

Appendix 1. Tree species 2013 basal area (m2 ha-1) across sites and plots in Serengeti NP.

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*Species key:*
Appendix 2: Cumulative germination proportions (viability) for (a) *A. robusta* (acarob) and (b) *A. tortilis* (acator) in 2013.
**Appendix 3**: Model fits for the effect of MAP, species, infestation and their interaction on seed mass for *A. robusta* and *A. tortilis*.

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