# DISSERTATION

# Moving Beyond the Aggregated Models: Woody Plant Size Influences on Savanna Function and Dynamics

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements for the Degree of Doctor of Philosophy

> Colorado State University Fort Collins, Colorado Spring 2008

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#### COLORADO STATE UNIVERSITY

December 17, 2007

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY WILLIAM BRIAN SEA MOVING BEYOND THE AGGREGATED MODELS: WOODY PLANT SIZE INFLUENCES ON SAVANNA FUNCTION AND DYNAMICS IN PARTIAL REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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# **ABSTRACT OF DISSERTATION**

# Moving Beyond the Aggregated Models: Woody Plant Size Influences on Savanna Function and Dynamics

Despite extensive global coverage and decades of research, the ecology of savannas remains poorly understood. Historically, models have played important roles in studying aspects of savannas, including tree-grass competition, fire, and plant-herbivore interactions. The models can be categorized as either 1) "aggregated" ones that neglect size structure but have the advantage of mathematical tractability or 2) complicated process-oriented ecosystem models incorporating mechanistic ecophysiology capturing greater ecological realism but constrained to simulation modeling. The aggregated class of models can be further separated into those that focus on resource utilization and treegrass competition ("resource-based models") and those that focus on demographic impacts of disturbances by fire and herbivory ("demographic bottleneck models"). The resource and demographic models separately consider important aspects of savanna ecology, yet the two approaches have rarely been integrated, resulting in a significant gap in our understanding of savannas.

For this study, I investigated the role of woody plant size in savanna ecology. Using extensive datasets along broad resource gradients of annual precipitation in southern Africa, I examined patterns of size-abundance for woody plants in relatively undisturbed savannas to see if relationships for savannas showed similar patterns to theoretical predictions for tropical forests. Contrary to assumptions and predictions made by aggregate savanna models, I found that the percentage of wood biomass subject to fire loss actually decreases in wetter savannas. Furthermore, woody biomass in annual dry season fires has actually increased over three decades. Since resource limitation and "thinning" have been mentioned as potential factors in savannas, I investigated the suitability of self-thinning in savannas. I developed a simple theoretical model hypothesizing three potential impacts of tree-grass interactions on the self-thinning relationship. Results from the analyses, testing with field data, suggest that tree-grass competition is asymmetric with respect to tree size.

For the formal modeling component of my dissertation, I developed a simple savanna model that integrates demographic bottleneck and resource-based approaches. The model is unique in that the woody carrying capacity has both resource and demographic constraints. Demographic bottlenecks occurred fairly easily in the model and were described mathematically by saddle node bifurcations resulting from small changes in adult mortality. Model simulations including stochastic variation showed that modest amounts of variation in adult mortality during fires and size-asymmetric tree-grass competition lead to very different model outcomes. The work opens up an entirely new class of ecological models for savanna ecology: analytically tractable with enough size structure to capture realistic savanna vegetation-disturbance interactions.

William Brian Sea Graduate Degree Program in Ecology Colorado State University Fort Collins, Colorado 80523 Spring 2008

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# Chapter 1

# Introduction

# 1.1 Summary

My dissertation work focuses on the role and importance of competition and disturbance in savannas related to size structure in the woody community. Three broad questions related to savannas are central to my research: 1) under what conditions savanna vegetation structure is more affected by competition or disturbance. Savanna models have generally focused on either competition or disturbance as the key driver, but it is likely that each may play a major role depending on environmental conditions; 2) -the role tree size has in determining the competitive advantage trees may have over grasses. Since most savanna models "aggregate" woody populations, and thus ignore any size effects, these models are unable to invoke any competitive advantage for larger trees, and finally, 3) -the role size structure of woody plants plays in mediating the impacts of disturbance. Models that assume fire typically leads to a 10-20% reduction in woody biomass may be in error, especially if large, fire-resistant individuals dominate the biomass.

The dissertation structure is outlined in Fig. 1.1. This chapter serves as an introduction to the dissertation by providing background literature, outlining chapter structure and goals, and highlighting chapter content. Chapter 2 includes a survey of

savanna models focusing on shortcoming of aggregated models that dominate the field. A new and innovative model that incorporates minimal size structure is introduced and analyzed. Chapter 3 examines the importance of size structure for woody plant communities via analyses of new and existing datasets from savanna sites in southern Africa (Zambia, Botswana, and South Africa). Chapter 4 investigates the use of the selfthinning concept for savannas to study how tree size effects tree-grass competition using new data from long-term experiments in the Kruger National Park, South Africa. In Chapter 5, I expand on the model introduced in Chapter 2 to examine how stochastic variation in fire interval and intensity, and size-dependent tree-grass competition, affects tree-grass coexistence in savannas. Finally, Chapter 6 synthesizes the key results for the dissertation.

#### **1.2 Background**

Tropical savannas cover extensive regions of the semi-arid and subhumid tropics (Bourliere and Hadley 1970, Huntley and Walker 1982), and savannas existing around the world implies the *coexistence* of woody and herbaceous plants. Much has been written on whether this coexistence is stable or unstable (e.g. Scholes and Archer 1997; Jeltsch et al. 1998; Sankaran et al. 2004) or indicates equilibrium, disequilibrium or nonequilibrium conditions (Ellis and Swift 1988; Illius and O'Connor 1999; Jeltsch et al. 2000). In many tropical savannas the woody component consists mostly of droughtdeciduous trees or shrubs, with the herbaceous layer dominated by annual or perennial grasses. Tree-grass coexistence theories for savannas stretch back to early German ecologists (Schimper 1903; Walter 1939) and to the recognition that water limitation



#### **Broad Savanna Questions**

Is savanna structure more affected by competition or disturbance? Is tree-grass competition in savannas asymmetric with respect to tree size? Are disturbance effects in savannas asymmetric with respect to tree size?



Figure 1.1 Conceptual outline for dissertation.

may play an important role in structuring semi-arid vegetation communities (Holdridge 1947). Subsequent versions of the Walter hypothesis (e.g. Walker et al. 1981; Walker and Noy-Meir 1982) postulated that niche separation between tree and grass roots leads to stable coexistence. Since fire and herbivory are so widespread in many savanna systems, and can greatly reduce woody density and cover, other researchers (Dublin 1990; Menaut et al. 1990; Higgins et al. 2000; Bond et al. 2005) have focused on disturbance as the primary mechanism that impedes woody population growth and thereby permits grass persistence. While competition among trees ("*balanced competition*") has been mentioned as a possible mechanism for coexistence in a few instances (Skarpe 1990; Scholes and Archer 1997), few experiments have examined the extent to which intra-specific competition may allow tree-grass coexistence.

Since many factors are involved in determining savanna structure and field data elucidating their individual and combined effects are in short suppply, models have played a crucial role in studying the ecology of savannas (House et al. 2003; Sankaran et al. 2004). While savanna models vary widely in their structure and level of complexity, they usually have focused either on the role of *resource competition* (water, nutrients, light) or *disturbances* (fire, herbivory, harvesting and climate variability that act as demographic bottlenecks at critical life stages) to explain tree-grass coexistence and the density and cover of trees and shrubs in different savanna systems Simple models that concentrate on resource competition have used differential (or difference) equations to study the "aggregate" woody and grass dynamics in savannas, whereas models that emphasize disturbance have used several size (or age) class equations for woody plants to examine how disturbances impede demographic transition of woody individuals from

seeding to reproductive adults. The use of two very different approaches for studying the "savanna problem" (Sarmiento 1984) has led to disagreements on how to characterize even general features of savanna vegetation. This can be most clearly exemplified in contrasting assumptions regarding competitive dominance of trees and grass. The resource competition models assume grass to be the better competitor with trees persisting only when provided access to resources (water) in deep soil layers. Disturbance-based models suggest that savanna tree-grass ratios are inherently unstable and woody plants are competitively superior to grasses such that grasses persist only when disturbances suppress the woody component (Higgins et al. 2000; House et al. 2003; Sankaran et al. 2004).

It has been argued elsewhere that greater emphasis needs to be placed on integrating and reconciling the two approaches for conceptual advances to take place in savanna ecology (Sankaran et al. 2004). Surprisingly no simple savanna model has incorporated enough demographic structure to adequately represent the impacts of disturbance (such as fire) on woody vegetation and also included realistic resource competition. Recent emphasis on demographic bottlenecks in savanna systems (e.g. Higgins et al. 2000) highlights the importance of plant size in woody population dynamics. Resource competition models neglecting size (Walker et al. 1981; Menaut et al. 1990; Ludwig et al. 1997; Anderies et al. 2002; D'Odorico et al. 2006; Williams et al. 2006; Beckage et al. 2007) are likely, therefore, to miss important size-related aspects of savanna ecology, especially ones related to disturbance and resource use. Conversely, savanna models focusing exclusively on demographic structure without implementing resource competition (Jeltsch et al. 1996; Jeltsch et al. 1998; Higgins et al. 2000; Baxter and Getz

2005; Gardner 2006) might not capture important aspects of resource limitation found in many water-limited savannas (Holdridge 1947; Walter 1971; Rodriguez-Iturbe et al. 1999; Sankaran et al. 2005; Bucini and Hanan 2007).

A number of studies have addressed tree-size structure in savannas (Scholes et al. 2002; Skarpe 1990; Wiegand et al. 2006; Higgins et al. 2000; Pellew 1983; Caylor et al. 2003; Kennedy and Potgieter 2003). However, general conclusions are confounded because most of these studies were restricted to short duration and over small spatial scales. Studies examining drier savannas (annual rainfall < 400 mm yr) suggest that tree size may be characterized by a single dominant size mode (Skarpe 1990; Wiegand et al. 2006), suggesting difficulties in recruitment for many years. However, in wetter savannas, where woody juvenile recruitment is less affected by drought, smaller individuals are generally more numerous than larger trees, and population structures often resemble distributions typical of continuous recruitment (Aubreville 1966; Bond and van Wilgen 1996; van de Vijver et al. 1999; Higgins et al. 2000; Higgins et al. 2007). Some savanna studies have proposed that, in addition to smaller trees dominating the number of individuals, they compose much of the woody biomass, and that this biomass is subject to high fire mortality (van de Vivjer et al. 1999; van Langevelde et al. 2003; Higgins et al. 2007). No study to date, however, has thoroughly examined size structure of savannas over a rainfall gradient (but see Scholes et al. 2002 who report that more humid savannas have greater mean tree height), and my subjective field observations suggest that larger trees comprise an increasing fraction of total biomass (though not necessarily an increasing fraction of total stems) with increasing rainfall.

Although tree size plays an important role in determining the response of individual trees with respect to growth, competition, and disturbance, patterns in woody population size structure across gradients of climate and disturbance remain largely unknown and unexplored. For example, tree size structure (the size and density of individuals in each size class) directly affects population level growth rates because larger trees tend to be slower growing as they invest greater resources to non-growth functions (e.g. respiration and reproduction, see Ryan et al. 1997) while smaller individuals are fast growing (Holdo 2006; Prior et al. 2006). Thus a population that consists of a few large trees may grow slower than a population of smaller trees with the same woody biomass or stem basal area. There is also a potential relationship between tree size and the strength of tree-tree and tree-grass competition (for water, nutrients, and light) and size affects the ability of trees to withstand various disturbance events related to herbivory, wind and fire.

In savanna systems where trees, by definition, share resources with an herbaceous layer, it seems probable that larger trees will have competitive advantages, relative to smaller trees and herbaceous vegetation, because of their more fully developed root systems. However, field data in support of the idea is still lacking (Scholes and Archer 1997; Sankaran et al. 2004). Perhaps woody plant size structure has its most observable impact in savanna fires because direct mortality and top-kill of trees during ground fires affects small individuals much more than larger individuals (Trollope 1982; Williams et al. 1999; Higgins et al. 2000). Furthermore, large trees sometimes decrease herbaceous production in mesic savannas, reducing fuel loads and increasing fuel moisture, both of which lead to lower intensity fires and reduced fire spread (Aubreville 1966, Walter

1971, Belsky 1994; Higgins et al. 2000). While savanna studies have increased focus on the importance of fire intensity (Higgins et al. 2000; Govender et al. 2006), greater understanding of size structure of woody plants may prove critical in determining actual woody plant mortality because of nonlinear relationships that have small individuals in a population suffering relatively high fire mortality (> 95 %) while larger individuals are mainly fire resistant (Trollope 1982; Williams et al. 1999; Hoffmann 2003; Holdo 2006).

It is likely that savanna vegetation responds differently to disturbances with constant intensity and interval and to disturbances occurring with stochastic variation (Higgins et al. 2000; D'Odorico et al. 2006; Williams and Albertson 2006; Hanan et al. 2008). Studies have highlighted the importance of fire intensity on woody loss (Trollope 1982; Williams et al. 1999; Higgins et al. 2000; Govender et al. 2006), and small changes (1-2%) in fire mortality for the adult trees can have dramatic effects on steady state values in deterministic models (Chapter 2). Deterministic savanna models that incorporate sizeasymmetric fire effects on woody plants can be expected to display "demographic bottleneck" features, as observed in nature, where smaller tree individuals are continually suppressed by fire, and models may exhibit very different outcomes as stochastic models exhibiting variation in fire intensity and interval than for mean-value versions.

# **1.3 Chapter Summaries**

#### Chapter Two

In Chapter 2 I address some of the problems apparent in "aggregated" savanna models and introduce a novel simple savanna model that incorporates minimal size structure (juveniles and adults) and logistic tree-grass resource competition. By necessity,

aggregated savanna models lump all individual and population level processes together for all aspects of growth, resource use and competition. While aggregated savanna models have proven useful for examining the role of resource competition in tree-grass coexistence, the models are unable to incorporate tree size relationships for resource use, competition and disturbances. It is possible that these shortcomings may lead the models to predict unrealistic results. For example, savanna fires typically lead to mortality rates of 50 % (or higher) for juvenile woody plants, while adult trees suffer minimal fire mortality. Thus an "average" fire loss of 10% of some models (e.g. D'Odorico et al. 2006) may substantially underestimate fire loss if a stand is dominated by small woody plants, but may overestimate if the stand has large woody plants. My model is different from previous savanna models because its woody maximum basal area depends on the number of adults. Thus my model avoids the problem of other logistic models that allow a few individuals to grow to the maximum basal area when no young trees are recruited. I examine the steady state solutions of the model in order to examine how the intensity of tree-grass competition and disturbance lead to changes in observed steady values for woody basal area.

#### Chapter Three

Chapter 3 makes use of several long-term and large-scale tree data sets to address the fundamental role of tree size in savannas. First, I examine tree size structure in relatively undisturbed (fire suppression for over 50 years) savannas to see if size-abundance relationships converge towards the power law distribution typically observed in tropical forests and predicted by metabolic theory. Next, I test the hypothesis that along a broad resource gradient of increasing average annual rainfall, a greater proportion of woody

biomass is contained in fire-resistant individuals, which is contrary to studies that suggest smaller trees dominate woody biomass of savannas. Finally, I make use of a long term fire study to examine if, contrary to most existing savanna models, prescribed annual burning over as many as 50 years may have little effect on woody biomass, or may actually lead to an increase, since fire-resistant trees continue to grow while smaller individuals are suppressed by fire. Although it is likely that the eventual outcome for these sites is long-term woody collapse, the demographic "bottleneck" can buffer the woody population for many years thus delaying sustained fire reduction envisioned by many existing models.

#### Chapter Four

Chapter 4 examines the feasibility of applying self-thinning concepts to savannas and how competition with herbaceous vegetation may modify self-thinning patterns among woody plants in these ecosystems. Competition among woody plants has seldom been invoked as a major explanation for the persistence of herbaceous vegetation in mixed tree-grass ecosystems. On the contrary, the primary resource-based explanations for tree-grass coexistence are based on tree-grass competition (niche-separation) that assumes that trees are inferior competitors unless deeper rooting depths provide them exclusive access to water. Alternative non-resource based hypotheses postulate that trees are the better competitors, but that tree populations are suppressed by mortality related to fire, herbivores and other disturbances. It is surprising that no substantive study has used a self-thinning approach to infer tree-on-tree competition in savannas, particularly since self-thinning studies in forests are so abundant in the ecological literature. If selfthinning of woody plants can be detected in savannas, stronger evidence for resource-

limitation and competitive interactions among woody plants would suggest that the primary models of savannas need to be adjusted. I present data from savanna sites in South Africa that suggest that self-thinning among woody plants can be detected in lowdisturbance situations, while also showing signs that juvenile trees, more so than adults, are suppressed when growing with herbaceous vegetation in these ecosystems.

#### Chapter Five

In Chapter 5 I expand my modeling work from Chapter 2 to examine the effects of stochastic fire disturbance and size asymmetric tree-grass competition on tree-grass coexistence. It is likely that savanna vegetation responds differently to fire disturbance with constant intensity and interval (i.e. mean-value conditions) and disturbance with stochastic variation in intensity and interval. I use simulations to examine how changes in parameters influencing mean fire intensity and interval affect long-term (3000 years) stability in tree-grass coexistence. By making fire a stochastic loss term with given annual probability of occurrence and by varying the fire mortality around mean values, I investigate if increases in fire mortality variability can lead to a "collapse" of the woody population and how these model results compare with a model having no size structure. I compare the results for model changes for adult and juvenile mortality and conclude that savanna vegetation is very sensitive to changes in adult mortality, but relatively resistant in the model to changes in juvenile mortality. Since my model dynamically keeps track of both number of adult individuals and total basal area, I am able to monitor "average" tree size and further investigate how small changes in tree-grass competitive advantage for larger trees may lead to changes in steady state basal area values, thus treegrass ratios. Finally, I investigate how the structure of my model with size classes is

affected by fires with different interval but the same long term average fire loss. I anticipate that there will be little impact on a traditional logistic model but that the demographic model will display a "bottleneck" feature for shorter fire intervals.

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# Chapter 2

### Integrating Demography and Competition in a Simple Savanna Model

#### **2.1 Introduction**

The ecology of savannas remains poorly understood despite approximately 20% coverage of terrestrial ecosystems globally by area and substantially higher coverage in Africa, Australia, and South America. Savannas can be broadly characterized as ecosystems having a nearly continuous grass layer with discontinuous tree canopy (Bourliere and Hadley 1970; Frost et al. 1986) but no apparent dominance of either the woody or grass component (Scholes and Archer 1997). Studies provide contrasting, and sometimes contradictory, information on the determinants of savanna structure and function (Scholes and Archer 1997; Sankaran et al. 2004). There is consensus among ecologists on the suite of factors thought important for promoting coexistence of trees and grass in savannas: water, nutrients, fire, and herbivory, but considerable disagreement and uncertainty on the relative importance of each factor in different locations and continents where soils, climate, physiology, and disturbance dynamics are different (Scholes and Walker 1993; Scholes and Archer 1997; House et al. 2003; Bond et al. 2003). Water and nutrient resources are referred to as *primary* factors because they likely set the upper bound for biomass, leading to stronger competition as resources become limiting (Holdridge 1947; Walter 1971; Rodriguez-Iturbe et al. 1999; Sankaran et al. 2005, Bond et al. 2005). Secondary factors, primarily fire, herbivory and human

actions, act as disturbances that, in most cases, reduce and determine actual biomass (Dublin et al. 1990; Higgins et al. 2000; Sankaran et al. 2004; Bond et al. 2005; Bucini and Hanan 2007).

Given the range of factors involved in determining savanna structure, combined with a shortage of quality field data, models have played an important role in studying the ecology of savannas (House et al. 2003; Sankaran et al. 2004). Although savanna models vary widely in their structure and level of complexity, they generally have focused either on the role of resource competition (water, nutrients, light) or disturbances (fire, herbivory and climate variability that act as demographic bottlenecks at critical life stages) in order to explain coexistence of trees and grass. Low dimensional models concentrating on resource competition have used differential (or difference) equations to examine the "aggregate" woody and grass dynamics in savannas, whereas models emphasizing disturbance have used several size (or age) class equations for woody plants to study how disturbances impede demographic transition of woody individuals from seed to sapling to reproductive adults. The use of these two very different approaches for studying the "savanna problem" (Sarmiento 1984) has led to widespread disagreements on how to characterize even general features of savanna vegetation. This may be most clearly exemplified in contrasting assumptions regarding competitive dominance of tree and grass. The resource competition models assume that grass is the better competitor with trees persisting only when provided access to resources (water) in deep soil layers. Disturbance-based models postulate that savanna tree-grass ratios are inherently unstable and woody plants are competitively superior to grasses, and grasses only persist because

disturbances suppress the woody community (Higgins et al. 2000; Jeltsch et al. 2000; House et al. 2003; Sankaran et al. 2004).

It has been argued elsewhere that greater emphasis needs to be placed on integrating the two approaches before further conceptual advances can occur in savanna ecology (Sankaran et al. 2004). Surprisingly no simple savanna model has incorporated enough demographic structure to adequately represent the impacts of disturbance (such as fire) on woody vegetation while also including realistic resource competition. Recent emphasis on demographic bottlenecks in savanna systems (e.g. Higgins et al. 2000) have demonstrated the importance of plant size in woody population dynamics. Resource competition models that neglect size (Walker et al. 1981; Menaut et al. 1990; Ludwig et al. 1997; Anderies et al. 2002; D'Odorico et al. 2006; Williams et al. 2006; Beckage et al. 2007) are likely, therefore, to miss key size-related aspects of savanna ecology, especially ones related to disturbance and resource use. Conversely, savanna models that focus exclusively on demographic structure without implementing resource competition (Jeltsch et al. 1998; Higgins et al. 2000; Baxter and Getz 2005; Gardner 2006) may not capture important aspects of resource limitation found in many water-limited savannas (Holdridge 1947; Walter 1971; Rodriguez-Iturbe et al. 1999; Sankaran et al. 2005; Bucini and Hanan 2007).

Although simple "aggregated" models have been highly influential in shaping how we think savannas behave dynamically, especially with respect to the implications for rangeland management in grazing systems with alternate stable states (Noy-Meir 1975; Walker et al. 1981; Ellis and Swift 1988; Scholes and Archer 1997; van Langevelde et al. 2003; Rietkerk et al. 2004; Sankaran et al. 2004), more progress is needed in integrating

demographic and competition approaches in models that remain relatively simple and analytically tractable. The major objective for this study is the introduction of an innovative new savanna model to address these needs. The new model should serve to stimulate greater discussion and highlight problems using simple models to explore vegetation dynamics in savannas. My model integrates demography, disturbance, and competition, striking a balance between conventional resource competition models that neglect size structure and demographic-bottleneck models that incorporate size structure but lack realistic resource competition. The model is thus able to address a suite of important outstanding questions on how woody plant size affects growth, competition, and fire mortality in savannas.

### 2.2 Existing Aggregated Savanna Models

#### 2.2.1 Aggregated Models and Resource Use

Aggregated savanna models generally use a single differential equation to represent woody vegetation dynamics in savannas. However, there is strong evidence that a single woody equation cannot properly represent relationships relating to resource use, fire loss, and tree-grass competition for both woody and herbaceous vegetation (Scholes and Archer 1997; Sankaran et al. 2004; Hanan et al. 2007).

Aggregated resource competition savanna models (e.g. Walker et al. 1981; Ludwig et al. 1997; Anderies et al. 2002, Beckage et al. 2006; D'Odorico et al. 2006; Williams and Albertson 2006) have taken two contrasting, and contradictory, approaches to defining how resource use relates to existing plant biomass. I define these approaches as the "resource implicit" and "resource explicit" approaches.

Assuming that resource use scales linearly with plant biomass the *resource implicit* approach makes use of a coupled logistic competition model (also known as Lotka-Volterra competition), with one differential equation each for wood and grass dynamics, and extra terms characterizing disturbances such as fire, grazing, and browsing (Ludwig et al. 1997; Anderies et al. 2002; Beckage et al. 2006; D'Odorico et al. 2006; Williams and Albertson 2006). Although the form of these models is mathematically identical to Lotka-Volterra, there is an important ecological difference that has not been thoroughly discussed in the literature. The logistic model is normally used to describe a population in terms of number density, with individuals assumed to be roughly similar size, and an intrinsic growth rate representing net balance between births and death in a population. By contrast, savanna logistic models lump all individual and population level processes into state variables characterizing population biomass (not density) for woody and herbaceous plants and the intrinsic growth rate now represents net biomass accumulation. In most of these models, competition between tree and grass is represented using a coefficient (e.g.  $c_{wg}$  refers to the net competitive effect of woody plants on herbaceous production while c<sub>gw</sub> indicates the effect of herbaceous plants on woody production; Fig. 2.1) that linearly reduces the amount of available resources for either woody or herbaceous growth based on the biomass of the other.

Assuming that plant resources are all used for new plant growth, the *resource explicit* approach originated from an earlier model (Walker et al. 1981) that was based largely on the two-layer savanna model (Walter 1971). Developed to test a general hypothesis that increased grazing leads to a positive feedback in infiltration that changes the water balance between trees and grass, soil water in the lower layer of the

based largely on the two-layer savanna model (Walter 1971). Developed to test a general hypothesis that increased grazing leads to a positive feedback in infiltration that changes the water balance between trees and grass, soil water in the lower layer of the model is available exclusively for woody plant growth. Water in the upper layer is partitioned competitively between trees and grass at a variable ratio depending on existing woody and herbaceous biomass. The model was recently extended to include the impacts of fire and herbivory (van Langevelde et al. 2003).

These models use a few differential equations to represent woody and grass vegetation dynamics, as in the logistic models, but tree-grass competition has somewhat greater mechanistic justification since all the available soil moisture is partitioned between trees and grass and used exclusively for either woody or herbaceous plant growth. The approach is considered *resource explicit* because a relationship, based on studies of water use efficiencies for grass and woody production, determines grass and wood production. A recent study, however, found large variability in water use efficiency for different species of woody plants, with some woody plant species having similar values to grass species (Cernusak et al. 2006). This fact poses problems for the aggregated resource explicit models and more specifically for models that assume that much higher water use efficiencies for grasses than trees is a prerequisite for niche-partitioning and tree-grass coexistence (Walker et al. 1981; van Langevelde et al. 2003).

Recent theoretical and observational studies call into question the basic assumptions of both approaches and argue for a nonlinear power law relationship (3/4 power) between



Figure 2.1. Conceptual tree-grass competitive interactions and growth rates for woody and herbaceous plants. Herbaceous plants have much faster intrinsic growth rates  $(r_g)$ than woody plants  $(r_w)$ . The competition coefficients  $c_{gg}$  and  $c_{ww}$  refer to intra-form competition, i.e. grass-grass and tree-tree competition, while  $c_{wg}$  refers to tree-on-grass competition and  $c_{gw}$  to grass-on-tree competition. Since large trees invest more heavily in ligneous stem and branch structure, the slower growth rate is compensated by higher competitiveness for the trees against the grass. The higher competitiveness may be associated with better access to light resources, particularly during more water efficient periods in the morning when temperatures are lower. Large trees have competitive advantages because of more extensive rooting patterns for water and nutrient resources relative to leaf mass. The competitive advantage may also result because additional protection from fire and mammalian herbivores. The relationships are formalized mathematically in a demographic-competition model (Fig. 2.2).

individual plant weight and resource use (Enquist et al. 1998; Enquist and Niklas 2002). This implies that woody maximum basal area depends on the size structure in the woody plant community (see Chapter 4). Thus in a system dominated by small woody individuals, which have a quasi-linear relationship between plant weight and resource use, the logistic model may provide an adequate description of resource use and competition. However, in savanna woody communities with complicated size structure, woody plants ranging in size from saplings of a few kilograms to adults weighing much more than a ton dry mass, there would likely be different resource demands given the same "aggregate" woody plant weight, in so far as biomass in a single large tree may not have the same unit resource demand as biomass in many small trees. In this study, I use tree basal area (rather than woody biomass) as a better measure of woody resource demand (Enquist et al. 1998), with the advantage of being a frequently measured quantity in field studies and a quasi-linear resource use relationship (see Appendix 1).

#### 2.2.2 Aggregated Models and Fire

Decades of field research suggest that aggregated models without size structure in the woody plant community cannot adequately model the fire ecology of savannas (Trollope 1982; Bond and van Wilgen 1996; Higgins et al. 2000; Govender et al. 2006). These studies show that fire acts as a "demographic bottleneck" to impede growth of trees into fire-resistant size classes, and that the effect of fire intensity on tree mortality is more important than fire interval in determining savanna size structure. Perhaps of greater importance than fire intensity, however, is the size structure of vegetation subject to fires (Frost and Robertson 1987), in which small woody individuals generally suffer very high

mortality (over 50%), but larger plants are mostly fire resistant (< 2%). Models using a single woody equation (e.g. van Langevelde et al. 2003) suggest that loss of woody biomass during fires of similar intensity increases with standing biomass because fire intensity is used to define a fractional wood loss term. However, if sites with higher wood biomass also have a higher fraction of large (fire-tolerant) individuals, biomass losses during fires could actually decrease with increasing standing biomass.

#### 2.2.3 Aggregated Models and Tree-grass Competition

Although the majority of studies on woody-herbaceous interactions have focused on the effects of trees on grasses, relatively few have looked at grass competitive effects on woody plants (Belsky 1990; Scholes and Archer 1997; House et al. 2003; Simmons et al. 2007). The few studies showing negative impacts of grass biomass on tree seedling establishment generally find that seedling abundance is strongly suppressed at higher grass biomass levels because of light, nutrient, and water competition (Davis et al. 1998; Higgins et al. 2000; Weltzin et al. 2000; Simmons et al. 2007). Vigorous competition between small woody plants and grass in savannas for water resources has also been hypothesized elsewhere (Walter 1971; Scholes and Archer 1997), but results of grass removal studies on adult trees have had mixed results, with some studies showing strong woody growth with grass removal (Davis et al. 1998; Simmons et al. 2007) and other results suggesting little or no effect on tree growth rates (Smit and Rethman 2000; Bond et al. 2007 unpublished data).

Aggregated savanna models assume faster growth rates for grasses than for woody plants, but they neglect differences in life strategy between trees and grasses and omit

potential changes in competitive interactions related to tree size. Trees and grass differ greatly in patterns of resource allocation and life strategy. For example, not having to invest in ligneous stem tissues, grass plants devote greater resources for the production of photosynthetically-active above ground leaves. Observational and theoretical studies on tree-grass interactions show strong support for higher grass production rates than for woody plants (Scholes and Walker 1993; Scholes and Archer 1997). Models reflect this difference by assuming higher intrinsic growth rates for grass production than for trees (Walker et al. 1981; Walker and Noy-Meir 1982; Anderies et al. 2002; van Langevelde et al. 2003; Williams and Albertson 2006). The aggregated savanna models prescribe fixed competition coefficients that linearly partition available resources to trees and grass (Ludwig et al. 1997; Anderies et al. 2002; Williams and Albertson 2006) or as a nonlinear function depending on woody biomass (Walker et al. 1981; van Langevelde 2003). However, while greater structural (ligneous stems) allocation generally leads to lower total photosynthesis rates for trees, as reflected in the models, trees with larger canopy and root systems may be stronger competitors for light, water and nutrients. This demographic asymmetry is not reflected in current aggregated savanna models (Fig. 2.1).

#### 2.3 Model Formulation

My demographic-competition model uniquely couples a minimal size-structured demographic model with a logistic tree-grass resource competition model (Fig. 2.2). In the demographic portion of the model, separate differential equations are used to model the number density of juveniles (J) and adults (A) with fecundity (m) and promotion (p) rates to allow for "births" of new juveniles and transition of juveniles into adult size
class. The resource competition portion of the model is a standard logistic tree-grass competition model (e.g. Ludwig et al. 1997; Anderies et al. 2002). However, in order to avoid nonlinear tree size versus resource use problems using biomass, I use tree basal area (B) that is assumed to scale linearly with resource demand. Furthermore, since above ground grass biomass is ephemeral in both annual and perennial grasslands, and since grass resource demand may not scale linearly with above ground biomass, in this study, I use grass root biomass (G) as the primary index of grass abundance and assume that I am modeling a savanna with perennial grasses. The key difference between my model and others is that woody maximum basal area is a function of the number of adults. This change leads to stronger coupling in the model between the number of trees and the maximum basal area. There is also strong coupling between competition and demographic state variables through reduced fecundity and promotion, and through grass-on-seedling ( $\alpha$ ) and tree-on-seedling ( $\beta$ ) competition. Mortality for all equations is envisioned as a total mortality ( $\mu$ ) that encompasses "natural" mortality and mortality during disturbances such as fire, herbivory, and severe drought. For a fuller description of the model equations, see Fig. 2.2.

Using a woody maximum basal area that is a function of the total number of adults in a population is integral to creating demographic bottleneck conditions in the model. Each adult (individuals reaching fire-resistant size) is theoretically allowed to reach its maximum size ( $B_0A \ll B_{max}$ ), for a maximum basal area ( $B_0A$ ), where A is the number of adults and  $B_{max}$  is a "landscape scale" resource-based potential maximum basal area. Ultimately, potential maximum basal area ( $B_{max}$ ) is constrained by a value representative of local and long-term climate and soil conditions. The model therefore

avoids the problem of a small number of trees being simulated to grow to potential maximum basal area (e.g. the unrealistic situation where A=1 and B=B<sub>max</sub>). Since there is a demographically-sensitive maximum basal area, woody population growth rates depend not only on total basal area as in other models (e.g. Gardner 2006) but also on the average tree size (B/A). As average tree size approaches B<sub>o</sub>, with B<sub>o</sub>A < B<sub>max</sub>, population growth rate reduces to zero. Likewise, in the model, when B<sub>o</sub>A converges to B<sub>max</sub>, the dynamics on B essentially decouple from the demographic portion of the model. Hence, under these conditions, basal area growth is insensitive to fecundity rates, juvenile promotion, and juvenile mortality rates.

### 2.4 Results

The demographic-competition model is particularly sensitive to small changes in adult mortality, whether due ultimately to fire, drought, browsing by elephants, or other causes. Model dynamics are characterized mathematically by a saddle node bifurcation with jump-like behavior around critical points (Fig. 2.3). Along the stable branch of the diagram (solid line in Fig. 2.3), increased adult mortality leads to monotonic decreases in the steady state values for basal area ( $B^*$ ). Additional mortality at the critical point ( $B_{cr}$ ) leads to collapse in B to zero. The jump-like behavior can be explained in the model by a feedback that reduces production of juveniles and adults, leading to rapid decline in A and consequently decreased maximum basal area ( $B_oA$ ). Longer juvenile promotion times (p), stronger grass-juvenile competition ( $\alpha$ ), and higher juvenile mortality ( $\mu_J$ ) enhance the feedback and likelihood of jump behavior (Fig. 2.3).

Although there are two mortality rates for adults ( $\mu_A$ ,  $\mu_B$ ) representing loss of



Figure 2.2. Equations for the demographic-competition model of savanna dynamics. The differential equations represent time rate of change for the densities of juveniles (J) and adults (A), and the basal area of trees (B) and root biomass of perennial grasses (G). Tree-grass and tree-tree competition are modeled using a logistic factor ( $\alpha$ ) that reduces juvenile recruitment and factor ( $\beta$ ) that reduces juvenile promotion. Units are arbitrarily individuals ha<sup>-1</sup> for J and A, m<sup>2</sup> ha<sup>-1</sup> for B, and kg ha<sup>-1</sup> for G. For parameter definitions and estimated values see Table 1.

Parameter	Symbol	Units	Default	Range	Source
Adult Mortality	$\mu_A$	yr <sup>-1</sup>	0.02	0.005-0.10	1
Juvenile Mortality	μ	yr <sup>-1</sup>	0.10	0.05-0.80	2
Basal Area Mortality	$\mu_{\mathrm{B}}$	yr <sup>-1</sup>	0.02	0.005-0.10	3
Grass Mortality	μ <sub>G</sub>	yr <sup>-1</sup>	0.10	0.10-0.90	4
Tree-grass competition	c <sub>wg</sub>	None	1.0	0.0-2.0	5
Grass-tree competition	c <sub>gw</sub>	None	1.0	0.0-1.0	6
Promotion Time	р	yr <sup>-1</sup>	0.05	0.02-0.20	7
Grass Growth Rate	r <sub>G</sub>	yr <sup>-1</sup>	1.0	0.25-1.50	8
Woody Growth Rate	r <sub>B</sub>	yr <sup>-1</sup>	0.10	0.05-0.25	9
Grass-Seedling	α	None	0.5	0.0-1.0	10
Tree-Seedling	β	None	1.0	0.0-1.0	10
Maximum Tree Size	Bo	m <sup>2</sup>	0.15	0.15	11
Maximum Basal Area	<b>B</b> <sub>max</sub>	m <sup>2</sup> ha <sup>-1</sup>	30	10-30	12
Maximum Grass Biomass	$G_{\text{max}}$	tons ha <sup>-1</sup>	5	1-10	4
Fecundity	m	Indiv m <sup>-2</sup>	20	0-100	13

1. Higgins et al. (2000)

- Prior et al. (2006); Holdo (2006) 2.
- 3. Higgins et al. (2000);
- van Langevelde et al. (2003); Williams and Albertson (2006) Ludwig et al. (1997); Williams and Albertson (2006) 4.
- 5.
- Ludwig et al. (1997); Williams and Albertson (2006) 6.
- 7. Therwell et al. (2007)
- 8. Anderies et al. (2002)
- 9. Anderies et al. (2002)
- 10. Arbitrary
- 11. Unpublished data (Sea et al. 2007; Bond et al. 2007)
- 12. Holdo et al. (2007); Scholes and House (2001)
- 13. Unpublished data (Sea et al. 2007; Bond et al. 2007)

Table 2.1. Parameters used for the study.

individuals in the demographic portion of the model and loss of basal area in the competition portion of the model, the two parameters are not independent of each other. There are several ecological reasons that justify differences between individual mortality ( $\mu_A$ ) and basal area mortality ( $\mu_B$ ). For example, if smaller adults have higher mortality rates than larger adults, then average mortality losses are greater for the number of individuals than for basal area, i.e.  $\mu_A > \mu_B$ . However, adult savanna trees often resprout after fires, which implies that the individual mortality rate is often much less than for losses in basal area, i.e.  $\mu_B > \mu_A$ . For the following analyses, I contrast three versions of the model where i.  $\mu_B = \mu_A$ , ii.  $\mu_B$  and  $\mu_A$  are not equal, and iii. model parameters that exclude the demography (i.e. solutions for Eq. 3-4, with  $B_oA=B_{max}$ ). A complete description of the equations and methods used to construct bifurcation diagrams appears in Appendix 2.

First I examine scenarios where tree-grass competition is excluded ( $\alpha = 0$ ,  $c_{gw} = 0$ ) in order to determine required juvenile and adult mortality for a given steady-state solution of basal area (B<sup>\*</sup>). Increased juvenile mortality (from 0.2-0.5) dramatically changes steady state basal area values (Fig. 2.4). Conversely, greater adult mortality is required to reduce steady-state basal area for a given juvenile mortality. For instance, at relatively low juvenile mortality ( $\mu_J = 0.2$  and  $\mu_J = 0.3$ ), unrealistically high adult mortality is required--(i.e.  $\mu_A > 0.30$ ) to drive the woody plants to extinction, i.e. B<sup>\*</sup> = 0. Such high adult mortality is unrealistic since it would be greater than for juveniles, which is very uncommon. By increasing  $\mu_J$  from 0.2, 0.3, 0.4 to 0.5 solutions for the demographic models converge towards the logistic model, which remains unchanged since  $c_{gw} = 0$ . The logistic model would suggest that woody plant exclusion, in the absence of tree-



Figure 2.3. Change in steady state woody basal area as function of adult mortality rate. Small changes in adult mortality in the model lead to "jump-like" behavior in bifurcation diagrams. Along the stable branch (solid line) of the diagram, small incremental changes in adult mortality display monotonic decreases in the steady-state solution for woody basal area (B<sup>\*</sup>). When a threshold in adult mortality ( $\mu_{cr}$ ) is exceeded, basal area values collapse to zero. Thereafter, an unstable branch (dotted line) hysteresis-effect governs the dynamics as a new lower threshold in mortality ( $\mu_o$ ) must be reduced to  $\mu_o$  or less to allow B<sup>\*</sup> to again approach the stable branch. Although it is unlikely that observed basal area values might actually collapse completely to zero, the figure illustrates a plausible scenario with rapid decline due to sensitivity to adult mortality in the population. grass competition, requires an annual adult mortality of at least 10%. This high mortality level in undisturbed systems seems unlikely. It could occur with severe disturbance such as caused by elephants (Dublin et al. 1990; Holdo 2006), or the combination of fire and elephants (Dublin et al. 1990; Baxter and Getz 2005). However, in low disturbance situations these results suggest that it may be necessary to invoke treegrass competition as well for the model to replicate observed basal area dynamics using field-based parameters.

Increasing tree-grass competition ( $c_{gw}$ ) leads to bistability in the model (Fig. 2.5). Here, I increased  $c_{gw}$  from 0.25, 0.5, 0.75 to 1.0 while keeping all other parameters fixed. At low  $c_{gw}$  results are qualitatively similar to the no tree-grass competition cases (Fig. 2.4), but lower adult mortality rates are sufficient to cause woody population collapse. Increasing  $c_{gw}$  (i.e. increasing the impact of grass on wood growth) leads to B<sup>\*</sup> solutions with increasing bifurcation tendencies, particularly for  $c_{gw}$  values above 0.50, with a stable upper branch (i.e. declining B<sup>\*</sup> values as adult mortality increases) and an unstable lower branch. Beyond the inflection point dividing the two branches, greater adult mortality leads to basal area collapses (B<sup>\*</sup> = 0). There are also striking differences in the three models as  $c_{gw}$  is increased. For example, by increasing  $c_{gw}$  to 1.0 leads to increase in the slope of the no demography model and at  $c_{wg} = 0$ , there is a singular point with no slope. Although the differences in adult mortality appear small (Fig. 2.5cd), small changes in adult mortality (2%) can be the difference between woody plant extinction and woodland conditions (B<sup>\*</sup> = 15.0 m<sup>2</sup> ha<sup>-1</sup>).



Figure 2.4. Model bifurcation diagrams showing impact of increasing juvenile mortality parameter ( $\mu_J$ ) on steady-state solutions of basal area (B<sup>\*</sup>) for a model with no tree-grass competition. Increasing juvenile mortality ( $\mu_J = 0.2, 0.3, 0.4, 0.5$ ) and no tree-grass competition ( $\alpha = 0, c_{gw}=0$ ) lead to decreased values in the critical bifurcation parameter (adult mortality;  $\mu_A$ ). At low juvenile mortality, woody exclusion appears unlikely in the model as adult mortality required exceeds juvenile mortality; which is rarely observed. Three model types shows where i) basal area mortality ( $\mu_B$ ) does not equal adult mortality ( $\mu_A$ ) ii)  $\mu_A = \mu_B$  and iii) simulations approximating the logistic model with maximum basal area set to a fixed value  $B_{max}$  to decouple the basal area growth from the demographics of the juveniles and adults. All other parameters were set to default values (Table 1).

In addition to tree-grass competition ( $c_{gw}$ ), there is also potential for strong competitive effects ( $\alpha$ ) of grass on juvenile recruitment, with numerous observations showing reduced seedling establishment at high standing herbaceous levels (Belsky 1994; Scholes and Archer 1997; Higgins et al. 2000; Simmons et al. 2007). There is a striking effect shown in the model when grass-juvenile competition  $\alpha$  is increased from 0.5, 0.75, 1.0 and 1.5 (Fig. 2.6). The last cases suggest that juvenile recruitment may reduce to zero when G<sup>\*</sup> < G<sub>max</sub>, as B<sup>\*</sup> solutions become increasingly nonlinear with population collapse thresholds occurring at lower adult mortality ( $\mu_A$ ) values as the grasson-juvenile parameter ( $\alpha$ ) is increased (Fig. 2.6). It is the inclusion of both tree grass competition values ( $\alpha$  and  $c_{gw}$ ) that allows reduction of the adult mortality parameter ( $\mu_A$ ) to levels approximating observed values (less than 2%). If there is very strong grassseedling competition ( $\alpha = 1.5$ ), in addition to the "jump" behavior described above, there is another stable state for B<sup>\*</sup> associated with the model when  $\mu_A = \mu_B$  (Fig. 2.6d).

### 2.5 Discussion

This work draws its motivation from a recent review (Sankaran et al. 2004) that called for greater integration of demographic stage structure and resource competition in savanna models. Although the review correctly identified that savanna models have too narrowly focused on either resource competition or demographic stage and disturbance as the key drivers of savanna structure and function, only one study (Gardner 2006) has been subsequently published that addresses, in part, some of the challenges posed in the review. While Sankaran et al. (2004) identified a significant gap in our ability to model savanna dynamics, they provided no details on how resource use, tree-



Figure 2.5. Model bifurcation diagrams showing impact of increasing tree-grass competition parameter ( $c_{gw}$ ) on steady-state solutions of basal area (B<sup>\*</sup>). Increasing tree-grass competition ( $c_{gw} = 0.25, 0.50, 0.75, 1.00$ ) leads to increased potential bistability in the model as solutions become more curvilinear. In the diagrams, stable steady-solutions of B<sup>\*</sup> are indicated with either solid or open circles or a solid line for the three different model versions as in Figure 4. Unstable solutions indicative of saddle-node bifurcations (see Fig. 2.3) are shown with dashed lines. All other parameters were set to default values (Table 2.1).



Figure 2.6. Model bifurcation diagrams showing impact of increasing tree-grass competition parameter ( $\alpha$ ) on steady-state solutions of basal area (B<sup>\*</sup>). Increasing grass-on-tree competition ( $\alpha = 0.50, 0.75, 1.00, 1.50$ ) leads to increased potential bistability in the model as solutions become more curvilinear. Fig 6d clearly indicates multiple potential stable states as the bifurcation diagrams takes on a reverse-S shape for the  $\mu_A = \mu_B$  model case. In the diagrams, stable steady-solutions of B<sup>\*</sup> are indicated with either solid or open circles or a solid line for the three different model versions as in Figure 2.4. Unstable solutions indicative of saddle-node bifurcations (see Fig. 2.3) are shown with dashed lines. All other parameters were set to default values (Table 2.1).

grass and tree-tree competition could be implemented jointly in a simple savanna model. I believe that, in order for a resource competition model to correctly represent tree-grass vegetation dynamics, resource use must allow for potential size asymmetric competitive relationships that are likely nonlinear in savannas.

The goal for this study was to introduce a new model and highlight some of the problems associated with more fully integrating resource competition and demography within simple savanna models. Observations from field studies suggest that aggregate savanna models without explicit treatment of size structure (Walker et al. 1981; Walker and Noy-Meir 1982; van Langevelde et al. 2003; D'Odorico et al. 2006; Williams and Albertson 2006) are unable to incorporate important size-specific processes such as fire that lead to high loss rates with small individuals and low loss rates with larger individuals (Trollope 1984; Williams et al. 1999; Higgins et al. 2000; Hoffmann et al. 2003; Holdo 2005; Hanan et al. 2007). Likewise, aggregate models cannot properly represent growth rates for a population of woody individuals where the smaller plants are fast growing and the large trees slow-growing (or not growing at all), with an average growth rate unable to appropriately depict the population level growth rate. Finally, since resource use generally scales nonlinearly with individual plant weight (Enquist et al. 1998), aggregate models (e.g. Anderies et al. 2002; Williams and Albertson) may exhibit large errors in potential biomass. Using basal area as the primary index of woody plant quantity, the linear resource use relationship (Enquist et al. 1998) alleviates problems using woody biomass.

I believe that my model innovatively combines the minimum demographic structure (two size classes) with realistic resource competition that offers a significant conceptual

advancement in savanna ecology. Instead of using a fixed maximum for woody biomass, as found in other savanna models, I allow the basal area maximum to be a function of the number of adult trees ( $B_0A$ ). Consequently, I avoid the potential problem of a single tree effectively growing to an arbitrary maximum basal area. Finally, my use of a variable maximum basal area (dependence on the number of adults) allows for better incorporation of size-specific growth rates as basal area growth slows to zero when average tree size reaches its maximum ( $B_0$ ).

I manipulated several aspects of tree mortality and competition in the new model to examine effects on steady state values of basal area (B<sup>\*</sup>). By increasing juvenile mortality but excluding tree-grass competition (Fig. 2.4), I was unable to reduce "required" adult mortality to observed natural levels (about 1%) except with very high B<sup>\*</sup> values. This suggests that, in the absence of disturbance, tree-grass competition, or grass-on-tree competition, plays an important role in savannas. The finding agrees well with several studies that show strong competition between trees and grass (Belsky 1994; Simmons et al. 2007). The addition of tree-grass competition (grass on juveniles and grass on adults) resulted in simulations that were qualitatively very different, shifting from monotonic behavior in the absence of tree-grass competition with small increases in adult mortality leading to lower basal area values (Fig. 2.3) to bistable behavior when tree-grass competition is included (where small changes in adult mortality beyond a critical point led to collapse of basal values to zero; Fig. 2.5). High, but ecologically plausible, values of grass-juvenile competition ( $\alpha$ ) led to alternate stable states in B<sup>\*</sup> (Fig. 2.6).

My results have potentially far reaching implications for improving global vegetation models that are currently trying to better incorporate savanna vegetation dynamics (e.g. Thornwicke et al. 2001; Bond et al. 2005). These dynamic global vegetation models (DGVMs) have been used to assess the relative importance of fire in determining existing vegetation structure in southern Africa savannas (Bond et al. 2003; Sankaran et al. 2005) and showed that fire is an important agent for determining vegetation structure worldwide, as without fire a considerable portion (33%) of existing mixed tree-grass ecosystems would become closed forests (Bond et al. 2005). Since DVGMs generally do not account for size structure in the woody plant community (only differentiate between plant functional types, e.g. woody plants & grasses), it is likely that the simple relationships for woody plant and grass resource use are unrealistic depictions for savanna vegetation dynamics, including the impacts of fires on savanna vegetation, and predicted woody biomass.

In modeling ecosystem dynamics, a balance must be found between simplicity and fully representing the complexity of real ecosystems. Although the use of simple, aggregated models can often lead to a clear message since the mathematical behavior has been well-studied, the message may also present a false sense of certainty since the foundational models have yet to be fully scrutinized with data. For example, simple logistic dynamics may be unable to faithfully represent a population of fast growing juveniles and slow or non-growing adults, nonlinear relationships between size and resource use that affect maximum basal area and competition, and nonlinear relationships between tree size and fire mortality. Furthermore, although some savanna trees live for thousands of years, woody plants are living organisms that have finite lifetimes, and

often a sizeable portion of the biomass of a population is contained in just a few individuals, such that mortality can lead to large change in biomass. In contrast to herbaceous plants, trees allocate greater resources to structural tissues to support an elevated canopy, which likely confers an advantage to woody plants over grasses.

Until now, new low-dimensional modeling approaches have not been forthcoming that couple resource competition and disturbance with the ability to incorporate sizeasymmetric processes in savannas. Throughout this study I have highlighted various shortcomings of aggregated savanna models. While there has been an evolution in savanna modeling using aggregated models making small adjustments to account for disturbance (Ludwig et al. 1997; van Langevelde et al. 2003) or stochastic processes (D' Odorico et al. 2006; Williams and Albertson 2006), it is possible that lack of formal criticism of the aggregated models may have hindered development of new models. Moreover, beyond mere critical analysis, using a minimalist approach I have provided an alternative perspective for modeling savannas, yielding a fully analytical solvable model that couples resource competition and disturbance yet also includes some demographic size-structure. The model is useful because of its ability to incorporate tree size, enabling investigations of size-asymmetric fire loss and tree-grass competition. The coupling of woody plant density and maximum basal area in the model displays, under a broad range of demographic and competition parameter values, demographic "bottleneck conditions" described mathematically as saddle node bifurcations and ecologically as alternate stable states. Thus, the model provides a new tool for investigations into a largely unexplored realm in savanna modeling between existing "aggregated" models and more complicated individual-based models.

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## **Appendix 1**

# Implications for Size, Tree-grass Competition, Maximum Basal Area

The single woody equation models differ substantially in how they consider resource use is affected by existing woody biomass. The resource implicit models (Anderies et al. 2002; Beckage et al. 2006; Williams and Anderson 2006) linearly scale resource use to plant biomass, while the resource explicit models (Walker et al. 1981; van Langevelde 2003; Holdo 2007) preclude water use by existing woody biomass and instead partition resources for new growth. Long term studies showing resource allocation and maintenance water use by savanna trees are currently unable to resolve the contradictions between these approaches (see February et al. 2006 for a 2-3 year study in Kruger National Park). Here, maintenance use is broadly defined as resource use required for woody plants, in the absence of any woody stem growth, but includes leaf and fine root production and maintenance water use in the absence of woody stem growth (e.g. Scholes and Walker 1993) because leaf production generally occurs at the beginning of the growing season before stem wood production.

In this study, I show that because of nonlinear relationships between plant weight and water resource use, "aggregated" savanna models using biomass carrying capacities cannot model tree-grass competition correctly. I use tree basal area as a better measure of woody quantity that has advantages of being a frequently measured quantity in field studies and a quasi-linear resource use relationship. There is a strong ( $r^2=0.96$ , p=0.001)

linear relationship between mean annual precipitation and tree basal area for fireprotected savanna sites (Fig. A1). This observation is consistent with theoretical studies (Enquist et al. 1998) and can be considered complementary to the relationship between mean annual precipitation and maximum tree cover found for African savannas (Sankaran et al. 2005). Four sites are located in the ecological burn plots (EBP) at Kruger National Park (KNP) in South Africa, with three locations measured recently and another survey taken in 1974. Another site used stem plot data from a fire-protection area of Hlhuluwe-Imfolozi Park in KwaZulu-Natal, South Africa (William Bond, personal communication). Fire has been protected from these sites for at least 50 years (Biggs et al. 2003; Higgins et al. 2007). For details of site locations see Table 2.

Observed woody biomass values in savannas (House and Scholes 1998; Higgins et al. 2007; Holdo 2005) are substantially higher than suggested by a resource explicit model (van Langevelde et al. 2003) for the case where model parameters have been changed to give trees exclusive access to all soil water (grass exclusion). For illustrative purposes to show the effect of tree size on woody maximum basal area, hypothetical maximum woody plant biomass (dry matter) was computed for different sized tree (uniform size) populations along a rainfall resource gradient. A simple allometric relationship (e.g. Higgins et al. 2007) determined the dry weight for tree individuals at four different tree diameters: 5 cm, 10 cm, 25 cm, and 50 cm keeping tree basal area constant at each mean annual precipitation (MAP). At lower MAP, the maximum woody plant weight differences are small, but the differences between tree sizes are substantial with increasing MAP (Fig. A2).

Although tree ring analyses have been used extensively as a proxy for past climatic fluctuations, particularly for precipitation (Therrell et al. 2006), tree rings can also be used as direct evidence of growth patterns, and with the aid of allometric relationships, to show how resource use and allocation shifts from woody growth to plant maintenance dominance as trees grow in size and in drought years. Here, I make use of published allometric relationships (Netshiluvhi and Scholes 2001; Shackleton 2002) between stem diameter with leaf mass and dry weight and an extensive tree ring data set (Stahle et al. 1999; collected from about 30 large trees in Hwange National Park, MAP=590 mm, representing over 100 years of tree growth) for a common savanna species (*Pterocarpus* angolensis) to better examine how water allocation patterns shift in tree individuals subject to climatic fluctuations over the course of many decades. Figure A3 shows tree growth trajectories through time and growth frequency distributions for *Pterocarpus* from the tree ring measurements. I then used the allometric equations to estimate from stem diameters to show: annual growth (biomass kg) for individual trees compared with tree size (Fig A3c), and estimated lead water partitioning. There is a remarkably strong correlation between age and diameter for relatively undisturbed trees ( $r^2=0.96$ ) and a lognormal distribution for diameter growth. Stem growth rates for *Pterocarpus* angolensis trees are typically 0.2-0.5 cm yr<sup>-1</sup>, translated into a growing period of 20-30 years to reach fire-resistant size. The results also show that, although relative growth woody growth rates may be largest for small trees, absolute growth (kg DM wood vr<sup>-1</sup>) in woody individuals tends to occur in medium sized trees (Fig. A3c). By assuming that water use costs for leaf production are lower than for wood production (van Langevelde et al. 2003; Cernasak et al. 2006), results here support the idea that for many large trees

in savannas a large portion of water use is devoted for maintenance functions, i.e. leaf and fine root production. This result cast doubts on the whether resource explicit models that neglect maintenance costs for woody vegetation realistically represent water resource use for woody plants in savannas (van Langevelde et al. 2003), particularly where large trees dominate the woody biomass.



Figure A1. Linear relationship between average precipitation and maximum basal area. Mean annual precipitation-basal area relationship is shown for highest recorded basal area in fire-protected sites (plot size  $\sim 0.25$  ha or larger). Four of the sites are in Kruger National Park: Pretoriuskop (725 MAP), Skukuza (625 MAP), Satara (550 MAP), and Mooiplaas (425 mm). The other site is a closed canopy forest at Hhluwe-Umfolozi Park in Kwazulu-Natal (900 MAP). For comparative purposes, basal area measurements are show for two extensive savanna transects in southern Africa (Kalahari Transect) and northern Australia (Northern Australian Terrestrial Transect). Observed basal areas for fire-protected sites in South Africa are considerably higher than for the other two transects.



Figure A2. Wood biomass is a function of rainfall and tree size. Climate-maximum tree biomass relationships for different average size classes: 5, 10, 25, and 50 cm using climate-basal area constraint (Fig. A1) and allometric relationship  $W_{kg}$ =0.035D<sup>2.67</sup>. The maximum woody biomass is also shown for results in van Langevelde et al. (2003) and for recent observations along a rainfall gradient in Kruger National Park.



Figure A3. Tree ring data (Stahle et al.1999) yields important long-term information about savanna growth rates and resource use. Trajectories of tree growth for *Pterocarpus angolensis* at Hwange National Park Zimbabwe show basically uniform growth rates over many decades (Fig. 4a). Growth rates for all trees are well characterized by a lognormal distribution of growth rates (4b). There is a strong relationship between previous growth and current growth (4c). Water allocation shifts to maintenance with larger tree size. Leaf-stem water partitioning for all trees is shown based on specific water use of 600 g g<sup>-1</sup> for leaf mass production and 1000 g g<sup>-1</sup> for stem wood production. Allometric relationships (Netshiluvhi and Scholes 2001): Leaf Biomass (in kg) =  $0.0017D^{2.63}$  and Wood Biomass (in kg) = $0.043D^{2.44}$ .

Site	Latitude	Longitude	Annual Rainfall (mm)	Dominant Vegetation	Source
Lishuwa Forest	14.42 S	23.52 E	970	1	SAFARI-2000
Mongu	15.44 S	23.25 E	879	2	SAFARI-2000
Senanga	15.86 S	23.34 E	811	2	SAFARI-2000
Maziba Bay	16.75 S	23.61 E	737	2	SAFARI-2000
Sachinga Station	17.70 S	24.08 E	707	3	SAFARI-2000
Pandamatenga	18.66 S	25.50 E	698	4	SAFARI-2000
Maun Centre	19.93 S	23.59 E	460	5	SAFARI-2000
Sandveld Station	22.02 S	19.17 E	409	6	SAFARI-2000
Tshane	24.17 S	21.89 E	365	7	SAFARI-2000
Vastrap Range	27.75 S	21.42 E	216	8	SAFARI-2000
Skukuza KNP	28.03 S	32.02 E	650	9	Sea et al.
Satara KNP	28.07 S	32.02 E	550	10	(unpublished) Bond et al. (unpublished)
Mopani KNP	28.13 S	31.48 E	425	11	Sea et al. (unpublished

<sup>1</sup> Evergreen Woodland (Cryptosepalem) <sup>2</sup> Miombo Woodland (Brachystegia)

<sup>3</sup> Woodland (Combretum)

- <sup>4</sup> Woodland (Schinziophyton, Baikiaea)
  <sup>5</sup> Woodland (Colospherum mopane)
- <sup>6</sup> Wooded grassland (Terminalia)
- <sup>7</sup> Wooded grassland (Acacia) <sup>8</sup> Scrub (Acacia)

<sup>9</sup> Woodland (Combretum)

<sup>10</sup> Woodland (Acacia/Marula)
 <sup>11</sup> Scrub (Colospherum mopane)

Table A1. Site locations for tree stem data.

# **Appendix 2**

In order to solve for steady state solutions in B<sup>\*</sup>, I first set the left hand sides of Eq. 1-4 to zero (see Fig. 2). Given that the characteristic polynomial for the system is fourth order, finding an explicit analytical solution for B<sup>\*</sup> in terms of the parameters is impossible. However, this representation allows us to determine the saddle node points for  $d\mu_A/dB^* = 0$ . Through algebraic manipulation I am able to obtain an equation that relates one parameter, adult mortality ( $\mu_A$ ) to all other parameters and B<sup>\*</sup>:

$$\mu_{A} = \frac{mB_{o}(c_{1}B^{*} + c_{2})(1 - \alpha + \alpha c_{wg}\frac{B^{*}}{B_{max}} + \alpha \frac{\mu_{G}}{r_{G}})(1 - \beta \frac{B^{*}}{B_{max}})}{1 - \frac{B}{B_{max}} + \frac{\mu_{J}}{p}}$$
(B1)

where 
$$c_1 = 1 - c_{gw} + c_{gw} \frac{\mu_G}{r_G} - \frac{\mu_B}{r_B}$$
 and  $c_2 = \frac{c_{gw}c_{wg}}{B_{max}}$ . (B2)

By substituting a range of  $B^*$  values into equation (B1), I am able to calculate exact implicit analytical solutions for adult mortality rates given other parameter values and  $B^*$  values. Conversely, and more important, I am able to compute all analytical solutions for  $B^*$  given parameter values.

## Chapter 3

# Tree Size Structure and Implications for Fire-vegetation Interactions in African Savannas

### **3.1 Introduction**

Although tree size plays a critical role in determining the response of individual trees with respect to growth, competition, and disturbance, the patterns in woody population size structure across gradients of climate and disturbance remain largely unknown and unexplored. For example, tree size structure (the size and density of individuals in each size class) directly affects population level growth rates because larger individuals tend to be slower growing as they invest greater resources to non-growth functions (e.g. respiration and reproduction, see Ryan et al. 1997) while smaller individuals are fast growing (Holdo 2006; Prior et al. 2006). Thus a population consisting of a few large trees may grow more slowly than a population of smaller trees with the same stem basal area. There is also a likely relationship between tree size and the strength of tree-tree and tree-grass competition (for water, nutrients, and light) and size affects the ability of trees to withstand various disturbance events related to herbivory, wind and fire.

In savanna systems where trees, by definition, share resources with an herbaceous layer, it seems likely that larger trees will have a competitive advantage, relative to

smaller trees and herbaceous vegetation, because of their more fully developed root systems. However, field data in support of the idea is lacking (Scholes and Archer 1997; Sankaran et al. 2004). Perhaps woody plant size structure has its most discernible impact in savanna fires because direct mortality and top-kill of trees during ground fires affects small individuals much more than larger individuals (Trollope 1982; Williams et al. 1999; Higgins et al. 2000). Furthermore, large trees sometimes reduce herbaceous production in mesic savannas, decreasing fuel loads and increasing fuel moisture, both of which lead to lower intensity fires and reduced fire spread (Aubreville 1966, Walter 1971, Belsky 1994; Higgins et al. 2000). While savanna studies are increasing focus on the importance of fire intensity (Higgins et al. 2000; Govender et al. 2006), greater understanding of size structure of woody plants may prove critical in determining actual woody plant mortality because of nonlinear relationships that have small individuals in a population suffering relatively high fire mortality (> 95 %) while larger individuals are mainly fire resistant (Trollope 1982; Williams et al. 1999; Hoffmann 2003; Holdo 2006).

A number of studies have addressed tree-size structure relationships in savannas (Scholes et al. 2002; Skarpe 1990; Wiegand et al. 2006; Higgins et al. 2000; Pellew 1983; Caylor et al. 2003; Kennedy and Potgieter 2003). However, general conclusions are confounded because most studies have been restricted to short duration and over small spatial scales. Studies examining drier savannas (annual rainfall < 400 mm yr) suggest that tree size is often characterized by a single dominant size mode (Skarpe 1990; Wiegand et al. 2006), suggesting that recruitment is difficult in many years. However, in wetter savannas, where woody juvenile recruitment is less limited by drought, smaller individuals are generally more numerous than larger trees, and

population structures can resemble distributions typical of continuous recruitment (Aubreville 1966; Bond and van Wilgen 1996; van de Vijver et al. 1999; Higgins et al. 2000; Higgins et al. 2007). Some savanna studies have proposed that, in addition to smaller trees dominating the number of individuals, they also compose much of the woody biomass, and that this biomass is subject to high fire losses (van de Vivjer et al. 1999; van Langevelde et al. 2003; Higgins et al. 2007). No study to date, however, has rigorously examined size structure of savannas over a rainfall gradient (but see Scholes et al. 2002 who report that more humid savannas have greater mean tree height), and my subjective field observations suggest that larger trees comprise an increasing fraction of total biomass with increasing rainfall (e.g. Fig. 3.1).

This study examines the role of tree size structure on the ecology and function of tropical savannas. While we may naturally, and correctly, view tree population size structure as a response to climate and disturbance factors, we often ignore the fact that the emergent tree size structure may come to dominate subsequent responses and thus have profound implications on savanna function. Given recent theoretical studies that link individual size and function to population and ecosystem structure (Enquist et al. 1998; Enquist and Niklas 2001), this paper will examine patterns specific to savanna systems. Although it is acknowledged that disturbance may play a large ecological role in savannas, with drought and fire being major factors leading to punctuated recruitment in drier and wetter savannas (e.g. Higgins et al. 2000), respectively, as a starting point, I explore demographic structures in relatively undisturbed savannas. I test three general hypotheses about how size structure in low disturbance systems responds to increasing rainfall, how woody biomass in fire-prone systems is partitioned between size classes,



Figure 3.1. Large fire-resistant trees often dominate woody biomass in savannas. The Makhohlola Exclosure site in Kruger National Park has excluded fire and elephants since 1971. Where elephants have been excluded, large trees dominate the woody biomass both for treatments including and excluding fire. The site receives an average annual rainfall of 550 mm, tree cover  $\sim 30\%$  with a basal area of 19.6 m<sup>2</sup> ha<sup>-1</sup>.

and finally how woody biomass response to an increase in disturbance (fire) can have transient effects with opposite sign to the long-term response.

### The three hypotheses are

- With increasing rainfall in tropical savannas, size-abundance relationships in protected locations shift from demographic structures characteristic of discontinuous ("punctuated") structure towards demographic structures more characteristic of continuous recruitment. Thus size-abundance relationships for the wetter savannas will converge with patterns in adjacent forest systems, i.e. a power law relationship with slope -2.
- 2) In savannas subject to fire, biomass is increasingly partitioned to fire-resistant size classes (larger trees) at sites with increasing average rainfall, where the interval between fires is shorter and fire intensity is greater.
- 3) In savannas subject to an increase in fire frequency, woody biomass can be maintained or even increase in the transient (e.g. > 30 years) as long-lived trees of fire-resistant size classes continue to grow.

## **3.2 Background**

### **3.2.1 Applications of Metabolic Theory to Savannas**

A recent theoretical framework based on plant energetics called *metabolic theory* makes testable predictions on how size affects resource use, growth and mortality rates both for individuals and translated into a theoretical equilibrial population size structure (Enquist et al. 1998). The theory predicts that plant resource use [R] for mass-specific production scales with mass [M] of an individual as a power law relationship:  $R = aM^{3/4}$ , where *a* is a constant of proportionality. However, because of the allometry between plant mass and other metrics, the power law implies a linear scaling with stem basal area and leaf mass (Enquist and Niklas 2002). In metabolic theory, growth rate is predicted to increase with stem diameter (D) as  $dD/dt=bD^{1/3}$ , and mortality rates decrease with increasing plant size as  $M(D)=cD^{-2/3}$ , where *b* and *c* are constants of proportionality. If growth rates and mortality rates are known, then the theory is able to predict a steady-state size distribution for a population as a power law relationship with slope –2 between basal diameter and abundance. The theory was tested extensively by Enquist and Niklas (2001) with an established global forest data set (Gentry 1995), confirming that the predicted power law size-abundance relationship with slope –2.0 fits the observations very well ( $r^2=0.90$  for most tropical forests in Africa) and is relatively unaffected by differing levels of species diversity, total standing biomass, sampling area, and latitude in all but the highest latitude sites (Enquist and Niklas 2001).

The results of Enquist and Niklas (2001) notwithstanding, there is vigorous debate on whether the predictions made by metabolic theory for growth and mortality rates, and size structure, are broadly and causally applicable or whether observed patterns approximate the theory because alternate processes (that happen to result in similar patterns) are active (Muller-Landau 2006a, Muller-Landau 2006b; Coomes 2006; Coomes and Allen 2007). These critics challenge that predictions are not applicable across all size classes: there is generally good agreement for small to medium sized trees, but less agreement in observations for largest size classes. Recent studies based on a meta-analysis of 10 large plots (20-50 ha each) at long term research sites in tropical forests reject a power law size-abundance relationship for old-growth forests (Muller-Landau et al. 2006a; Muller-Landau et al. 2006b). It was suggested that strong canopy effects influence the availability of light, and since small and large trees were subject to differing levels of light competition, this violates assumptions of relatively constant

available resources made by metabolic theory (Muller-Landau 2006ab; Coomes 2006). A recent review suggested that the predictions from metabolic theory may be more applicable when trees are growing in isolation from each other with respect to light competition (Coomes 2006). Coomes (2006), while critical of the generality of metabolic theory for tropical forests, highlights an opportunity and challenge for savanna ecologists to study tree structure more closely with respect to the current debate in theoretical plant ecology.

### 3.2.2 Using Allometry to Compute Woody Biomass

Allometric relationships have long been used for computing stand level woody biomass from size (diameter and height) of individual plants (Whittaker et al. 1974; Williams et al. 2004). However, field-derived allometric relationships exist for only a few tree species, and often the sample size is very low (fewer than 30 trees). A more practical route for using allometric relationships in savannas, where the relationships for many species are unknown, is to use a generalized allometric relationship for all species. Generalized allometry is particularly useful if differences in predicted weights between species for trees of similar size are smaller than differences with respect to plant size for the same species (Williams et al. 2004). The variation in allometry between species can be explained by differences in both wood density (specific gravity) and tree shape (Niklas 1994). Metabolic theory predicts a power law relationship (with slope 8/3) between stem diameter and plant dry mass (Enquist and Niklas 2002). For this study I use an allometric relationship between stem diameter (D in cm) and plant weight (W in

Kg): 
$$W = 0.04D^{8/3}$$
 (3.1)

where the slope is consistent with metabolic theory and the model predicts woody biomass consistent with published literature for savanna tree species (Netshiluvhi and Scholes 2001; Williams et al. 2004; House et al. 2007; Higgins et al. 2007; Fig. 3.2).

### 3.2.3 Fires in Savannas

Fire is thought to play a critical role in structuring savannas, particularly for wetter savannas where mean annual precipitation (MAP) is greater than 700 mm (Higgins et al. 2000; Scholes and Archer 1997; Bond et al. 2003; Sankaran et al. 2005; Holdo 2007). While earlier studies focused on threshold canopy height for protection from fire mortality (Trollope 1982), recent research has focused more on tree stem diameter as the critical size parameter that determines fire mortality (Williams et al. 1999; Hoffmann et al. 2003; Holdo 2006; Prior et al. 2006), because larger trees with thicker bark have greater protection from fire (Gignoux et al. 1997; Hoffmann et al. 2003). Although the effects of fire season and interval have long been studied (e.g. Trapnell 1959; Aubreville 1966), only recently has more effort been put into understanding the role of fire intensity in woody plant survival and mortality (Trollope and Tainton 1986; Frost and Robertson 1987; Trollope et al. 1995; Higgins et al. 2000; Govender et al. 2006). Fire intensity has been defined variously in the literature (Bond and van Wilgen 1996) as a function of fuel quantity and quality that is reflected in fuel load, heat yield, and spread rate (Byram 1959). Grass quantity largely reflects herbaceous production in response to growing season rainfall, although it may also be affected by tree-grass competition for water, nutrient, light resources, and grazing intensity. Grass fuel quality is a function of grass moisture content, which greatly impacts fire temperature and spread (Higgins et al. 2000;


Figure 3.2. Generalized allometric ( $W_{kg}=0.04D_{cm}^{8/3}$ ) and species-specific relationships between stem diameter and plant dry weight for several savanna tree species. The generalized model predicts small plant mass with small errors across all species. For larger trees, species-specific and generalized relationships diverge with relationships for several *Acacia species* (Goodman 1990), *Combretum species* (Scholes 1987, Shackleton 1988), *and Colophospermum* species (Scholes 1987) underestimated by the general model, and the general model overestimating biomass for *Sclerocarya birrea and Acacia Nigrescens*. The relationship is in good agreement with a recent study by House et al. (2007) and with respect to multiple species reported in Tietiema (1993).

Govender et al. 2006). Fire intensity has been defined variously in the literature (Bond and van Wilgen 1996) as a function of fuel quantity and quality that is reflected in fuel load, heat yield, and spread rate (Byram 1959). Grass quantity largely reflects herbaceous production in response to growing season rainfall, although it may also be affected by tree-grass competition for water, nutrient, light resources, and grazing intensity. Grass fuel quality is a function of grass moisture content, which greatly impacts fire temperature and spread (Higgins et al. 2000; Govender et al. 2006). Strong interannual variability in rainfall, coupled with variability in the timing of ignition and weather conditions at ignition, lead to large variability in fire intensity (Trollope 1982; Bond and van Wilgen 1996; Higgins et al. 2000).

Although the aforementioned sources of variability of fire intensity are of undoubted importance in determining fire mortality, a profound yet understated relationship (see Fig. 3.3) for savanna fire ecology is that fire mortality for individuals may be more determined by tree size than by either fire intensity or interval: small trees generally have high fire mortality regardless of fire intensity; larger trees have negligible fire mortality regardless of fire intensity or interval (Trollope and Tainton 1986; Trollope et al. 1995; Higgins et al. 2000). Thus the woody mass consumed during fires may depend equally, or more, on the structure of the woody vegetation than on the intensity or timing of the fire.

## **3.3 Site Data and Methods**

Several fire-excluded sites exist at savanna locations in southern Africa (Bond et al. 2003). These sites allow for testing the impacts of disturbance on tree-size distribution



Figure 3.3. Effect of stem diameter on probability of mortality during fire for savanna trees. All symbols represent a synthesis of several studies linking fire mortality for savanna trees. Field observations (symbols) are shown using data from Australia (Williams et al. 1999), Brazil (Hoffmann et al. 2003) and Zimbabwe (Holdo 2006), and for a savanna model (Higgins et al. 2000). Two of the studies represent variation in mortality for different tree species (Holdo 2006; Hoffmann and Solbrig 2003). Williams et al. (1999) used data from a high intensity (> 20,000 kW m<sup>-1</sup>) fire event that exhibits considerably higher mortality than the other studies even for larger trees. While mortality rates tend to agree well with each other at larger tree sizes (diameters> 15 cm), there is considerable variation in mortality for smaller trees due to species and site differences. The model (Higgins et al. 2000) fits the observations fairly well, but differences in computed mortality during intense fire (solid black circle) and week fires (open circle) are not strong in the model.

and whether tree-size structure in savannas, under low disturbance, is indistinguishable from tropical forests despite not having total canopy cover (Hypothesis 1). Table 1 details the sites and sources providing data for this study, and site locations are depicted in Figure 3.4.

### **3.3.1 Data for Testing First and Third Hypotheses**

The Kruger National Park (KNP) is situated in the northeast portion of South Africa and shares a border (Lobombo Mountains) with Mozambique to the east and a border with Zimbabwe to the north (Limpopo River). A series of long-term fire trials (the Ecological Burn Plots; EBP) was set up in 1954 at four locations in the park along a pronounced annual rainfall gradient (400-725 mm rainfall over 300 km) to assess the impact of burning interval and season on vegetation in KNP (see Kennedy and Potgieter 2003; Biggs et al. 2003 and Higgins et al. 2007 for further descriptions). Although the EBP project was not initially intended to be a long-term study, the study continues to this day and provides valuable information on the impacts of fire and climate on savanna structure.

In 1954 two perpendicular belt transects were deployed in each plot to sample tree species and size characteristics of each tree recorded (Biggs et al. 2003). Trees were not measured individually for stem diameter, but rather were enumerated into six different diameter classes if single-stemmed plants. During the 1970s, each plot was re-sampled on a 1 x 1 m grid within 50 x 50 m or 50 x 100 m subplots. In this case all stem diameters, crown diameters, and heights were recorded.

Site	Latitude	Longitude	Annual Rainfall	Vegetation	Source
			(mm)		
Lishuwa	14.42 S	23.52 E	970	1	SAFARI-2000
Mongu	15.44 S	23.25 E	879	2	SAFARI-2000
Senanga	15.86 S	23.34 E	811	2	SAFARI-2000
Maziba Bay	16.75 S	23.61 E	737	2	SAFARI-2000
Sachinga Station	17.70 S	24.08 E	707	3	SAFARI-2000
Pandamatenga	18.66 S	25.50 E	698	4	SAFARI-2000
Maun Centre	19.93 S	23.59 E	460	5	SAFARI-2000
Sandveld	22.02 S	19.17 E	409	6	SAFARI-2000
Tshane	24.17 S	21.89 E	365	7	SAFARI-2000
Vastrap Range	27.75 S	21.42 E	216	8	SAFARI-2000
Skukuza KNP	25.03 S	32.02 E	650	9	Sea et al.
					(unpublished)
Satara KNP	24.39 S	31.77 E	550	10	Bond et al.
Mopani KNP	23.53 S	31.40 E	425	11	Sea et al.
Pretoriuskop, KNP	25.14 S	31.26 E	725	12	Bond et al.

<sup>1</sup> Evergreen Woodland (Cryptosepalem)
<sup>2</sup> Miombo Woodland (Brachystegia)

<sup>3</sup> Woodland (Combretum)

Woodland (Combretum)
 <sup>4</sup> Woodland (Schinziophyton, Baikiaea)
 <sup>5</sup> Woodland (Colospherum mopane)
 <sup>6</sup> Wooded grassland (Terminalia)
 <sup>7</sup> Wooded grassland (Acacia)
 <sup>8</sup> Scrub (Acacia)
 <sup>9</sup> Woodland (Combretan)

<sup>9</sup> Woodland (Combretum)

<sup>10</sup> Woodland (Acacia/Marula)
 <sup>11</sup> Scrub (Mopane)
 <sup>12</sup> Woodland (Terminalia/Marula)

Table 3.1. Site locations for tree stem data.



Figure 3.4. Geographic locations for field sites in Kruger National Park contributing data to the study. Sites were part of a long term burning study and chosen along a pronounced rainfall gradient in the park, with wettest locations in the southwest of the park around Pretoriuskop (725 mm MAP) and driest in the north around Mopani (425 mm MAP). The four general study locations coincided with four principal landscapes in the park. Data were also obtained for 11 sites sites along the Kalahari Transect. For more details on the sites and data, see Table 1. Figure was adapted from Biggs et al. (2003). Reproduced with permission from Koedoe.

In 2002 and 2004, I resampled the woody vegetation in the EBP. At each plot site, original corner stakes (from the 1970s) were located. Not all corners stakes were in their original location, but by use of tree positions from the original survey in the 1970s and geometrical triangulation, missing corners were estimated. With the corners of each plot defined, a series of parallel transects was laid out using cables. Individual plots were resampled at 5 m x 5 m, a size that could easily be compared with an aggregation of the 1 m x 1m plots from the original sampling. For each subplot, I recorded tree location, height, number of stems, diameter of each stem at 30 cm (above any basal swelling), species, and maximum crown diameter. These measurements were directly comparable to those made in the 1970s for the sample plot. Since exact locations of plots were easily identifiable, this provided a unique opportunity to assess changes in savanna tree vegetation structure over a 26-33 year period.

These data were used to construct size-abundance curves for testing hypotheses 1 and 3 that increased average annual rainfall will lead to more continuous recruitment patterns characteristic of forests and that, while growth of woody biomass in smaller individuals is suppressed with continuous burning, fire resistant trees (>10 cm diameter) are able to grow despite fires, such that woody biomass is less sensitive to fire treatments than might otherwise be expected. Although I anticipated using all four sites for my analyses, I excluded one (Pretoriuskop) from hypothesis 1 because sampling area was much lower than for other sites (0.20 ha vs. 1.6-2.0 ha/site for other sites). However, for examining woody biomass changes over time in plots (hypothesis 3), Pretoriuskop had the most complete record for annual and triennial burns, both in the 1970s and in 2002,

particularly since burns at Pretoriuskop almost always occurred on time, in contrast to the other sites (see Biggs et al. 2003).

#### **3.3.2 Data for Testing Second Hypothesis**

The Kalahari Transect (KT) follows a north-south decline in mean annual rainfall from  $\sim$ 1000 mm/yr to  $\sim$ 250 mm/yr on homogenous sandy soils. The transect spans approximately 2000 km from Vastrap, South Africa in the south to Mongu, Zambia in the north (Table 3.1). The uniform soil conditions are a key advantage compared to data from Kruger National Park, where there is a pronounced west-east soil division, with granite soils dominating the western portion of the park and basalt soils dominating the eastern park (Fig. 3.4). Vegetation sampling was performed during 2001 in support of the Southern African Regional Science Initiative (SAFARI 2000) program. The data were obtained from the SAFARI 2000 database (for methods see Scholes et al. 2002). In order to test that increased annual precipitation leads to a higher proportion of woody biomass in fire resistant size classes (hypothesis 2), stem diameters at each plot were first converted into woody biomass by using the generalized allometric relationship (Fig. 3.2). Consistent with published literature (Trollope and Tainton 1986; Trollope et al. 1995; Williams et al. 1999; Higgins et al. 2000; Hoffmann et al. 2004; Holdo 2006) size thresholds were examined both in terms of tree height (> 5m) and stem diameters (7.5 cm diameter stem has high survival in low intensity fire; 15.0 cm diameter stem has high survival in high intensity fire).

## **3.4 Results**

*Hypothesis 1: With increasing rainfall woody plant size structure tends towards continuous distribution* 

There was good agreement with the first hypothesis that, with increasing rainfall, woody plant size structure in savannas tends toward a continuous distribution that resembles the power law relationship predicted by metabolic theory. Figure 5 shows size-abundance relationships for fire-free ecological burn plots across the rainfall gradient in Kruger National Park from the driest site (Mopani, 425 mm MAP) to wettest site (Skukuza, 625 mm MAP). Data were pooled from four replicate plots at each site to ensure sufficient individuals across all size classes. Because many sampled individuals contained multiple stems, data were analyzed both as single stems and aggregated individuals (sum of basal area of all stems) to test whether multiple-stemmed individuals function differently from single stemmed trees of similar basal area. Since resource use is expected to be similar for plants with equal basal area, differences in patterns for trees versus stems may indicate that multiple stemmed plants have different growth and mortality rates than equivalent single stemmed individuals. In the regression analysis, bin size was first attempted with different sized widths, but there is a compromise between having a sufficient number of individuals in each bin and having bin sizes too large incorporating too great a span of tree size. Overall, the pattern was qualitatively the same if a 1.0 or 2.0 cm bin width was used, so the smaller bin size was retained.

Results for the wettest site, Skukuza (625 mm) suggest good general agreement with metabolic theory which predicts a slope of -2 in a plot of log density versus log stem diameter for populations with continuous recruitment (Fig. 3.5a). When stems are aggregated for multi-stemmed trees, there is an excellent relationship between effective tree diameter and density (slope -2.02, r<sup>2</sup>=0.97, p < 0.001). Conversely, when analyzed for individual stems (i.e. each stem is treated as an individual tree), there is greater



Figure 3.5. Size abundance relationships in low-disturbance savannas converge to values predicted by metabolic theory in wetter systems but diverge in drier systems. Data are from a series of long-term fire-exclosures along a rainfall gradient in Kruger National Park, South Africa. At the wettest site (Skukuza; MAP =625 mm yr<sup>-1</sup>), data converge towards a well-defined power law distribution, with slope (-2.02) when stems of an individual are aggregated. This slope is close to the value predicted by metabolic theory. Drier sites (Satara; MAP=550 mm yr<sup>-1</sup> and Mopani; MAP=425 mm yr<sup>-1</sup>) do not conform so closely with the predicted -2.0 slope suggesting demographic bottlenecks to recruitment in younger size classes.

scatter in the data such that no single power law relationship adequately fits the data. Scatter in the observations may be associated with the larger number of very small stems (i.e. diameter < 1.0 cm) that are incorporated into larger (aggregate basal area) multistemmed individuals. At Satara (550 mm), it is clear (Fig 3.5b) that no single power law (with constant slope) can adequately fit the data across the range of tree size. At Satara, a demographic "bottleneck" is apparent for trees diameters between 4-10 cm, which for the smallest sizes (1-2 cm) may reflect difficulty in recruitment on fine-textured soil due to droughts occurring in the wet season. An alternative explanation for differences between Skukuza and Satara may be the higher level of elephant tree damage observed in the Satara ecological burn plots, where the larger trees have suffered high rates of top-kill by elephants (Holger Eckhardt, KNP Scientific Services, personal communication). At Mopani (425 mm), the results show several differences between tree and stem analyses where again no single power law adequately represents the size-abundance relationship across the entire range of stem diameters. Instead, it appears that two relationships are needed in order to fit the data reasonably well, one for smaller trees and one for larger trees. That no single power law can adequately represent size-abundance relationships agrees well with the findings of Muller-Landau et al. (2006ab), although they found the size threshold at about 30-40 cm stem diameter whereas at Mopani it was approximately 15-20 cm.

Thus analysis of woody demographics along the savanna rainfall gradient suggests that woody populations in wetter savannas resemble adjacent forest systems with quasi-

continuous recruitment. In drier savannas, demographic data show punctuated recruitment related to drought and climate variability in these systems.

*Hypothesis 2: Woody biomass fraction in fire resistant tree increases with mean annual rainfall* 

With increasing annual precipitation the fraction of woody biomass in fire resistant size classes increases dramatically (Fig. 3.6), confirming my second hypothesis. Fig. 3.6a shows the relationship between average annual precipitation and fraction of woody biomass associated with trees greater than 5 m in height considered fire resistant (Trollope and Tainton 1986; Trollope et al. 1995; Higgins et al. 2000). From 200-600 mm MAP, there is a linear increase in fire-resistant woody fraction. Above 600 mm MAP, there is little difference between the sites, with most (>95 %) of the woody biomass associated with large, fire-resistant trees. Since stem diameter is often considered to be a better predictor of fire survival probability. Figure 3.6b shows data on fraction of population woody biomass in larger stem diameter classes across the rainfall gradient. Two classes of woody plants exceeding size thresholds are shown, one representing trees likely to be resistant to medium intensity fires (7.5 cm) and a second (15.0 cm) representing trees likely to be resistant to high intensity fires (Williams et al. 1999; Higgins et al. 2000; Hoffmann et al. 2003; Holdo 2006). Figure 3.6b illustrates that, for sites on the Kalahari transect, most (>90%) wood biomass is associated with fire-resistant stem diameters (> 7.5 cm) at all but the driest sites (Vastrap). Thus relatively little woody biomass is subject to fire mortality.

The data in Fig. 3.6 suggest that, in wetter savannas (e.g.  $> \sim 500 \text{ mm MAP}$ ) most of the woody biomass exists in larger trees that rarely burn. The concentration of biomass



Figure 3.6. Relationship between mean annual precipitation (MAP) and the fraction of biomass in larger trees in unprotected sites on the Kalahari transect. With increasing MAP woody biomass tends to be increasingly concentrated in larger individuals whether represented by tree height (Figure 3.6a) or stem diameter (Figure 3.6b). The Kalahari Transect has relatively uniform coarse textured soils along its extent with average annual rainfall varying from 216 mm in the south to about 1000 mm in the north. Fig. 6a shows the woody biomass fraction for trees taller than 5 m with pronounced pattern of increased fraction with greater rainfall. Fig. 3.6b shows a similar pattern but with respect to stem diameter for two size thresholds that might define larger trees that are able to survive during moderate (7.5 cm) and severe (15 cm) fires. Overall, the majority of woody biomass is found in fire-resistant size classes at most sites, with exception of drier sites, where severe fires are unlikely to occur frequently. Mean values shown with standard deviations.

in larger individuals may occur, in part, because smaller size classes have burned in earlier fires. However, it serves to emphasize the point that biomass "available" for fires is generally a very small fraction of total biomass. In drier savannas (200-400 mm MAP) the fraction of woody biomass in large trees is much lower. When and if fires occur in these systems, the fractional loss of woody biomass, and mortality of trees, is likely to be high. However, fires are much less common in dry savannas because of low herbaceous fuel load that is rarely sufficient for fires to propagate in the landscape.

*Hypothesis 3: Woody growth continues in regularly (annually) burned savanna sites* From my original hypothesis, I anticipated that, with continued burning over a long period, increases in woody biomass in fire-resistant size classes may temporally stabilize total woody biomass, reducing biomass loss and potentially even allowing for increasing biomass with fire. I found excellent support for this hypothesis in data from the annual and triennial burn trials that Kruger National Park has maintained since 1954 (Fig. 3.7). The 100m x 50 m plots were originally sampled in 1970s for stem diameters and resampled in 2002. Despite annual dry season burns, the plots gained total biomass with particularly noticeable increases in tree size class 10-30 cm (Fig. 3.7a). Smaller size classes showed slightly decreased biomass or remained unchanged. A similar pattern emerged with the triennial burns, as the 10-30 cm tree size classes gained biomass but there were not significant differences in total woody biomass changes between annual and triennial fire intervals.



Figure 3.7. Woody biomass in savanna plots subject to annual burns (a) and three year burns (b) over a 27 year period. Data are from the Kruger Park EBP experiment at Pretoriuskop, in South Africa. Mean plot biomass for each size class is shown for two sampling periods along with standard error. Despite annual August dry season burns, overall biomass increased in the plots during the period, with noticeable biomass increases for tree size classes 10-30 cm. Smaller tree size classes showed slightly decreased biomass or remained unchanged. Similar pattern observed for triennial burns (Fig. 3.7b).

### **3.5 Discussion**

My results emphasize the functional significance of tree size in savannas. Although tree size is neglected in many savanna studies, and in many savanna models, our understanding of the role of size in fire responses suggests that savanna ecosystems cannot be examined outside the context of what potentially is subject to mortality during each fire (Williams et al. 1999; Higgins et al. 2000; Holdo 2006). While several studies have suggested that impact of fire depends crucially on fire intensity (e.g. Higgins et al. 2000; Govender et al. 2006), I suggest that the impacts fire on woody loss in savannas also very much depend on the size composition of the woody plant community: a system dominated be smaller trees is likely to have biomass reductions in excess of 10%, while a large tree system may see a reduction less than 1%.

While several influential savanna models (e.g. Walker et al. 1981; Walker and Noy-Meir 1982; van Langevelde et al. 2003; D'Odorico et al. 2006) neglect size differences of woody plants to study the behavior of tree-grass dynamics of an "aggregated" woody component, my results suggest that these studies may fail to capture some of the essential features of savanna functioning. These models suggest that the primary impact of savanna fires is to directly reduce woody biomass. Observational studies suggest otherwise: that fire acts primarily as a "demographic bottleneck" to suppress the recruitment of woody individuals from reaching fire- resistant size (Higgins et al. 2000; Higgins et al. 2007). Such demographic interruptions can eventually lead to collapse of woody plant populations but over much longer time scales than might generally be expected (Trollope 1982; Higgins et al. 2000; Hoffmann et al. 2003; Hanan et al. 2007). My results also suggest that, although intensity and frequency of fires may increase

across the rainfall gradient, the impact of these fires on woody biomass may not increase since the fraction of total biomass that is fire-sensitive decreases with rainfall.

My finding that woody plant size-abundance relationships at wetter locations tend toward expected values for tropical forests has important implications for better understanding woody plant function in savannas. Although drier savannas tend to have size-abundance relationships better characterized by limited recruitment (e.g. caused by drought-induced mortality), I found that, when fires are excluded in wetter savannas, size-abundance relationships tend towards a power exponent equaling the predicted value of -2 for tropical forests (Fig. 3.5). Recently it was suggested (Muller-Landau et al. 2006a) that size-abundance predictions made by metabolic theory for tropical forests (Enquist and Niklas 2001) are largely invalid because resource availability for individual trees is not constant. Resources, particularly light, decrease towards the forest floor, and observations at many tropical sites diverge from metabolic theory (Muller-Landau 2006a). Coomes et al. (2006) pointed out that a better test for metabolic theory would likely occur where canopy conditions are relatively open so that light limitation through the canopy is not so important. My results support this contention and suggest that the predictions of metabolic theory may indeed hold true in mesic savannas (> 650 MAP) in locations where the major disturbance factors (notably fire, but also herbivory) are excluded. This result indicates that resource limitation, density dependence, and competition among trees are important factors in wetter savanna systems, just as they are in adjacent moist forests. By contrast, in drier savannas, climate and climate variability may impose bottlenecks to recruitment of young trees that reduce the intensity of competition among adult trees.

My study found that, along a gradient of increasing annual rainfall, a greater percentage of woody biomass is contained in relatively fire-resistant size classes. This contradicts recent studies that assume that most of the woody biomass in savannas in found in smaller, fire-prone size classes (van de Vivjer et al. 1999; van Langevelde et al. 2003). My results (Fig. 3.6) suggest that general statements about woody plant size and biomass made previously are either likely to be site-specific or apply only to savannas with shorter trees, i.e., shrublands. My results also contradict studies (e.g. D'Odorico et al. 2006), that suggest that savanna fires cause significant reductions in woody biomass (e.g. > 10 % biomass loss in each fire), and I agree with earlier studies (e. g. Higgins et al. 2000) that the main function of fire in savannas is instead as a demographic "bottleneck" that prevents the promotion of smaller individuals into fire-resistant size classes (Trollope and Tainton 1986; Trollope et al. 1995; Higgins et al. 2000). Hence, although woody community structure can be greatly affected by fire, woody biomass tends to be relatively insensitive with respect to individual fires

I also found that although fire continued annually at sites in Kruger National Park, woody biomass significantly increased in plots re-sampled in 2002 after ~ 30 years of annual prescribed burns. This result contradicts other earlier modeling work that neglects size structure (Bond et al. 2003; Bond et al. 2005; van Langevelde et al. 2003; D'Odorico et al. 2006) that, in large part because the woody population is modeled as an aggregate, suggesting that fires dramatically decrease woody biomass in savannas in the short term. My results showed sensitivity to tree size as there tended to be little or no changes in biomass for smaller size classes (< 10 cm) but significantly increased biomass in medium-sized (10 cm < diameter < 25 cm) trees that were largely fire-resistant.

Reductions in the largest tree classes may have been due to additional damage from increased elephant populations or due to fire-elephant interactions (Dublin et al. 1994; Holdo 2007).

Patterns of population size structure and resource competition in wetter savannas resemble forests when disturbance is reduced, and dry systems do not. This result agrees with a previous study (Sankaran et al. 2005) that suggested wetter savannas may be characterized as "unstable" and fires provoke changes in size woody structure that then greatly affect their response to additional fires. This means that aggregated models and concepts need to be expanded to accommodate demographic/size effects. At a minimum models need to differentiate at least two size classes with high and low mortality.

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# **Chapter 4**

# Self-thinning and Tree-tree Competition in Savannas

## 4.1 Introduction

Tropical savannas occupy large areas of the semi-arid and subhumid tropics (Bourliere and Hadley 1970, Huntley and Walker 1982). The existence of savannas around the world implies the *coexistence* of woody and herbaceous plants, and much has been written on whether such coexistence is stable or unstable (e.g. Scholes and Archer 1997; Jeltsch et al. 1998; Sankaran et al. 2004) or indicative of equilibrium, disequilibrium or non-equilibrium conditions (Illius and O'Connor 1999; Jeltsch et al. 2000). In most tropical savannas the woody component consists of drought-deciduous trees or shrubs, with the herbaceous layer dominated by annual or perennial grasses. Theories for treegrass coexistence in savannas stretch back to early German ecologists (Schimper 1903; Walter 1939) and the recognition that water limitation may play an important role in structuring semi-arid vegetation communities (Holdridge 1947). Subsequent versions of the Walter hypothesis (e.g. Walker et al. 1981; Walker and Noy-Meir 1982) postulate that niche separation between tree and grass roots leads to stable coexistence. However, since fire and herbivory are so widespread in many savanna systems, and can greatly reduce woody density and cover, other researchers (Dublin 1990; Menaut et al. 1990;

Higgins et al. 2000; Bond et al. 2005) have focused on disturbance as a primary mechanism that impedes woody population growth and thereby permits grass persistence. Although competition among trees ("*balanced competition*") has been mentioned as a possible mechanism for coexistence in a few instances (Skarpe 1990; Scholes and Archer 1997), few experiments have explicitly examined the extent to which intra-specific competition may allow tree-grass coexistence, and no mathematical models of savannas that I am aware of include realistic tree-tree competition as a mechanism limiting maximum tree cover or facilitating grass persistence.

Results from a recent analysis of data from a large number of sites in Africa (Sankaran et al. 2005) show a distinct upper bound for tree cover in the semi-arid savannas (<650 mm mean annual precipitation (MAP)) that correlates with rainfall (Fig. 4.1). While several theories might explain this apparent rainfall limitation on tree cover, competitive interactions among trees would seem to be a leading candidate.

The goal of this paper is to examine the applicability of self-thinning concepts as a diagnostic for intraspecific tree-tree competition in mixed tree-grass systems. I review existing evidence for intraspecific competition in savanna systems and contrast self-thinning in savannas to forest systems in light of differences in stand complexity, including tree-grass competition and spatial heterogeneity, that are likely to be more significant in savannas than forests. I postulate that the slope and linearity of self-thinning relationships (plotted on log-log scales) assessed for the woody component of savannas will contain information on the nature of tree-grass interactions, and should allow us to test a number of general hypotheses about how water resources are partitioned between trees and grasses. For demonstration purposes, I present a simplified



Figure 4.1. Change in woody cover of African savannas as a function of mean annual precipitation (after Sankaran et al. 2005). Maximum tree cover is represented using a 99th quantile piecewise linear regression. Data come from 854 sites across Africa, including a number of sites with low and absent disturbance by fire, herbivory and harvest. See Sankaran et al. (2005) for full discussion and datasets.

model to illustrate how the impacts of tree-grass and tree-tree competition might impact self- thinning patterns in savannas. Finally I test for self-thinning in savannas by using data from a 50-year fire-exclosure study in Kruger National Park, South Africa.

## 4.2 Self-thinning as an Indicator of Intra-specific Competition

The self-thinning concept was originally proposed for single species plant cohorts with uniform size structure (Yoda et al. 1963) and has been promoted as a conceptual framework for studying stand level carrying capacity (Westoby 1981). A power law characterizes self-thinning lines relating plant size and density, with a higher density of small trees supported than large trees, and predictable trajectories of mortality occurring as mean plant size increases. The emergence of such patterns is often taken as a diagnostic of competition among plants in forest systems (Kenkel 1988).

The slope of the thinning relationship between log density and the log of mean plant size reveals how size affects plant resource use, and the intercept can be interpreted as representative of a long-term carrying capacity. Yoda et al. (1963) proposed a slope of -3/2 between log plant weight and log density to describe, geometrically, how a two dimensional resource such as incident light is distributed functionally into three-dimensional plant space. Recent ecological scaling arguments using fractal geometry, and based on hydraulic constraints to optimize resource distribution, suggest a slope of -4/3 is more appropriate and that the relationship spans roughly twelve orders of magnitude in plant size (West et al. 1997; Enquist et al. 1998). Debate about the correctness and generality of self-thinning slopes (e.g. Lonsdale 1991; Weller 1991) has led to several recent attempts to find new methods of computing the self-thinning slope

and intercept (Bi et al. 2000; Cade and Guo 2000). Though most often used for dense forests and plantations, there is no reason that self-thinning concepts need not apply to more open semi-arid canopies where strong competition for water may occur and thus limit population size, density, and cover.

To my knowledge, a quantitatively rigorous self-thinning approach has not previously been used to infer intraspecific (or intra-life form) competition in savannas. However, if intraspecific tree-tree competition does occur in savannas, then self-thinning may provide a diagnostic test for this form of competitive interaction. I argue that, while such patterns may only be found in locations where disturbances have been low and woody density is relatively high, their presence will be instructive to our understanding of the underlying function of savanna systems, particularly since tree-tree competition has, until now, been largely neglected as a mechanism structuring savannas and permitting grass persistence.

Self-thinning has been criticized when applied to natural ecosystems that are less homogeneous than plantations in terms of spatial distribution, species composition and age (Weller 1989; Midgley 2001; Reynolds and Ford 2005). Reynolds and Ford (2005) suggest that assumptions normally made for the self-thinning process may not be justified in natural systems. This includes (a) using mean size as an index of resource use in multi-age stands, (b) assuming that all limiting resources are accessed and used by the plant community, and (c) that resource acquisition takes place in only two dimensions. Other criticism points out the possibility that each species may have its own self-thinning relationship (Weller 1989) and that, as trees age, size-resource relationships change (Midgley 2001). I discuss each of these criticisms, and how they may relate to self-thinning applications in savannas, below.

4.2.1 Mean Size as an Index of Total Resource Use in Mixed-age Tree Populations Recent studies on ecological scaling (Enquist et al. 1998; Enquist and Niklas 2002), suggest that equations may be obtained to relate various indices of tree size (e.g. leaf area, biomass, basal area, or basal circumference) to resource use. If the relationship between the size of an individual and resource demand is non-linear, however, then total resource demand in mixed-sized stands cannot be uniquely represented by mean size (Reynolds and Ford 2005). If, on the other hand, the index of woody plant size is carefully chosen to have a linear relationship with resource demand, then the average size of a population of trees in mixed-age populations can be used to represent total resource demand. In this situation I argue that thinning relationships between log density and log mean size remain valid even for mixed size populations. Water use by trees has been shown to increase linearly with sapwood area and basal area across a number of sites and tree species (Cook et al. 2002; Meizner 2003). If mean basal area of a mixedage population of trees provides a linear index of total resource usage, then it can be appropriately correlated with woody plant density in self-thinning analyses (e.g. plots of log mean basal area against log density). The simple models presented in Section 4 describe self-thinning in savannas and the impacts of grass competitors and disturbance assume, a priori, that the chosen index of tree size and resource demand scale linearly with each other.

#### **4.2.2 Full Resource Use by the Plant Community**

In semi-arid savannas, the assumption of full resource use (water in these water-limited ecosystems) may be more reasonable than for forests. In most semi-arid ecosystems,

rainfall is partitioned primarily to evaporation and transpiration by plants: deep drainage and surface runoff are limited except during very intense storms (Scholes and Walker 1993; Huxman et al. 2005). Furthermore, soil evaporation often occurs for a few days after rainfall, but as the soil surface dries out, total evapotranspiration is mainly driven by plant transpiration (Huxman et al. 2005). Thus, while some fraction of the limiting resource (water) may be lost and unavailable for vegetation growth, and grasses may compete for water, there is little long-term storage of water in most savannas, and rainfall during the wet season is mostly used by the plant community during that year.

### 4.2.3 Horizontal Resource Acquisition

Tree canopies in forests tend to have strong vertical gradients in resource availability, with light intensity decaying exponentially down to the floor, and hydraulic resistance (and thus resistance to transport of water and nutrients) increasing with height in the canopy. Ford and Reynolds (2005) pointed out that most self-thinning studies neglect that trees grow in three dimensions in response to a complex 3-dimensional light environment. In savanna systems, however, water is a primary resource limiting production and water is generally limited to a relatively shallow rooting zone, thus the assumption of horizontal resource acquisition for water by woody plants may be more reasonable for savannas than forests.

The use of self-thinning concepts in savanna ecosystems does, however, present a number of differences and potential new problems relative to applications in forests and plantations. These relate to the presence of herbaceous vegetation that may reduce tree growth or cause mortality (discussed further below), increased spatial heterogeneity in

the establishment and growth of woody species, and the importance of disturbances (e.g. fire, browsers, wood harvest and agricultural clearance) that often act to reduce woody density and cover. Savanna vegetation communities vary widely in both density and spatial distribution of trees and shrubs in the landscape. Some consist of scattered trees in essentially continuous grassland. Others are better characterized as clumped woodlands with large expanses of grass in between the trees. The spatial distribution of woody plants in savannas can become aggregated through physical (e.g. soil depth or water redistribution) and biological (e.g. seed source or animal redistribution) processes (Rietkerk et al. 2002). In extreme cases (e.g. tiger bush, forest savanna mosaics and gallery forests), this can result in distinct woody communities that are functionally better considered as separate patches of forest and grassland. Highly aggregated systems of this sort are not considered in this paper. Disturbances (e.g. fire) can lead to either a reduction in tree-tree competition for resources or to a reduction in the competition between trees and grasses (grazers). While I fully acknowledge the importance of disturbance processes (particularly fire, browsers and humans) in structuring savannas, and reducing competition among trees, the focus of this paper is on the potential underlying limitation to woody biomass, density and cover related to intraspecific treetree and tree-grass competition for water resources in low disturbance situations.

## **4.3 Evidence for Tree-tree Competition in Savannas**

Competition in savannas generally takes place underground for water and nutrients (Scholes and Archer 1997). In arid and semi-arid ecosystems, root profiles sometimes extend laterally ten or more times height of trees (Segheiri 1995; Smit and Rethman

1998; Casper and Jackson 2000; Smit and Rethman 1998). Comprehensive studies of rooting volumes and lateral extent are rare, and actual rooting radii of individual trees remain an active area of pursuit in plant ecology (Casper et al. 2003). The sparse available data, however, tends to support the idea that, while above ground canopy cover may be low in savannas, underground root distributions are much more extensive and in many cases may have sufficient overlap for competition between neighboring trees to be significant (Smit and Rethman 1998; Schenk and Jackson 2002).

In many savannas, woody plants are distributed widely in the landscape, with distributions that are random to only slightly aggregated (Fowler 1986; Jeltsch et al. 1998). Nearest neighbor methods and spatial pattern analysis have explored tree spacing in savannas to assess competition between woody plants (Smith and Goodman 1985; Penridge et al. 1986, Grundy et al. 1994; Couteron amd Kokou 1997; MacGregor and O'Connor 2002; Shackelton 2002; Caylor et al. 2004). However, the results of these studies have been inconclusive or open to alternative interpretation. A regular spatial pattern may indicate the presence of competition, but the absence of such a pattern does not exclude the possibility for competition (Smith and Goodman 1985; Grundy et al. 1994). These studies have also been faulted for not adequately taking into account the effects of size structure and for neglecting the importance of small trees (Shackleton 2002). Lack of a regular or uniform spacing of trees may also reflect irregular root volumes that may not be sampled adequately using conventional methods (Casper et al 2003). In these savannas it would be most unusual for woody plant populations to approach the very regular distributions typical of plantations where self-thinning patterns are most readily applicable (Reynolds and Ford 2005). The lack of spatial regularity,

particularly in mixed age stands of trees, means that many individual trees are exposed to a competitive environment (defined by the number and size of neighbors) that may be considerably weaker or stronger than the mean for the stand.

Tree thinning experiments in a few semiarid to mesic tropical savannas generally lead to increased growth in remaining trees or greater grass biomass (Chikmunbo et al. 1999; Smit and Rethman 1998; Smit and Rethman 2000; Loaga et al. 2004; Wiegand et al. 2005), suggesting that competition between trees, and between trees and grasses, limits growth. In temperate mixed systems, regrowth of chaparral trees after fire quickly reaches a maximum biomass, after which density-dependent processes reduce tree density (Guo 1998). Mortality of adult trees in tropical savannas has also been shown to exhibit density-dependence during drought periods (Fensham and Holman 1999; McGregor and O'Connor 2002). Patterns of woody plants in shrublands appear to become increasingly subject to density dependent limitation with increasing biomass, followed by overall decreases in plant density (Skarpe 1990; Pyke and Archer 1991; Wiegand et al. 2005; Wiegand et al. 2006).

## 4.4 Water Balance Model for Self-thinning in Savannas

Existing literature suggests that water availability limits both grass and woody production in savannas (Scholes and Archer 1997; Rodriguez-Iturbe et al. 1999). The exact nature of how trees and grass in savannas compete for those water resources remains, however, an important and unresolved issue (Scholes and Archer 1997; House et al. 2003). While a number of studies have found vigorous competition between tree seedlings and grass plants, the majority have studied the impacts of adult trees on grass

production (Davis et al. 1998; House et al. 2003). The effects of tree size on tree-grass interactions are not well known.

Here, I present a simplified model to examine the potential effects of tree size on treegrass and tree-tree competition on hypothetical self-thinning conditions in savannas. If water demand and use by trees in the absence of competition is linearly related to some size attribute, such as basal area, then a simple model can be used to illustrate the effects of tree-grass competition on self-thinning relationships in savannas. Such a model can also be used to examine size dependent tree-grass interactions. For simplicity I consider mean annual rainfall as the limiting resource, while recognizing that rainfall variability, particularly wet season droughts, is of central importance in reproduction and seedling dynamics (O'Connor 1995; Higgins et al. 2000) in semi-arid savanna systems.

Let *w* be a long-term mean annual precipitation. A certain amount of the precipitation,  $w_e$ , falls in small events such that the moisture either evaporates directly from grass and tree canopies or from the soil to the atmosphere, and the water is not available for plant growth. Suppose also that another portion,  $w_g$ , falls in low intensity rainfall events that become available only for grass production, but not for trees.

The long-term plant available moisture for tree or grass production,  $w_a$ , can then be defined by a simple water balance equation

$$w_a = w - w_e - w_g \tag{4.1}$$

Equation 4.1 assumes that runoff and deep water percolation are relatively small components of the hydrological balance in semi-arid savannas, although such terms could of course be added to Equation 4.1 as appropriate.

If resource use in the absence of grass competitors scales linearly with size,  $T_s$ , then mean water use for a population of trees of given mean  $T_s$  can be defined by a mean water use term,  $\mu_{Ts} = T_s \mu^*$ , where  $\mu^*$  is a water demand parameter (for example, kg H<sub>2</sub>O/cm<sup>2</sup> basal area/year). The water use for an individual grass plant is  $\mu_G$ , where I assume constant size and water demand for all individual grasses. A competitive interaction ratio,  $C_{TG}$ , represents the partitioning of available water,  $w_a$ , between trees of a particular size-class (s) and grass at equilibrium:

$$C_{T_sG} = \frac{D_{T_s}\mu_{T_s}}{D_{G_s}\mu_{G_s}}$$
(4.2)

where  $D_{Ts}$  is the density of trees of size  $T_s$  and  $D_{G1}$  is the density of grass plants that are competing with trees for  $w_a$ . The density of grass plants supported by  $w_g$  is represented by  $D_{G2}$ . Given that  $w_a = D_{Ts}\mu_{Ts} + D_{G1}\mu_G$  and  $w_g = D_{G2}\mu_G$ , I solve for the density of trees and grasses:

$$D_{T_s} = \frac{w_a C_{T_s G}}{\mu_{T_s} (C_{T_s G} + 1)} \quad \text{and} \quad D_G = \frac{w_a}{\mu_G (C_{T_s G} + 1)} + \frac{w_g}{\mu_G}$$
(4.3)

Three hypotheses are suggested here that relate tree-grass competition to self-thinning relationships. In symmetric competition the presence of grass in savannas reduces the total soil water availability for trees irrespective of the mean size or age of the trees. This constant reduction in resource availability will reduce the intercept of the self-thinning relationship but the slope should remain the same as for a grass-free system (Fig. 4.2a). For size-dependent asymmetric competition, growth and survival of larger trees are little affected by grass competitors, but competition increases linearly for smaller trees. In this case the self-thinning relationship in the presence of a grass
competitor changes as a function of mean tree size, with fewer small trees supported (Fig. 4.2b). For life stage-dependent asymmetric competition, growth and survival of established adults (and perhaps saplings) is little affected by the presence of grasses. However, seedling (perhaps sapling) growth and survival is reduced in a threshold response that may be related to development of root systems in older life-stages that effectively minimize competition with grass (Fig. 4.2c). Figure 4.2d shows the values of  $C_{TG}$  used to generate the hypothetical tree-grass competition curves in Figs. 4.2a-c.

## 4.5 A Test for Self-thinning in Savannas

#### 4.5.1 Site and Methods

Ideally, data for testing self-thinning in savannas would come from systems that are free from disturbance such that there can be some reasonable expectation that basal area values are at, or near, resource-limiting levels. Finding such data in savannas is, however, difficult because of the numerous natural and human disturbances that affect most savanna areas (Sankaran et al. 2005). A review of the literature (e.g. Trapnell 1959; Swaine et al. 1992; Biggs et al. 2003; Bond et al. 2003) suggests, however, that there may be opportunities in locations that have, for various reasons, been protected from fire, herbivory, and other major disturbances. In southern Africa, the long-term fire experiments in the Kruger National Park (KNP) present an excellent opportunity since the study includes fire exclosures that have been maintained continuously for over 50 years (Biggs et al. 2003; Higgins et al. 2007).

The KNP fire experiments began in 1954 at four different locations (each with four site replicates) along a pronounced north-south rainfall gradient (from 350 mm mean



Figure 4.2. The hypothetical effects of adding a grass competitor on self-thinning relationships among shrubs and trees in savanna systems. Solid lines show hypothetical self-thinning relationships in the absence of grass competition. Dotted lines show postulated treegrass interaction effects. (a) symmetrical tree-grass competition, where grass competitors reduce resource availability equally for all tree size classes, (b) size-dependent asymmetrical tree-grass competition, with smaller trees increasingly more affected by grasses than larger trees, (c) life stage-dependent asymmetrical tree-grass competition, where seedlings (and perhaps also saplings) are affected by grass competition, but grasses have relatively little impact on growth and mortality of adult trees. (d) shows the size-dependent values of  $C_{TG}$  (Equation 4.2) used to generate the hypothetical relationships shown in Figs. 4.2a-c: symmetrical competition (Fig. 4.2a, solid), asymmetric size-dependent competition (Fig. 4.4b, dashed), and symmetric life stage-dependent competition (Fig. 4.2c, dotted).

annual precipitation in the north of the park to about 700 mm in the south). The locations were chosen to represent several of the most important landscapes found in the KNP. For this study, a field survey was conducted in July and August 2004 on the "no-fire" (control) treatments where fire has been excluded (except for some accidents) for > 50 years. On each (6-10 ha) plot, all stem diameters were measured (at 30 cm above ground level) in contiguous 5 m x 5 m subplots within larger sample plots (50 m x 50 m or larger). The sampling method was designed, in part, to take advantage of previous sampling (30 years ago) at the same sites in order to assess changes in woody biomass in the burn plots. More importantly, however, the arrangement of contiguous subplots within a larger plot allowed a multi-scale assessment of the appropriate sampling scale for these systems.

## 4.5.2 Results

Choosing an appropriate spatial scale for sampling presents difficulties for heterogeneous woody vegetation in savannas. In contrast to plantations, the distribution of individual plants in natural systems is generally irregular. Thus sampling at too fine a spatial scale may result in plot values that are high or low relative to the mean resource-limited value (with the extreme case occurring at very fine scales (e.g. 1 cm<sup>2</sup>) where the basal area assessment would return either 1 or 0 depending on stem location. Conversely, sampling at too coarse a scale will likely incorporate landscape and geomorphological heterogeneity that might confound detection of patterns of plant competition. In order to determine a suitable spatial scale for my study, I examined variability in basal area observations in subplots at different aggregation scales (5-25m). I anticipated that the

standard error in basal area would be highest at fine sampling scales where within-stand heterogeneity dominates, and decline at coarse scales as the subplot size better represents the inherent heterogeneity of the community (Fig. 4.3). Figure 4.3 indicates that plot size of 15 m or more is sufficient to represent the heterogeneous community. Since the number of plots available for analysis decreases with increased aggregated plot size, I chose the minimum acceptable length scale (15 m) to carry out self-thinning analysis.

Regression analysis supports the general hypothesis that savanna tree-grass competition is size-asymmetric, with results from all three sites having slopes more negative than –1 (Fig. 4.4). This result suggests that smaller trees are competitively disadvantaged. The results also suggest that the self-thinning intercepts indicative of woody carrying capacity, under prevailing long-term rainfall, tend to be positively correlated with mean annual precipitation. However, the intercept values represent large extrapolations from the observed data and thus, while providing qualitative assessment of resource-based limits on the woody community, may not provide meaningful quantitative assessment. Differences between the intercepts may also be a reflection of different soil types, coarse vs. fine–textured soils, or that the calculated intercepts are very sensitive to the slope. Since the intercept extrapolates to predict maximum basal area that could be supported, because intercepts are sensitive to nonlinear slopes, there are likely insufficient plot samples in this study to realistically extrapolate intercepts to a meaningful maximum basal area.



Figure 4.3. Impact of plot size on variability of basal area measurements. There is considerable variability at the 5 m scale in the standard error of basal area (mean values shown with +/-1 standard error). An intermediate scale (15 m) was chosen as a favorable compromise because results were statistically distinguishable from smaller plots but with a sufficient number of plots for regression analysis.



Figure 4.4. Self-thinning analysis for savanna in Kruger National Park, South Africa. For each relationship for all data pooled at each location (a) Mopani (425 mm MAP) (b) Satara (550 mm MAP), and (c) Skukuza (625 mm MAP). The calculated slopes indicate asymmetric tree-grass competition, with each site having slopes significantly more negative than -1. The calculated intercepts suggest increasing carrying capacity with mean annual precipitation.

# 4.6. Discussion

It is not currently known how much, or how often, tree-tree competition plays a role in limiting woody basal area in tropical savannas. Clearly many, probably most, savannas are subject to disturbance (fire, herbivory and harvest) that suppress tree cover below any postulated climate-related potential (e.g. most data points in Fig. 4.1). That said, however, the correlation between maximum cover and rainfall in Fig. 4.1 also provides compelling evidence that water availability may be important in determining maximum woody cover. But the mechanisms behind the observed relationship across the rainfall gradient are poorly understood. While in this paper I postulate that tree-tree competition may be important, it is also likely that tree-grass competition or bottlenecks to woody establishment and survival that correlate with mean rainfall are also active, particularly at the dry end of the rainfall gradient where woody cover is so low that strong tree-tree competition seems unlikely.

The potential of extending self-thinning concepts from traditional forest situations into the savannas lies in the possibility that such analyses may provide a useful diagnostic for the presence or absence of tree-tree competition, particularly in locations that have been protected from disturbance for some time and where the woody community is not suppressed by other, non-resource based, mechanisms. In such sites I would expect that measurements of woody size and density (taken at an appropriate spatial scale) would begin to show thinning relationships if tree-tree competition is occurring. To minimize the effect of spatial heterogeneity, woody populations should be sampled at spatial scales appropriate to the length scale of the heterogeneity to thus minimize its influence. The plot size should, however, not be so large that it captures

landscape scale heterogeneity related to geomorphology or topography. The appropriate plot size for heterogeneous plant communities can be assessed using a multi-scale block sampling methodology such that fine scale data can be aggregated to larger plot sizes until the between plot variability (standard error) reaches a minimum, at which further aggregation no longer decreases the variance.

The characteristics of the self-thinning line (slope, intercept, and linearity) may reveal information on how competition between trees and grasses changes with tree age and size (Fig. 4.2). It is likely that competition with grasses may result in both increased mortality and growth suppression for seedlings and young trees. For adults the effect of grass competitors, if significant at all, would likely express through reductions in growth rather than in increased mortality. Little or no experimental data on the competitive effects of grass on tree growth and mortality across age and size-classes is available. However, the results shown in Fig. 4.4 suggest that the tree-grass competitive interaction is asymmetric with respect to tree size, with the data tending to support the hypothetical response shown in Fig. 4.2b. Thus, while analysis of self-thinning relationships will not provide definitive answers on how trees in savannas respond to grass competitors, across rainfall gradients and across tree size or age-class, I suggest the approach does provide useful qualitative information on the processes and mechanisms of savanna structure and function.

An abundance of studies have stressed the critical importance of disturbance to the development and maintenance of savannas, particularly fire (Higgins et al. 2000; Bond et al. 2005), browsing (Dublin 1990; Prins and Vanderjeugd 1993) and grazing (Walker et al. 1981). Fires and browsers directly impact the biomass, growth and survival of trees

and thus they are expected to reduce tree-tree competition. In such cases, though treetree competition may be an underlying mechanism limiting maximum woody density and cover, the woody community in most savanna locations is often well below the maximum (e.g. Fig. 4.1). Grazing, on the other hand, is expected to reduce grass-on-tree competition and thus increase resource available to the woody vegetation. The probable impacts of grazing on maximum woody density and basal area are to increase water availability to the trees, as illustrated in the hypothetical tree-grass competition diagrams of Figs. 4.2a-c. Furthermore, grazing tends to reduce fire occurrence such that tree-tree competition and self-thinning may be more relevant in sites that are grazed (particularly heavily grazed) than in ungrazed sites. Grazing would thus be expected to increase woody cover, as has often been reported in the literature as "shrub encroachment" (Archer 1989; van Auken 2000; Jurena et al. 2003; Fensham et al. 2005). However, if there is an underlying resource limitation (as apparent in Fig. 4.1 for Africa savannas where MAP<600 mm), the increase in density and cover of woody plants, even under heavy grazing, may still be bounded below canopy closure as competition among trees increases.

The negative correlation between tree size and density, so common in forest and plantation ecosystems, appears also to occur in savannas. Such self-thinning relationships provide evidence that competition among trees may be a significant factor in savanna ecosystem function. It may be that this tree-tree interaction only occurs in situations where disturbance by fire, herbivory and humans has been historically low. However, while most savannas are subject to a variety of disturbance factors, the identification of an underlying resource-limitation to woody population dynamics is of

great significance to our understanding of savanna systems and our ability to model and predict their behavior under varying land use and climate conditions. In particular, most models of savanna ecosystem dynamics pay relatively little attention to tree-tree competition and concentrate instead on tree-grass interactions and/or disturbance dynamics (e.g. Higgins et al. 2000; Bond et al. 2005). The incorporation of tree-tree competition in such models may be very important as a stabilizing factor enhancing and promoting tree-grass coexistence. This would help explain why the arid and semi-arid tropical savannas (<650 mm MAP) are relatively stable in the sense that, while dynamic in response to climate fluctuations and disturbance, trees rarely come to dominate and tree-grass coexistence, and the tropical savanna biome is persistent both in Africa and elsewhere around the globe.

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# **Chapter 5**

# Dynamical Investigations Using a Demographic-Competition Savanna Model

# **5.1 Introduction**

Simple (or aggregated) modeling approaches for savanna ecology have traditionally focused on either resource competition or disturbance to explain coexistence of trees and grass (Chapter 2; Belsky 1990; Scholes and Archer 1997; Sankaran et al. 2004). Simple savanna models have further been differentiated into models aggregating demographic processes and models that use size classes to incorporate demographic bottlenecks (Sankaran et al. 2004). Differences in these approaches stem primarily from widespread disagreements between savanna ecologists on even the most basic features of savanna ecology, including whether woody or herbaceous plants are competitively superior, and if so, under what environmental conditions, e.g. soil texture, rainfall variability, herbivory, fire (Frost and Robertson; Scholes and Archer 1997; Williams and Albertson 2006). Fundamental disagreements on whether savanna tree-grass ratios, in the absence of disturbance, are inherently stable (Walter 1971; Walker et al. 1981; Eagleson and Segarra 1985; Rodriguez-Iturbe et al. 1999; van Langevelde et al. 2003; Sankaran et al. 2006) also

continue to pose challenges for savanna ecology. Recently, there have been calls for greater integration of modeling approaches currently dividing savanna ecology, with the view that this is needed before further advancement can take place (Sankaran et al. 2004).

Progress on integrating demographic and competition approaches in simple models has been slow to date (Sankaran et al. 2004; Gardner 2006). Several reasons might explain why this is the case. Although it is relatively easy, provided there is sufficient data for parameterization, to incorporate size class equations to represent demography (growth and mortality rates) of woody plants in savannas, modeling competition properly is especially difficult, in large part because of size-specific asymmetries in tree-grass competition (Belsky 1994; Scholes and Archer 1997; Simmons et al. 2007) and resource use (Enquist et al. 1998). Modeling disturbance effects on woody populations is also non-trivial because fire impact on individual trees depends largely on size (Williams et al. 1999; Higgins et al. 2000; Hoffmann et al. 2003; Holdo 2006; Hanan et al. 2007). Existing savanna models that have water resource use scaling linearly with woody plant weight (e.g. Ludwig et al. 1997; Anderies et al. 2002; Williams and Albertson 2006) or avoid considering plant maintenance costs altogether (e.g. Walker et al. 1981; van Langevelde et al. 2003; Holdo et al. 2007) may not realistically capture important nonlinear plant size-resource use effects, especially important for larger (Enquist et al. 2001; Meinzer et al. 2003) or older (Ryan et al. 1997) trees (chapters 3 and 4). In early simple savanna models tree-grass competition was greatly simplified (e. g. Walker et al. 1981) with fixed tree-grass competition coefficients, even though it is likely that the competitive advantage for woody plants may be a nonlinear function of tree-grass ratios

(Scholes 2003) or shift as tree individuals grow in size (Sea and Hanan 2007; Chapter 4). While early savanna modelers clearly recognized that such representations of competition among trees and grasses may be overly simplistic, several decades later, model representation of tree-grass and tree-tree competition have advanced little, especially with respect to asymmetric tree-grass competition as a function of woody plant size (Sankaran et al. 2004; Sea and Hanan 2007). Further, although numerous studies report that woody plant size is especially important in determining individual mortality from fire (Trollope 1982; Williams et al. 1999; Higgins et al. 2000; Hoffmann et al. 2003; Holdo 2006; chapter 3), many savanna models continue to neglect the role plant size in disturbance responses (Anderies et al. 2002; van Langevelde et al. 2003; Beckage et al. 2006; Williams and Albertson 2006; Holdo et al. 2007). It is likely that these models fail to properly account for fire loss in woody communities (Hanan et al. 2007; Sea et al. 2007)

A recent analytical modeling study introduced a minimal savanna model to more fully integrate size structure (demography) and resource competition (Sea et al. 2007; Chapter 2). The model accounted for size-related asymmetric resource use (Enquist et al. 1998; Meinzer 2003) in the tree population by using woody basal area instead of plant weight as the primary index of plant size. Resource use in individual trees is approximately linear with basal area allowing simple averaging of population-level resource use. Because a number of recent studies suggest relatively constant tree stem growth rates for adult savanna trees (Stahle et al. 1999; Therwell et al. 2007), the model included only two size classes (juveniles and adults) to focus more specifically on the asymmetries in growth and fire mortality among juveniles (which grow rapidly but are fire susceptible)

and adult trees (which grow slowly but are fire resistant; Williams et al. 1999; Higgins et al. 2000; Hoffmann et al. 2003; Holdo 2006). In Chapter 2 (Sea et al. 2007), tree-grass competition was modeled between adult trees and grasses and as competition between trees that affected recruitment rates of juveniles and promotion of juveniles into fire-resistant adult size class. Tree-grass competition in the model, both grass-on-juvenile and grass-on-adult, were important in altering vegetation dynamics, as illustrated by nonlinear bifurcation diagrams that showed how changes in some parameters led to potential alternate woody stable states: relatively high or low woody values (or exclusion). With increased competition, stable tree-grass mixtures were possible for a large range of parameter values. At critical points, small changes in parameter values, especially adult mortality, led to threshold behavior, with sudden collapses in woody populations thus enhancing the possibility for alternate stable states. In contrast, a logistic model without demography is unable to capture the dynamic effects of competition and demographic processes.

The primary goal of this chapter is to expand on my earlier work with a simple savanna model (Sea et al. 2007). Here, I focus on exploring the role played by two key features of savannas systems that have received little attention to date but that I postulate may be important, both individually and in concert, for the dynamics and functioning of savanna systems: stochastic fire disturbance and size-asymmetric competition. It is likely that savanna vegetation responds differently to disturbances occurring with constant intensity and interval compared to disturbances occurring with stochastic variation as in real savannas (Higgins et al.2000; D'Odorico et al. 2006; Williams and Albertson 2006; Hanan et al. 2008). Recent studies have found that the timing and

intensity of fires may play a pivotal role in fire loss, with higher grass production, related to variability in rainfall, leading to greater likelihood of fire spread and increased intensity. This variability in rainfall that characterizes savannas and semi-arid regions suggests that stochastic modeling may need to play a larger role in savanna modeling (Higgins et al. 2000; D'Odorico et al. 2006; Williams and Albertson 2006). Stochastic models that include variation in fire intensity and interval may exhibit different outcomes from deterministic versions. There is, in addition to the importance of stochastic variability in fire effects, great uncertainty on the direction of plant competition between trees and grass, especially on the factors responsible for shifting the advantage from one plant form to the other. These factors include woody plant size, rainfall variability, and variations in the timing and intensity of fires.

In this study I extend the model of Chapter 2 (Sea et al. 2007) to examine four interesting questions related to demographic size structure, stochastic disturbance, and asymmetric competition.

- 1. *Mortality:* How do increases in tree mortality (juvenile and adult) change steady state woody basal area in a demographic-competition model compared with a traditional aggregated logistic model?
- 2. *Stochasticity:* How does stochasticity in fire intensity and frequency impact woody dynamics relative to mean-value simulations?
- 3. *Initial Values:* How do changes in initial values of basal area B<sup>\*</sup> affect the steady state basal area values B<sup>\*</sup> in the demographic model compared with the logistic model?
- 4. *Competition Asymmetry:* How do changes in the magnitude of asymmetric tree-grass competition lead to changes in steady state basal area values?

I provide a detailed description of the model in the next section. In subsequent sections, I describe modeling tests used to address the questions. Using the model, I

examine how changing demographic and competition parameters leads to different outcomes for a model with demography (juveniles and adults) compared to an aggregated model with more traditional logistic competition. Since my model keeps track of both the number of adults and total basal area, I am able use a simple function for tree-grass competition that is a function of mean tree size. Finally, I address how sensitive the model is to small changes in fire intensity (mortality) and interval, with contrasts between the demographic-competition and logistic model.

## 5.2 Model

#### 5.2.1 Background

#### 5.2.1.1 Competition in Savannas

There is poor understanding of how trees and grass compete for limited resources in savannas, especially when subject to spatially and temporally variable resources and differing levels of competition intensity that depend on the size of trees (Scholes and Archer 1997; House et al. 2003). Few simple models explicitly examine resource variability and competition in space and time (e.g. Higgins et al. 2000; Williams and Albertson 2006), and no published study has thoroughly addressed the impacts of tree size on competition (but see Chapter 4). Current simple savanna models prescribe fixed competition coefficients that linearly reduce available resources for trees and grass as a function of biomass for each functional group (Ludwig et al. 1997; Anderies et al. 2002; Williams and Albertson 2006) or as a nonlinear function depending on the landscape-scale biomass of trees and grass (Walker et al. 1981; van Langevelde 2003). It is likely, however, that tree-grass competition is not symmetric with respect to tree size, and some

savanna literature suggests that large trees are competitively superior to grass through advantages such as larger rooting volumes (Seghieri 1995) or shading of light resources in wetter savannas (Belsky 1994).

Early tree-grass interaction studies emphasized how invasion (or encroachment) of woody plants into rangeland degraded grazing conditions through depressed herbaceous production or decreased foraging efficiency of grazing animals (Walter 1971; Walker et al. 1981; Walker and Noy-Meir 1982). Hence, the majority of studies on woodyherbaceous interactions have focused on the effects of trees on grasses and relatively few have looked at grass effects on adult trees (House et al. 2003; Simmons et al. 2007). In Chapter 4, the competitive effects of grass on trees were hypothesized to be a function of tree size, and my analyses suggest that larger trees are mostly insensitive to grass competition while smaller trees are strongly impacted. In addition to tree-grass resource competition, the competitive impact of herbaceous plants on woody plants is accomplished in the model through a reduction of fecundity rates (i.e. reducing seedling establishment). Vigorous competition has been hypothesized between small woody plants and grass for water and nutrients (Walter 1971; Fowler 1986; Belsky 1990; Scholes and Archer 1997; Sea and Hanan 2007), as herbaceous plants compete intensively for shallow water resources that could also be used by smaller woody plants. However, relatively few studies have actually demonstrated negative impacts of grass biomass on tree seedlings (Davis et al. 1998; Weltzin et al. 1998; Higgins et al. 2000; Sea and Hanan 2007; Simmons et al. 2007). The results of a number of grass removal studies have had mixed results with some studies showing increased woody growth with grass

removal (Davis et al. 1998; Simmons et al. 2007), but others suggesting little or no effect on tree growth rates (Smit and Rethman 2000).

#### 5.2.1.2 Savanna Fires

Decades of field research shows that fire acts as a "demographic bottleneck" to impede growth of small trees into fire-resistant size classes, and that the effects of fire intensity on individual tree mortality are likely greater than fire interval in structuring savanna vegetation (Trollope 1982; Bond and van Wilgen 1996; Higgins et al. 2000; Govender et al. 2006). Perhaps of greater importance than fire intensity, however, is the size structure of vegetation subject to fires (Frost and Robertson 1987; Chapter 3) because small woody individuals generally suffer very high mortality (> 50%), but larger plants are mostly fire resistant (< 2% mortality). Results from models using a single woody equation model (e.g. van Langevelde et al. 2003) suggest that if fire occurs at higher woody biomass, then there is greater absolute woody biomass loss at the same fire intensity. If increases in population woody biomass, however, tend to be associated with larger trees, then fires occurring in high biomass locations may consume less wood than in low biomass sites (where more trees are likely to be fire sensitive). This situation seems most likely in savannas containing larger trees and suggests that, to properly model savanna vegetation, additional demographic structure is required in models.

#### **5.2.2 Model Formulation**

My savanna model incorporates a minimal size-structured demography along with logistic tree-grass resource competition (Fig. 5.1). The demographic portion of the

model uses separate differential equations to model the number density of juveniles (J) and adults (A), with fecundity (m) and promotion (p) rates allowing for births of new juveniles and transition of juveniles into the adult size class. The resource competition portion of the model uses a standard logistic tree-grass competition model (e.g. Ludwig et al. 1997; Anderies et al. 2002; Williams and Albertson 2006). In order to avoid nonlinear tree size resource use problems using biomass, I use tree basal area (B) which scales ~linearly with resource demand (Enquist et al. 1998). Furthermore, since grass resource use may not scale linearly with above ground biomass and above ground biomass is ephemeral, I model grass dynamics as a function of root biomass (G) assuming the system is composed of perennial grasses in which only roots persist from year to year.

The major difference between my model and other models is that the woody maximum basal area is a function of the number of adults. This change strengthens the coupling between the number of trees and the maximum basal area. There is also strong coupling between demographic and competition state variables that reduces fecundity and promotion through grass-seedling ( $\alpha$ ) and tree-seedling ( $\beta$ ) competition. Mortality for all equations is envisioned as encompassing both "natural" mortality ( $\mu$ ) and mortality from disturbances (F) such as fire. For full model equations, see Fig. 5.1.

Using a woody maximum basal area that is a function of the total number of adults in a population is crucial to creating demographic bottleneck conditions in the model. Each adult (individuals reaching fire-resistant size) is theoretically allowed to attain its maximum size ( $B_0$ ), for a maximum basal area ( $B_0A$ ), where A is the number of adults. Ultimately, potential maximum basal area ( $B_{max}$ ) is bounded by a value representative of

local climate and soil conditions. The model thus avoids the problem of a little woody biomass (say a single tree) continuing to grow even when disturbance or climate conditions preclude recruitment of new individuals. Since there is a demographicallysensitive maximum basal area, woody population growth rates depend not only on total basal area, as in other models (e.g. Gardner 2006), but also on the average tree size (B/A). As average tree size approaches  $B_0$ , population growth can only occur through recruitment of new adults, even though the resource-based potential maximum basal area of the site may not have been reached (i.e.  $B_0A < B_{max}$ ). Likewise, in the model, when  $B_0A$  converges to  $B_{max}$ , the dynamics decouple from the demographic portion of the model. Hence, basal area growth is insensitive to fecundity rates, juvenile promotion, and juvenile mortality rates.

Fire loss is modeled as a factor (F) that reduces woody basal area, number of adults and juveniles, and grass root biomass (Fig. 5.1). A priori, I assume low mortality for trees and grasses, with high mortality for juveniles. Since observations indicate that fires in savannas tend to occur at most once a year during the dry season, I model fire as a stochastic process with a probability (p) that a fire occurs in a given year. For example if p = 0.5, then fires may occur in successive years, but the long-term average interval is two years. My fire model differs somewhat from D'Odorico et al. (2006) in that they used an exponentially distributed variable that determines the time between fire events, allowing for possibility of very long intervals between fires but also a substantial number of fires occurring within 6 months of each other, which is not realistic for savanna fires. A number of field and modeling studies support the idea of savannas fires having a normally distributed variable, with relatively low values (~ 0.02) for adult trees and high



Figure 5.1. Detailed description of the model. Each differential equation represents time rate of change for the number densities of juveniles (J) and adults (A), respectively, and B and G represent the basal area and grass root biomass. Tree-grass and tree-tree competition are modeled using a logistic factor ( $\alpha$ ) that reduces juvenile recruitment and factor ( $\beta$ ) that reduces juvenile promotion. Fire is modeled offline from the differential equation model by allowing for a one discrete event to occur each year with probability p. The fire mortality is modeled as a normally distributed random variable with mean  $f_A$ ,  $f_J$ ,  $f_B$ ,  $f_G$  for the state variables in the model. The mean fire loss term is  $F_A = f_A I$ , where I is average adult fire interval and  $f_J I$ ,  $f_B I$ ,  $f_G I$  representing fire loss in the other state variables. For greater discussion of parameter definitions and values see Table 5.1. values (> 0.50) for juveniles (Higgins et al. 2000; Govender et al. 2006; Hanan et al. 2008).

## **5.3 Model Tests**

Using analytic techniques, we found that the model is very sensitive to small changes in adult mortality, whether caused by fire, drought, browsing by elephants, or other means (Chapter 2). Model dynamics can be characterized analytically as a saddle node bifurcation with jump-like behavior around critical points (Fig. 5.2). Along the stable branch of the bifurcation diagram (solid line in Fig. 5.2), increased adult mortality leads to monotonic decreases in the steady state values for basal area ( $B^*$ ). Additional mortality at the critical point ( $B_{cr}$ ) leads to a collapse in B. The jump-like behavior may be explained as a feedback that reduces production of juveniles and adults leading to decreased maximum basal area ( $B_oA$ ). Increased juvenile promotion times (p), stronger grass-juvenile competition ( $\alpha$ ), and higher juvenile mortality ( $\mu_J$ ) enhance the feedback and likelihood of jump behavior (Fig. 5.2).

The following sub-sections detail simulation model experiments designed to answer key questions given in Section 5.1. Simulations referring to the demographic model use maximum basal area ( $B_0A$ ), while simulations referring to the logistic model use potential maximum basal area ( $B_{max}$ ).

Parameter	Symbol	Units	Default	Range	Source
Adult Mortality	$\mu_A$	yr <sup>-1</sup>	0.02	0.005-0.10	1
Juvenile Mortality	$\mu_J$	yr <sup>-1</sup>	0.10	0.05-0.80	2
Basal Area Mortality	$\mu_{\mathrm{B}}$	yr <sup>-1</sup>	0.02	0.005-0.10	3
Grass Mortality	μ <sub>G</sub>	yr <sup>-1</sup>	0.10	0.10-0.90	4
Tree-grass competition	c <sub>wg</sub>	None	1.0	0.0-2.0	5
Grass-tree competition	c <sub>gw</sub>	None	1.0	0.0-1.0	6
Promotion Time	р	yr <sup>-1</sup>	0.05	0.02-0.20	7
Grass Growth Rate	r <sub>G</sub>	yr <sup>-1</sup>	1.0	0.25-1.50	8
Woody Growth Rate	r <sub>B</sub>	yr <sup>-1</sup>	0.10	0.05-0.25	9
Grass-Seedling	α	None	0.5	0.0-1.0	10
Tree-Seedling Competition	β	None	1.0	0.0-1.0	10
Maximum Tree Size	B <sub>o</sub>	m <sup>2</sup>	0.15	0.15	11
Maximum Basal Area	<b>B</b> <sub>max</sub>	m <sup>2</sup> ha <sup>-1</sup>	30	10-30	12
Maximum Grass Biomass	G <sub>max</sub>	tons ha <sub>-1</sub>	5	1-10	4
Fecundity	m	Indiv m <sup>-2</sup>	20	0-100	13

1. Higgins et al. (2000)

- 2. Prior et al. (2006); Holdo (2006)
- 3. Higgins et al. (2000);
- 4. van Langevelde et al. (2003); Williams and Albertson (2006)
- 5. Ludwig et al. (1997); Williams and Albertson (2006)
- 6. Ludwig et al. (1997); Williams and Albertson (2006)
- 7. Therwell et al. (2007)
- 8. Anderies et al. (2002)
- 9. Anderies et al. (2002)
- 10. Arbitrary
- 11. Unpublished data (Sea et al. 2007; Bond et al. 2007)
- 12. Holdo et al. (2007); Scholes and House (2001)
- 13. Unpublished data (Sea et al. 2007; Bond et al. 2007)

Table 5.1. Parameters used for the study.



Figure 5.2. Generalized bifurcation diagram for the demographic-competition model between *critical bifurcation parameter* (adult mortality  $\mu_A$ ) and equilibrium basal area (B<sup>\*</sup>). Small changes in adult mortality in the model lead to "jump-like" behavior in bifurcation diagrams. Along the stable branch (solid line) of the diagram, small incremental changes in adult mortality display monotonic decreases in the steady-state solution for woody basal area (B<sup>\*</sup>). When a threshold in adult mortality ( $\mu_{cr}$ ) is exceeded, basal area values collapse to zero. Thereafter, an unstable branch (dotted line) hysteresis-effect governs the dynamics as a new lower threshold in mortality ( $\mu_o$ ) is required for non-zero B<sup>\*</sup> values.

#### 5.3.1 Mortality of Juveniles and Adults

Results from previous work using a similar model (Hanan et al. 2008) suggested that very small changes in the adult fire mortality could be the difference between long term tree-grass coexistence and woody population collapses. I first analyzed mean-value conditions for the model using a fixed two-year fire interval and constant juvenile and adult mortality. Two-year fire interval averages are fairly typical for wetter savanna regions in Africa (Higgins et al. 2000). Using the equations from Fig. 1, model simulations were performed for 2000 years. The length of the simulations was sufficient for steady state conditions to occur. By increasing adult mortality slightly, I expected large changes to occur in steady state basal area values, i.e. small changes in fire intensity lead to long-term collapse of woody population reflected in basal area. I further expected that the changes would be larger for the demographic-competition model than for the logistic model. As in Hanan et al. (2007), I expected that large changes in juvenile fire mortality would lead to only small or no changes in steady state basal area values. The mean-value analyses provided useful comparisons to stochastic simulations.

#### 5.3.2 Stochasticity

In order to examine the effect of stochastic variation in fire interval and intensity, model simulations were performed for 2000 years as before, but allowing for random fluctuations in fire mortality and/or interval. Fire mortality was modeled as a normally distributed random variable having a mean value comparable to the mean-value analyses, i.e. 1-3%. Variability in fire intensity was measured by standard deviation in the means. Fire interval was randomized in the simulations using a normally distributed random

number generator that determined whether an individual fire occurred during a model year. For example, in any given model year, a discrete fire event (with random mortality loss) occurred with probability p, i.e. for 3 year burn interval, p = 0.333. Hence, consecutive fire years are as likely as are consecutive years without fire. Since the deterministic analyses (Chapter 2) suggest that the basal area in the model was very sensitive to small changes in adult (and basal) mortality, I anticipated that, with random fluctuations in intensity, some fire events occurring with greater intensity (loss rate) might impact the woody population greater in the demographic-competition model than for the logistic model. Mathematically, this can be described as a *stochastic shift* in basin of attraction (Fig 5.2) from higher to lower attractors (bottom solid line).

I also examined the impact of increasing the average fire interval from two to five years with fixed high adult mortality (0.05). This adult mortality can be considered representative of severe savanna fires (Williams et al. 1999; Higgins et al. 2000). While I expected that high fire severity in adult tree mortality might quickly lead to collapse in the woody population, I expected that the two models (demographic and logistic) would behave somewhat differently, as the logistic model should be able to persist at low basal areas while the demographic model cannot (without the addition of an immigration term).

## 5.3.3 Initial Values

A number of modeling and observational studies (Trollope 1982; Bond and van Wilgen 1996; Higgins et al. 2000) have suggested that demographic "bottlenecks" commonly occur in savannas, as smaller trees are unable to promote to larger size classes because of

competitive interactions and disturbance. Since the logistic version of my model is decoupled from the demographic equations for juveniles and adults, it is insensitive to demographic parameter changes. In the demographic version of my model, parameter changes that lead to lower recruitment of adult trees will increase demographic constraints (bottleneck), and in effect, reduce the woody maximum basal area ( $B_0A < B_{max}$ ). This interaction between the number and size of individuals and the capacity for population growth (the "effective carrying capacity") is likely to be a major difference between my model and previous models.

I conducted a series of simulations to examine the impact of changing initial basal area values comparing my demographic-competition model with a more conventional logistic growth model (using the same model but setting the maximum basal area to a fixed value B<sub>max</sub>). Simulations were carried out for 2000 years for each parameter combination. Mean basal area and standard deviations were recorded for the last 500 model years for 100 model replications. Initial basal area values were chosen from 1-20 m<sup>2</sup> ha<sup>-1</sup>. To examine the effects of demographic conditions, three different fecundity values were chosen to represent lower (m=10), medium (m=15), and higher (m=20)demographic cases. It was anticipated that there may be a lower demographic threshold (in m), at which all initial values in basal area lead to woody population collapses. Likewise, it was expected that for more favorable demographic parameter values the demographic model will closely resemble the logistic model. At intermediate demographic conditions, however, I expect, based on earlier analyses, alternate stable states with higher and lower basal area values and increased higher variance of steady state basal area values.

#### **5.3.4 Competition Asymmetry**

Many low dimensional savanna models have no implementation of size for woody plants, but instead use an aggregate such as woody biomass. It is impossible, however, to incorporate tree size-effects in tree-grass competition model where there is no "size" in the model. Through use of demographic accounting for juveniles and adults and with logistic modeling of woody basal area, I have a measure for average adult tree size (B/A) that can be used in size-competition relationship. In this study, I chose asymmetric treegrass competition to be a Michaelis-Menten saturation function (described in Fig. 5.9), where the competitive effect ( $c_{wg}$ ) of smaller adult trees on grass production (G) is smaller (e.g.  $c_{wg} < 1.0$ ; the effect on grass production for an equal biomass of grass  $c_{gg}$ = 1.0) and larger adult trees having a greater effect (e.g.  $c_{wg} > 1.0$ ) on grass production. I examined the effect of using a Michaelis-Menten type relationship between woody plant size and tree-competition having a 5%, 10%, and 20% advantages for the largest trees but keeping the overall  $c_{wg}$  equal to 1.0.

# **5.4 Results**

## 5.4.1 Mortality of Juveniles and Adults

Small changes in adult mortality ( $\mu_A$ ) for the model led to dramatically changed steadystate values in B<sup>\*</sup>, with a 1 % change in tree mortality for biennial fires being the difference between long-term tree-grass coexistence (at 2 % mortality) between fires and long-term extinction (3 % mortality) of woody plants. Fig. 5.3 compares mean-value runs for the demographic and logistic models with two-year fire intervals and increased adult fire mortality (1%, 2%, and 3% respectively). The results show that for 1% and 2% adult fire mortality, the two models yield nearly identical results, with 1% fire mortality leading to a relatively high woody state (~ 70% basal area maximum) and 2% mortality leading to roughly even tree-grass distribution. When fire mortality is increased to 3%, the two models diverge in steady-state values with the demographic model having a woody collapse at about 800 years, while the logistic model has woody persistence at a somewhat low level (~20% B<sub>max</sub>). The results are similar when fire interval alone is made a stochastic random variable, i.e. the probability of fire is a given year is 50% for biannual burns, 33% for triennial burns, etc. as the simulations indicated only small variations around the mean value (Fig. 5.4). There was a small but noticeable difference between the mean-value and stochastic runs for 3% adult fire mortality in the demographic model (compare Fig. 5.4E and Fig. 5.4E), as the stochastic case persisted at higher basal area followed by a more sudden drop.

#### **5.4.2 Stochasticity**

When the fire intensity (adult mortality) was allowed to be random (normally distributed variable with mean = 0.02), differences became clearly apparent between the mean-value and stochastic models. Fig. 5.4 exhibits results for the demographic and logistic models with stochastically varying fire intensity with mean 2% adult fire mortality. For direct comparison, compare the results to Fig. 5.3 C-D, which show relatively even tree-grass mixtures. By increasing the stochastic variability of fire intensity with small increases in the adult fire mortality standard deviation from 0.02 to 0.03 to 0.04, keeping the same mean value (2%), greater variability in fire intensity leads to lower steady state values in basal area for both models (Fig. 5.5). At relatively high variability ( $\sigma_{\mu\Lambda} = 0.04$ ), the demographic model has a woody basal area collapse after about 800 model years,



Figure 5.3. Model simulations showing the effect of increased adult mortality ( $\mu_A$ ) on tree basal area and grass root biomass. 5.3A. For the demographic-competition model,  $\mu_A$ = 0.01 leads to high values of tree basal area. Mean field simulation of 2000 years uses equations in Fig. 5.1. The green line depicts grass root biomass (%max) and the black line tree basal area (%max). 5.3B. As in 5.3A but using logistic model leads to identical results with 5.3A. The logistic model uses equations in Fig. 1 but replaces B<sub>o</sub>A with B<sub>max</sub>. 5.3C. For  $\mu_A$  = 0.02, the demographic-competition model has steady state solutions with approximately equal treegrass ratio. 5.3D. As in 5.5C but using logistic model leads to identical results with 5.3C. 5.3E. For  $\mu_A$  = 0.03 in the demographic-competition model leads to steady state tree-grass persistence. Other model parameters used default values (Table 5.1).


Figure 5.4. Model simulations showing the effect of increased adult fire mortality ( $\mu_A$ ) with stochastic fire interval (but constant adult fire mortality) on tree basal area and grass root biomass. For 5.4A-F, results for tree basal area are essentially the same as in mean-value analyses (Figure 5.3). Model simulations of 2000 years use equations as in Figure 1. The green line depicts grass root biomass (%max) and the black line tree basal area (% max). Standard deviation of adult mortality,  $\sigma_{\mu A} = 0.02 \text{ yr}^{-1}$ . Other model parameters use default values (Table 5.1).

whereas the logistic model is able to persist at relatively low woody levels (15-25% maximum).

As expected results for juvenile mortality indicated that even large changes in juvenile mortality had little or no effect on the model behavior for stochastic runs having twoyear fire intervals, and similar results were exhibited at various fire intervals. Fig. 5.6 displays results with increased juvenile mortality from 60% to 90% in the demographic model with constant 2% adult mortality. Even at high juvenile mortality in the model (80%), the results were similar to cases with lower juvenile mortality (see Fig. 5.6C). Only at the highest juvenile mortality (90%) does the model exhibit woody collapse, but after almost 2000 model years. Increasing the stochastic variability in juvenile fire mortality does not appreciably change model behavior (not shown), contrary to the results for adult fire mortality (Fig. 5.5). These results confirm the importance of adult trees in "storing" (Warren and Chesson 1985; Higgins et al. 2000) growth potential for trees in savannas and making them relatively insensitive to juvenile mortality whether it is caused by drought, fire or other factors.

Figure 5.7 shows the effects of increasing average fire interval for intense fires (adult fire mortality ~ 5%) in the demographic model. At two-year fire intervals there is steady decline in woody basal area, with extinction taking place in about 200 years. This result suggests that the use of extreme burning events alone is unlikely to remove woody plants within a human lifetime. At successively longer fire intervals, woody plants are able to persist for longer time periods (3 year ~ 500 years; 4 year ~ 1000 years). Although the trajectory of woodiness is decidedly downward in both cases, the decline is gradual, and woody exclusion by fire only is doubtful over ecologically relevant time scales (decades



Figure 5.5 Model simulations showing the effect of increased stochastic variability in adult fire mortality on tree basal area and grass root biomass. For all simulations parameter values were identical to simulations as in Figure 5.4C-D (e.g.  $\mu_A = 0.02$ ). 5.5A. In the demographic-competition model, with standard deviation ,  $\sigma_{\mu A} = 0.02$  leads to slightly depressed basal area values compared to simulations with constant fire mortality (see Figure 5.3C). 5.5B. As in 5.5A but using logistic model leads to identical results compared with 5.5A. 5.5C. Increasing  $\sigma_{\mu A}$  to 0.03 in the demographic-competition model leads to further decreases in basal area values compared with 5.5A. 5.5D. As in 5.5C but using logistic model yields similar results to 5.5C. 5.5E. At  $\sigma_{\mu A} = 0.04$  in the demographic-competition model leads to woody basal area collapse. 5.5F. As in 5.5E but with logistic model with leads to steady state tree-grass persistence. Other model parameters use default values (Table 5.1).



Figure 5.6. Model simulations showing the effect of increased juvenile mortality  $(\mu_J)$  on tree basal area and grass root biomass in the demographic-competition model. Except for juvenile mortality, all other parameter values use default values as in Figure 4C (Table 1). 5.6A-C. Model was largely insensitive to changes in juvenile mortality, except at the highest levels. 5.6D. Only at very high juvenile mortality (90%) did the tree basal area collapse.



Figure 5.7. Model simulations showing the effect of increased fire return time on basal area and grass root biomass in the demographic-competition model. For the simulations adult mortality was increased to 0.05 to examine if woody persistence could occur by increasing average fire interval alone. All other parameter used default values (Table 5.1). 5.7A. At two-year fire interval average, tree basal area extinction took place in about 200 model years. 5.7B. At three-year fire interval average, tree basal area extinction took place in about 600 model years. 5.7C. At four-year fire interval average, tree basal area extinction takes place in about 1000 model years. 5.7D. Trees are able to persist indefinitely in the model with 5-year return time (at about 20% maximum basal area).

to centuries), especially given potential for immigration that is not implemented in this model or if environmental changes lead to increased woody dominance. Finally, at five-year fire interval, woody plants are able to persist with intense fire, even though at relatively low values (about 20 %  $B_{max}$ ).

#### 5.4.3 Initial Values

Changes to parameters affecting initial conditions and fecundity rates significantly altered steady state solutions for basal area values. Fig. 5.8 depicts the contrast between a purely logistic model (labeled  $B_{max}$ ) and a demographic model. Simulations were run for 2000 model years, increasing initial mean basal area values from 1-20 m<sup>2</sup> ha<sup>-1</sup>, with mean basal area and standard error values recorded for 100 replicates. The demographic model using high fecundity rate (m=20) is similar to the logistic model, as there appears to be little demographic constraint, except for low initial basal area values  $(B < 4 m^2)$  $ha^{-1}$ ). For model runs with reduced fecundity (m=10), however, all initial basal values  $(B = 1-20 \text{ m}^2 \text{ ha}^{-1})$  led to woody plant exclusion under steady state conditions. The intermediate fecundity case displays somewhat different behavior from the other two cases, as there is greater variability (measured by the standard error) and significantly reduced steady-state basal area values compared with the logistic model. A possible explanation for the intermediate case (m=15) results may be that, although the mean steady state values were often non-zero, some of the runs led to woody extinction, which inflated the variance in basal area. Similar results were observed for modeling runs that included changes to promotion rate (p) and grass-juvenile competition ( $\alpha$ ).



Figure 5.8. The effect of initial conditions (and fecundity parameter m) on steady-state values of basal area in the demographic-competition model. Simulations were performed for 2000 model years using default values (see Table 5.1) with circles representing mean values for 100 replicates and error bars representing  $\pm$ - one standard deviation. Three different scenarios are shown with lower (m=10), medium (m=15), and higher (m=20). At low fecundity, the population collapses to a wood-free state regardless of initial conditions. At intermediate fecundity, there is higher variability (measured by standard deviation) in the steady-state basal area values, with reduced B<sup>\*</sup> values until starting values about 10 m<sup>2</sup> ha<sup>-1</sup>. The higher fecundity case has slightly (but significant) lower values than the B<sub>max</sub> model. Results are also shown for the logistic model (B<sub>max</sub>).

#### **5.4.4 Competition Asymmetry**

Including size-effect on tree-grass competition had a large effect on the steady state solution of basal area. Four different cases were examined: largest trees having 20% advantage, 10 % advantage, 5 % advantage, and no advantage. The effect of tree size on competition was compared across various grass-tree competition ( $c_{gw}$ )

from none to strong (Fig. 5.9). There were only small differences between the two cases when there was relatively weak  $c_{gw}$  (i.e.  $c_{gw} < 0.3$ ). But for increasingly large grass-ontree competition, the differences between the four cases grow larger, as higher grass-tree competition strongly depresses B<sup>\*</sup> values for the model without a competitive advantage for larger trees. Figure 5.9 illustrates that even if large trees have a small competitive advantage (10%) over grasses, the effect on steady state basal area is strong, especially if grasses also have a strong influence on woody production, i.e.  $c_{gw} > 0.5$ . The results highlight the importance of size structure of woody plants and reinforce that aggregate models using fixed competition parameters may not capture basic features of savannas ecology.

### **5.5 Discussion**

In this study I used numerical simulations to investigate further the dynamics of my demographic-competition model. I focused specifically on two interesting but little studied aspects of savanna ecology: stochastic variation in fires and asymmetric tree-grass competition. Most studies using simple "aggregated" models with no size structure (e.g. Anderies et al. 2002; van Langevelde et al. 2003) have examined only



Figure 5.9. The effect of size-asymmetric competition (in  $c_{wg}$ ) on steady state solutions of basal area in the demographic-competition model. Simulations were performed as in Figure 5.8. Three different Michaelis-Menten relationships ( $C_{wgi} = B_i/(a + B_i) + b$ ) were used to represent three levels of competitive asymmetry for  $c_{wg}$  with parameters *a* and *b* chosen to give largest adult trees advantages: 5%, 10%, 20%. The 20% case (e.g. largest trees have  $c_{wg} = 1.2$ ) indicates that there is little reduction in B<sup>\*</sup> for a wide range of grasson-tree ( $c_{gw}$ ) values, but a sharp decrease for higher  $c_{gw}(c_{gw} > 0.9)$ . With even a small competitive advantage (5% case), there is a change in B<sup>\*</sup> values for  $c_{gw}=0.7$  and  $c_{gw}=0.8$ compared with model simulations with no size-asymmetric competition (No size with fixed  $c_{wg}=1$ .). Circles represent mean values for 100 replicates and error bars represent +/- one standard deviation.

steady-state solutions, although there are a few recent exceptions (D'Odorico et al. 2006; Williams and Albertson 2006). This is surprising since variations in fire intensity (Higgins et al. 2000; Govender et al. 2006) and the impacts of climate change are rapidly becoming two important themes for savanna research (Tietjen and Jeltsch 2007). The potential for size-asymmetric tree-grass competition remains largely untested (but see Chapter 4; Sea and Hanan 2008) in field studies and was not incorporated explicitly in simple savanna models until its introduction in my model (Chapter 2). While traditional mathematical analyses of steady-state solutions have yielded important insights into the dynamics of the aggregated models, numerical simulations can provide important information on how stochastic factors such as fire and climate can impact model dynamics. Future savanna modeling studies will likely focus more on the importance of stochastic factors, including examinations into thresholds (magnitude) needed to generate alternate stable states as the model dynamics shift from one basin of attraction to another (D'Odorico et al. 2006; Williams and Albertson 2006; Hanan et al. 2008).

My model displayed strong sensitivity to small parameter changes in adult fire mortality. When adult fire mortality parameter values changed from 1% to 2% to 3% mortality in biannual fires, steady state basal area went from relatively high woodiness to even tree-grass ratio to woody exclusion, respectively (Fig. 5.3). Results are in general agreement with observational studies for savanna fires that indicate relatively low adult mortality despite considerable interannual variability in fuel load (Higgins et al. 2000; Hoffmann et al. 2003; Abbadie et al. 2006; Holdo 2006). Although another study (Williams et al. 1999) suggested that adult fire mortality can be quite high (~10%), these results were from a fire with unprecedented intensity in an Australian savanna.

Furthermore, field studies that relate fire mortality to tree size have generally been shortterm, often less than a decade and sometimes representing a single fire season or two (Holdo 2006). Since adult fire mortality is such a critical parameter to measure, and given the paucity of data, I suggest that efforts intensify in this area. My study complements short-term studies of the effects of fire on savanna vegetation structure (e.g. Hoffmann et al. 2003; Holdo 2006) by simulating fires stochastically that occur over periods from decades to longer time scales.

Observational and modeling studies support the idea that savanna vegetation responds differently to fires occurring with stochastic variability in intensity and interval compared with fires exhibiting mean-value characteristics, i.e. having fixed fire intensity and interval (Higgins et al. 2000; D'Odorico et al. 2006; Hanan et al. 2008). Models that incorporate size structure in the woody plant community are able to better represent the fire ecology of savannas since fire mortality for trees is largely a function of tree size (Williams et al. 1999; Higgins et al. 2000; Hoffmann et al. 2003; Holdo 2006; Hanan et al. 2008). My modeling results were able to confirm that a modest amount of variability in adult and basal fire mortality led to dramatically different long-term patterns of tree-grass persistence compared with model runs having fixed adult fire mortality (Fig. 5.3). As expected, the demographic-competition model is insensitive to large mortality in juveniles (Warner and Chesson 1985; Higgins et al. 2000), thus making juvenile fire mortality stochastic did not change steady state basal area values, nor did making adult fire interval alone stochastic (Fig. 5.4).

It is possible that larger trees enjoy some competitive advantage over grass for water, light and nutrient resources in savannas. Savanna models that do not incorporate size

structure (Walker et al. 1981; Walker and Noy-Meir 1982; Ludwig et al. 1997; Anderies et al. 2002; van Langevelde et al. 2003; D'Odorico et al. 2006; Williams and Albertson 2006) are unable to address size asymmetric tree-grass competition. Since my model keeps track simultaneously of both number of adults and total basal area, I am able to use a simple metric for average tree size. I was able to show in my model that even a small competitive advantage (10%) for the largest trees, with no overall advantage for the trees over the grass across the total size range, led to large differences in steady state basal area values (Fig. 5.9). It may be possible that the advantage for larger trees is even greater than implied by my modeling analyses. I suggest that models not incorporating size asymmetric competition may ignore an important feature of tree-grass competition in savannas, especially in semiarid and mesic savannas where larger trees can dominate the woody biomass.

Results from my modeling study have broader implications for the current discussions on how woody encroachment in savanna rangelands might be used to sequester carbon long-term in woody plants. A number of observations suggest that savannas and dry woodlands may be a net carbon sink worldwide through sequestration of carbon in woody plants (van Auken 2000; Jackson et al. 2004; Bond et al. 2003). Recent studies (e.g. Beringer et al. 2006) suggest that significant carbon uptake is still possible for annual low-intensity fires. Such fires tend to effectively remove herbaceous fuel quantity while causing little damage to adult woody plants. Fire-prone savannas are unlikely to be net carbon sinks, however, if unplanned high intensity fires dramatically reduce carbon stocks in above ground vegetation. Fire management strategies that focus on fire exclusion may, in fact, lead to eventual woody collapses either through large

unplanned fire events that impact adult trees or long-term demographic collapses. My work can provide information to help fire management determine an optimal fire strategy to maximize carbon storage in savannas and woodlands. Based on my modeling results, it is important that management strategies incorporate size demographic structure in modeling tools that are used to ensure that carbon gains are sustainable.

Results from this study have several implications for savanna modeling and could potentially change how savannas are modeled in the future. There has long been division in savanna modeling between theoretical modelers using simple "aggregated" lowdimensional models to explore the stability of savannas and modelers using complicated process-oriented models that are excellent tools to examine scenarios for a given location. The dichotomy is that simple models seldom, if ever, are confronted with data and that complicated models suffer from insufficient data for parameterization. Furthermore, the two modeling approaches have seldom been integrated, and an intermediate class of models, retaining some analytical tractability and realistic aspects of size structure, has not been forthcoming. In this study, by adding minimal sizestructure, size asymmetric tree-grass competition, and stochastic variation in fires to my model, I was able to examine more fully how some largely unexplored aspects of savanna ecology may be important both in a simple "demographic bottleneck" model and in real savannas.

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# Chapter 6

# Conclusions

# 6.1 Summary

My dissertation work has focused on how tree size may affect vegetation relationships in savannas. In Chapter 2, I developed a new demographic-competition model that integrated minimal aspects of woody plant size with resource competition. This allowed several improvements in modeling potential size-asymmetric relationships pertaining to resource use and fire. For example, instead of modeling fire as a simple reduction factor as in many simple "aggregated" models, the impact of fire in the demographiccompetition model is largely demographic and reflects better "demographic bottlenecks" found in observational studies. In Chapter 3, I made use of several data sets, collected by myself and others, to assess how tree size structure and size-partitioning of woody biomass changes along a rainfall gradient and how long term increases in biomass are possible even in plots subject to constant (annual) fire disturbance. In Chapter 4, I explored the potential that a foundational concept in plant ecology, self-thinning, might be applied to savannas, especially with respect to size-asymmetric tree-grass competition. Finally, in Chapter 5, I explored the transient dynamics of tree-grass-fire interactions for the demographic-competition model by making stochastic changes in fire intensity and interval and allowing for size-asymmetric tree-grass competition to the model.

This work draws on motivation from a recent review (Sankaran et al. 2004) that called for greater integration of demographic stage structure and resource competition in savanna models, identifying a significant gap in our ability to model savanna dynamics. The review correctly identified that savanna models have too narrowly focused on either resource competition or demographic stage and disturbance as the key drivers of savanna structure and function, but provided no details on how resource use, tree-grass and treetree competition could be implemented jointly in a simple savanna model. In order for a resource competition model to correctly represent tree-grass vegetation dynamics, resource use must allow for potential size asymmetric competitive relationships that are likely nonlinear in savannas. My proposed new model innovatively combines the minimum demographic structure (two size classes) with realistic resource competition that offers a significant conceptual advancement in savanna ecology.

By manipulating several aspects of tree mortality and competition in the new model (Chapter 2), I examined effects on steady-state values of basal area (B<sup>\*</sup>). Increasing juvenile mortality but excluding tree-grass competition, I was unable to reduce "required" adult mortality to observed natural levels (about 1%) without the model predicting very high B<sup>\*</sup> values suggesting, in effect, a closed woodland condition rather than a savanna. Given that savannas are widespread and persistent in the semi-arid tropics, this suggests that that tree-grass competition, or juvenile-grass competition, plays an important role in savannas. The finding agrees well with several studies that show strong competition between trees and grass (Belsky 1994; Simmons et al. 2007). When tree-competition (grass on juveniles and grass on adults) was included in model, simulations were qualitatively very different, shifting from monotonic behavior in the

absence of tree-grass competition with small increases in adult mortality leading to lower basal area values to bistable behavior when tree-grass competition is included, where small changes in adult mortality beyond a critical point led to collapse of basal values to zero. High, but ecologically plausible, values of grass-juvenile competition ( $\alpha$ ) led to alternate stable states in B<sup>\*</sup>. The results of this chapter suggest that aggregated models may need to be altered to include aspects asymmetric aspects of tree-grass competition and disturbance.

The results in Chapter 3 emphasize the functional significance of tree size in savannas. Finding that woody plant size-abundance relationships at wetter locations tend toward expected values for tropical forests has important implications for better understanding woody plant function in savannas. I found that, when fires are excluded in wetter savannas, size-abundance relationships tended towards a power exponent equaling the predicted value of -2 for tropical forests (Enquist et al. 1998). Results further suggest that the predictions of metabolic theory may indeed hold true in mesic savannas (> 650 MAP) in locations where disturbance factors (notably fire, but also herbivory) are excluded. This result indicates that resource limitation, density dependence, and competition among trees are important factors in wetter savanna systems, just as they are in adjacent moist forests. My study found that, along a gradient of increasing annual rainfall, a greater percentage of woody biomass is contained in relatively fire-resistant size classes. This contradicts recent studies that assume that most of the woody biomass in savannas in found in smaller, fire-prone size classes. Results suggest that general statements about woody plant size and biomass made previously are either likely to be site-specific or apply only to savannas with shorter trees, i.e., shrublands. The results

also contradict studies (e.g. D'Odorico et al. 2006), that suggest that savanna fires cause significant reductions in woody biomass (e.g. > 10 % biomass loss in each fire), and agree with earlier studies (e. g. Higgins et al. 2000) that the main function of fire in savannas is instead as a demographic "bottleneck" that prevents the promotion of smaller individuals into fire-resistant size classes. I also found that although fire continued annually at sites in Kruger National Park, woody biomass significantly increased in plots re-sampled in 2002 after ~ 30 years of annual prescribed burns. This result contradicts previous modeling work (van Langevelde et al. 2003; D'Odorico et al. 2006) that neglects size structure and, in large part, because the woody population is modeled as an aggregate, suggest that fires dramatically decrease woody biomass in savannas in the short term.

The negative correlation between tree size and density, self-thinning relationship, so common in forest and plantation ecosystems, appears also to occur in savannas. The potential of extending self-thinning concepts from traditional forest situations into the savannas lies in the possibility that such analyses may provide a useful diagnostic for the presence or absence of tree-tree competition, particularly in locations that have been protected from disturbance for some time and where the woody community is not suppressed by other, non-resource based, mechanisms. The characteristics of the self-thinning line (slope, intercept, and linearity) may reveal information on how competition between trees and grasses changes with tree age and size. It is likely that competition with grasses may result in both increased mortality and growth suppression for seedlings and young trees. For adults the effect of grass competitors, if significant at all, would likely be expressed through reductions in growth rather than in increased mortality.

Little or no experimental data on the competitive effects of grass on tree growth and mortality across age and size-classes is available. However, results in Chapter 4 suggest that the tree-grass competitive interaction is asymmetric with respect to tree size, with the data tending to support the hypothetical response in my conceptual model. It may be that this tree-tree interaction only occurs in situations where disturbance by fire, herbivory and humans has been historically low. However, while most savannas are subject to a variety of disturbance factors, the identification of an underlying resourcelimitation to woody population dynamics is of great significance to our understanding of savanna systems and our ability to model and predict their behavior under varying land use and climate.

In Chapter 5, the transient effects of tree-grass-fire interactions were explored in the demographic-competition model by making stochastic changes in fire intensity and interval and allowing for size-asymmetric tree-grass competition to the model. Modeling results were able to confirm that a modest amount of variability in adult mortality led to dramatically different long-term patterns of tree-grass persistence compared with model simulations having fixed adult fire mortality. The model displayed strong sensitivity to small parameter changes in adult fire mortality. When adult fire mortality parameter values changed from 1% to 2% to 3% mortality in biannual fires, steady state basal area went from relatively high to woody exclusion. These results were in general agreement to a previous modeling study (Hanan et al. 2008). The results highlight sensitivity in the model to adult mortality, and given the paucity of size-mortality data for savanna trees, suggest the need for further studies. I was able to show that even a small competitive advantage (10%) for the largest trees led to large differences in steady state basal area

values. Models not incorporating size asymmetric competition may ignore an important feature of tree-grass competition in savannas, especially in semiarid and mesic savannas where larger trees can dominate the woody biomass.

## 6.2 Simple vs. Complex Model Discussion

Models for exploring savanna vegetation dynamics vary greatly in complexity from the simplest one equation aggregate versions (e.g. D'Odorico et al. 2006) to highly mechanized process-oriented models (e.g. Coughenour 1993; Simioni et al. 2000; Boone et al. 2004; Liedloff and Cook 2007) that use ecophysiological principles to explore water, nutrient, and light resource partitioning between trees and grass. Although simple, aggregated models are easier to use since the mathematical behavior has been well-studied, they ignore all the complexity /biology that may buffer the real system so that it could easily be argued that may (or may not) make simple models ineffectual or worthless since these models have not been scrutinized with data. The intense data requirements for parameterizing process-oriented models, however, often cannot be met with existing data, and the cost of acquiring new data is often prohibitively expensive.

The simple models have number of advantages and disadvantages that need to be considered depending the scope and nature of the savanna question.

#### **Advantages**

*Easier to build and understand* Simple models often have only a few equations, sometimes only one. The equations can be modeled as a regression equation, or as

differential or difference equation, or as a system of equations. As May (1976) showed, simple models may still display a rich assortment of behavior, even unexpectedly so, where in some respects the complex models, and the real systems, may not exhibit the rich assortment because neither the complex models nor the real ecosystems are simple. The dynamics of the simple models are very easy to understand for those individuals comfortable with elementary calculus and differential equations. *Total closed-form solutions*. Simple analytical models have closed-form solutions. In closed-form, all solutions are known for all parameter values. Basic mathematical analysis can be used to examine the steady state solutions. *Generalization*. Simple models are a nice starting point for investigations. If the assumptions are explicitly known and stated, investigation can use the simple model as a null-model. For instance, a simple model can take a mean-value approach with no explicit treatment of spatial heterogeneity. Departures from a null model may suggest processes not accounted for such as the influences of spatial or temporal heterogeneity.

#### **Disadvantages**

*Hidden Assumptions.* In order to make a model as simple as possible, a number of assumptions are necessary. For example, the logistic competition model needs only two differential equations. The intrinsic growth rate, r, is a complicated process, certainly seldom ever fixed, and carrying capacity, K, often changes with the environment and is temporally and spatially varying. Finally, competition is a very complex process, potentially poorly modeled with a single competition coefficient. *Does the model represent the system?* Simple models can only be taken so far and can never expect to

model the immense complexity of an ecosystem. At best a simple model can represent a portion of the ecosystem or a highly abstracted version of one. *Error propagation*. Complex models often have multiple negative feedbacks that can minimize compounding errors. Simple models with nonlinear terms often have computational difficulties, and small errors can become magnified.

The complex models have number of advantages and disadvantages.

#### <u>Advantages</u>

Logical, like science. A mechanistic, process-oriented simulation model based should potentially be constructed from scratch usually a logical step-by-step fashion. Simulation models can be used to test basic scientific hypothesis by making changes to model parameters. Bond et al. (2005) world fire suppression is an excellent example of a clear, simple scientific question address with a simulation model. *Transparent*. Although complex simulation models can be large, there is no reason to believe that a model should not be comprehensible by a patient person. There are fewer hidden assumptions in complex models. The structure of computer languages requires that logic be followed. With proper commenting, anyone should be able to understand the basic features of a model and what it is trying to be accomplished. *Modular and hierarchical*. Complex models can be built in modular form. Each section can be added quasiindependently of other. Other models can be added to an existing model. The hierarchical structure of complex models allows for the possibility of addressing

problems at multiple scales. Patterns can emerge at higher levels. Top-down and bottom-up control are effectively modeled using simulation tools.

#### Disadvantages of complex models

*Steep learning curve*. There is a steep learning curve with complex simulation models. People not familiar with the science behind the model can be intimidated by the model complexity. Complex models in ecology tend to be written by biologically-oriented modelers. *Data Hungry*. There is a perception that complex simulation models are data hungry. A simple rule has suggested that a greater number of parameters in a model should require a greater amount of data. This rule tends to come from people who believe in parsimonious modeling and emphasize prediction. However, complex modelers tend to believe that scientific understanding is more important than prediction. *Expensive to make*. Building a complex simulation model can take a long time. Many hours are needed for coding and debugging a model. Building a complex simulation requires strong programming skills.

SAVANNA is such a spatially-explicit, process-oriented model (Coughenour 1993; Boone et al. 2004). The model simulates ecological processes at landscape through regional scales over annual to decade time scales. The model treats ecological processes at an intermediate level of resolution: spatially explicit at the landscape scale and spatially implicit at the patch scale. Monthly climate data is implemented into a soil water submodel that determines water availability for a net primary production submodel. Tree populations are divided into six age/size classes; and establishment is affected by competition with herbaceous plants. Provided there is sufficient data from

model parameterization, SAVANNA is particularly well suited for addressing questions such as: *Does competition for water and light affect the relative numbers and sizes of different functional groups of plants?* 

# **6.3 Broader Implications**

My dissertation work provides new insights into how ecologists might change their thinking about savannas. Previously, savanna ecology tended largely to view savannas from a *myopic*, community level perspective dominated by field studies or from a *hyperopic*, ecosystem level perspective dominated by modeling studies. I suggest that savanna ecologists need to broaden their perspective beyond a single scale of analysis towards greater synthesis of other studies and make use of interdisciplinary approaches to solving more complex problems. For example, based on results from this study, we need to incorporate certain aspects of population level detail including woody plant size distribution and how it affects patterns of growth, resource use, carrying capacity and is affected by disturbance. Furthermore, my results on self-thinning and size-abundance relationships in undisturbed savannas should encourage other ecologists to consider using savannas to test general theories in plant ecology and, hopefully, also encourage savanna ecologists to think harder about how savanna ecology studies may play a greater role in theoretical plant ecology.

My dissertation work has several implications for savanna modeling and can potentially change how savannas are modeled in the future. There has long been a division in savanna modeling between theoretical modelers that use simple "aggregated" low-dimensional models to explore stability of savannas and modelers that use

complicated process-oriented models that are excellent tools to examine scenarios for a given location. Both modeling approaches have advantages and disadvantages. The dichotomy is that the simple models seldom are confronted with data and the complicated models seldom have sufficient data for parameterization. An intermediate class of models until now has not emerged that retains analytical tractability of the simple models and overcomes the obvious shortcomings of "aggregated" models that do not realistically capture key aspects of savanna ecology, including growth, resource use, competition, and disturbance. By adding minimal size-structure to the simple models I am able to fully explore how changes in a few parameter values affect a model that capture the realism of a "demographic bottleneck" in more complicated models (e.g. Higgins et al. 2000).

My dissertation work has ecological applications in how we manage savannas, particularly with respect to fire. Traditionally, environmental managers have used knowledge about how fire frequency affects savanna vegetation structure, especially to prevent woody encroachment (and dominance) into valuable grazing lands. More recent studies have increased focus on determining how fire intensity leads to structural changes in the woody community (Higgins et al. 2000; Higgins et al. 2007). Results from this study have two major implications for the management of savananas: 1) The effects of fire on woody vegetation loss depend more on the size structure of the woody community than on either the fire intensity or interval; 2) Fire management strategies, based on results from my dissertation, would suggest that the timeframe to reduce or eliminate woody plants from a system may be too long for success using fire alone. Instead, a strategy that makes use of relatively inexpensive fires and proactive harvesting

of adult trees may lead to the desired outcome of rapid declines in the woody plants. Finally, the management strategy for long-term carbon sequestration in woody plants (and soils) for savannas will need to incorporate ideas from this dissertation, most notably the optimization of fire interval and intensity to increase carbon gains.

### 6.4 Future Work

A goal of my dissertation work was the development of the first analytically tractable savanna model that incorporates some size-structure but also implements realistic resource competition. Work expanding on my dissertation studies could follow several promising paths. 1) Developing analytical (or numerically-equivalent) solutions for the stochastic version of the model. A similar (but much simpler) study was published recently in D'Odorico et al. (2006). 2) Fully implementing stochastic rainfall variability as an ecological driver. Currently the model (Chapter 5) implements stochastic variability in fire mortality and return time. A more mechanistic version of the model would allow herbaceous (and possibly woody) production to be a function of rainfall and allow fire intensity to be a function of herbaceous biomass as in other models (e.g. Higgins et al. 2000). 3) Making the minimal demographic-competition model into spatially explicit model while retaining its analytical properties. 4) Reducing a higher dimensional demographic savanna model (e.g. Higgins et al. 2000) to an equivalent lowdimension model such as the one in my dissertation.

# 6.5 References

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