

# Competitive interactions between savanna trees

**Tiffany Prileeni Pillay**

Submitted in partial fulfilment of the academic requirements for the degree of

Master of Science

in the Discipline of Botany

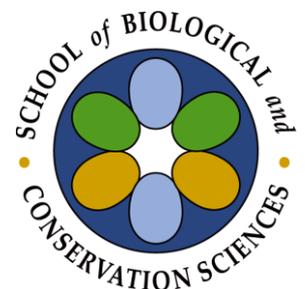
School of Biological and Conservation Sciences

Faculty of Science and Agriculture

University of KwaZulu-Natal

Pietermaritzburg

2011



## SUMMARY

Savannas are socio-economically important ecosystems, which support high floral and faunal diversity. This biome covers large areas of Africa, Australia, South America, India and parts of North America, and is comprised of a mixture of grasses and woody plant biomass. Most empirical studies of savanna ecology have focused primarily on the interactions between trees and grasses, especially at the seedling stage where recruitment is regarded as a key driver of savanna dynamics. However, studies of interactions between woody savanna plants, such as competition and facilitation, are less common in the literature. Considering the increasingly negative effects of woody plant encroachment and global climate change, interactions between woody plants need to be closely monitored and evaluated.

In this thesis, I investigated the effects of neighbourhood competition on four dominant tree species from humid savannas (receiving more than 1000 mm of mean annual rainfall, hereafter referred to as “humid species”) and four dominant tree species from mesic savannas (receiving around 650 mm of mean annual rainfall, hereafter referred to as “mesic species”). I employed a greenhouse-based study to examine the effects of neighbour density on the growth, survival and biomass of savanna tree seedling species. I quantified two aspects of competitive ability (competitive effect and response), and compiled competitive hierarchies for both groups. In addition, I correlated competitive ability with several plant traits. Using field surveys of natural stands of *Acacia karroo* from humid savanna sites across KwaZulu-Natal, South Africa, I examined the spatial patterns and competitive interactions between trees.

A greenhouse experiment revealed that mesic species suffered high levels of mortality when exposed to increasing neighbour density, while humid species were relatively unaffected in terms of survival. However, mesic species were able to maintain constant relative growth rates (RGR)

despite increasing neighbourhood competition while the RGR of humid species decreased as neighbour density increased. The total biomass of both humid and mesic species also declined as the neighbourhood competition increased. In terms of competitive effect and response, we found that these two aspects of competitive ability were not concordant (i.e. good effect competitors were not necessarily good response competitors). Lastly, we found that plant traits such as specific leaf area and above-ground features (e.g. shoot biomass and leaf number) were significantly related to the competitive *response* or *effect* of savanna tree seedlings.

Spatial distribution patterns of a dominant humid savanna species, *Acacia karroo*, revealed that juvenile plants are aggregated, as expected due to facilitation, seed dispersal and vegetative reproduction. However, the regular spacing of larger individuals due to competition and density-dependant mortality were not detected. We found, using nearest neighbour analysis, that trees with closer neighbours had smaller canopy diameters. This suggests that while competitive interactions are present, they may be weak and insufficient to cause mortality, rather resulting in decreased plant performance.

Overall, I found that, at the seedling stage, neighbourhood competition was particularly important for both humid and mesic savanna trees. Competitive interactions between mesic seedlings resulted in significantly higher mortality rates, greatly reducing the recruitment of these species. Humid species, although able to successfully recruit, experienced reduced growth rates under dense neighbourhood competition. In the field, patterns of competitive interactions were difficult to detect using spatial statistics alone. However, we did find evidence of weak competitive interactions among humid savanna trees. In summary, competitive interactions were important for all savanna species at the crucial seedling stage. However, field comparisons showed that competitive interactions were relatively weak in *A. karroo* and resulted in reduced performance rather than differential mortality.

## PREFACE

The work described in the thesis was carried out at the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from January 2010 to November 2011, under the supervision of Prof. David Ward.

This thesis, submitted for the degree of Master of Science in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the author and has not been submitted in any form to another university. Where use was made of the work of others, it has been duly acknowledged in the text.

Chapter 2 and 3 in this thesis were written in paper format following the format of the journal they were/will be submitted to.



.....  
Tiffany P. Pillay  
December 2011

I certify that the above statement is correct

.....  
Professor David Ward  
Supervisor  
December 2011

# FACULTY OF SCIENCE AND AGRICULTURE

## DECLARATION 1 - PLAGIARISM

I, Tiffany P. Pillay, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
  - a. Their words have been re-written but the general information attributed to them has been referenced.
  - b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.
5. This thesis does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

Signed:



.....

Tiffany P. Pillay

December 2011

# FACULTY OF SCIENCE AND AGRICULTURE

## DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

### Publication 1

T P Pillay and D Ward. **Competitive *effect and response* of savanna tree seedlings: Comparison of survival, growth and associated functional traits**

Submitted to *Journal of Vegetation Science*

*Author contributions:*

TPP conceived the paper with DW. TPP collected and analysed the data, and wrote the paper. DW contributed valuable comments to the manuscript.

### Publication 2

T P Pillay and D Ward. **Spatial pattern analysis and competition between *Acacia karroo* trees in humid savannas**

Submitted to the journal *Ecography*

*Author contributions:*

TPP conceived the paper with DW. TPP collected and analysed the data, and wrote the paper. DW contributed valuable comments to the manuscript.

Signed:



.....  
Tiffany P. Pillay

December 2011

## **Dedication**

This thesis is dedicated to my mother...for imparting onto me the hunger for success...and for holding my hand through it all.

*It is in fact a part of the function of education to help us escape, not from our own time — for we are bound by that — but from the intellectual and emotional limitations of our time.*

**T.S. Eliot**

## ACKNOWLEDGMENTS

The culmination of this thesis has truly been a life-changing experience, unachievable without the grace of God and His immense blessings, for which I am eternally grateful.

I am also deeply grateful to my supervisor, Professor David Ward, firstly for having faith in my abilities and also for his hard work and dedication. Prof Ward has been exceptional throughout the course of this MSc; most especially in reviewing chapters, with prompt response and insightful comments. It has been an honour working with a researcher of his calibre.

The technical staff at UKZN have been very helpful, in terms of the experimental setup and data collection. I thank Alison Young, Stephne Stuart and Vanessa Stuart for sharing their expertise on irrigation and planting techniques. I am also thankful to Andile Shange, Welcome Ncgobo and the late Freedom Linda for their hardwork on data collection and harvesting.

My days at UKZN certainly would not have been complete without the antics of my colleagues Snehalatha Vadigi, Desale Okubamichael, Kyle Tomlinson, Halima Abdillahi, Mayashree Chinsamy and Zivanai Tsvuura. I would like to thank them all for always encouraging me through my numerous phases of despondence. I am also grateful to my dear friends, Fathima and the late A.V. Murchie for their emmense blessings and prayers during the course of this MSc.

Lastly, I would like to extend my deepest gratitude to my loving family, who have indeed felt the brunt of my anxiety during the preparation of this thesis. To my parents, I am thankful for all the opportunities you have given me, and the sacrifices that were made for my benefit. To my sister Daria, I am grateful to you for always reminding me of my worth. To Zunaïd, thank you for your undying love and support.

# TABLE OF CONTENTS

SUMMARY .....	i
PREFACE .....	iii
DECLARATION 1 - PLAGIARISM.....	iv
DECLARATION 2 - PUBLICATIONS .....	v
DEDICATION .....	vi
ACKNOWLEDGEMENTS .....	vii
TABLE OF CONTENTS .....	viii

## CHAPTER 1:

### Literature review: An overview of inter-tree competition in savannas .....1

Savanna ecology .....	1
Competition .....	2
Tree-grass competition .....	3
Tree-tree competition.....	4
Tree spacing.....	5
Evidence for tree-tree competition .....	7
Importance of competition in humid savanna .....	9
Field methods of detecting competition .....	11
Neighbour removal.....	11
Nearest neighbour analysis.....	12
Point pattern analysis.....	12
Greenhouse methods of studying competition .....	14
Competitive effect and response .....	14
Competitive hierarchies and trait-based frameworks .....	16
Linking species traits to abundance/performance .....	16
Woody plant encroachment .....	17
Research gaps, problem statement and justification.....	18
Species notes.....	19
Structure of the thesis .....	21
References.....	23

## CHAPTER 2:

### Competitive response and effect of savanna tree seedlings: Comparison of survival, growth and associated functional traits .....34

Abstract.....	35
Introduction.....	37
Materials and Methods .....	40
Study species .....	39
Experimental setup .....	39
Data collection.....	41
Statistical analysis .....	42
Results .....	43
Discussion.....	46
Conclusions .....	51
Acknowledgements.....	52
References.....	53
Tables.....	59
Figures .....	61

### CHAPTER 3:

#### Spatial pattern analysis and competition between *Acacia karroo* trees in humid savannas .....

Abstract.....	74
Introduction.....	75
Materials and Methods .....	78
Study species .....	78
Study sites and data collection .....	78
Data analysis .....	79
Results .....	82
Discussion.....	83
Acknowledgements.....	87
References.....	87
Tables.....	91
Figure legends.....	92
Figures .....	94

### CHAPTER 4:

#### Conclusions and future research .....

Conclusions .....	100
Future research.....	103
References.....	104

# Chapter 1

## Literature review: An overview of inter-tree competition in savannas

### Savanna ecology

Savannas are broadly defined as landscapes composed of a continuous grass layer and scattered trees (Walter 1939; Skarpe 1991; Scholes & Archer 1997; Higgins, Bond & Trollope 2000). However, the relative representation of these life-forms varies considerably across savanna types (Scholes & Archer 1997; Sankaran, Ratnam & Hanan 2004; Calabrese *et al.* 2010). The savanna biome covers about 13% of the global land surface and about half of the area of Africa, Australia, and South America (Scholes & Archer 1997). In South Africa, the savanna biome spans an area of about 410 000 km<sup>2</sup>, which is approximately 33.5 % of the country (Smit 1999). Savannas are known to support high faunal and floral diversity, and are also of great socioeconomic importance (Young & Solbrig 1993) in terms of agriculture and eco-tourism. Considering the significance of this biome, much effort is placed on research towards the conservation of savannas.

Savannas are dynamic on both temporal and spatial scales, and vary with changes in climate (primarily rainfall), soil nutrient content, fire regime, herbivory and physical disturbance (Walker 1987; Scholes & Archer 1997; Calabrese *et al.* 2010). The availability of resources (water and nutrients) and disturbances (fire and large mammalian herbivory) have been identified as interactive mechanisms that regulate savanna structure (Walter 1971; Scholes & Archer 1997; Higgins, Bond & Trollope 2000; Jeltsch *et al.* 1996; Weber & Grimm 2000). Primary areas of research surrounding savanna ecology are the mechanisms of coexistence of two contrasting life forms (grass and trees), and the factors that influence the relative abundance of each life form (Sankaran, Ratnam & Hanan 2004).

Many studies have investigated the factors that influence the relative abundance of the grass and woody components in African savannas (Skarpe 1991; Higgins *et al.* 2000; Jeltsch, Webber & Grimm 2000; Sankaran, Ratnam & Hanan 2004; Kraaij & Ward 2006). Two broad explanations for the persistence of trees and grasses in savannas can be distinguished, following Sankaran, Ratnam & Hanan (2004), as competition-based models and demographic bottleneck models (Chesson 2000; Sankaran, Ratnam & Hanan 2004). In the competition-based models, the importance of competitive interactions is emphasized as playing a fundamental role in savanna maintenance (Walter 1971, Walker *et al.* 1981, Walker & Noy-Meir 1982). In these models, rainfall and nutrient availability are seen as key drivers of the tree-grass continuum. The demographic bottleneck models focus on factors that limit the establishment and subsequent survival of the woody plants in the savanna ecosystem (Higgins, Bond & Trollope 2000; Sankaran, Ratnam & Hanan 2004). Disturbances such as fire and herbivory are factors that are emphasized in the demographic bottleneck models. Although both types of models differ in their emphases on key processes, both model types show how the factors affecting tree seedling recruitment have a key impact on savanna dynamics. Tree seedling recruitment is therefore an integral research priority for understanding savanna ecosystems, as asserted by several other studies (Higgins, Bond & Trollope 2000; Jeltsch *et al.* 1996; Weber & Grimm 2000; Wiegand, Saltz & Ward 2006).

## **Competition**

Competition occurs when adjacent plants are forced to share the limited resources of a restricted area (Tilman 1982; Suding, Goldberg & Hartman 2003). Resource-mediated competition occurs when individual plants consume resources, thereby depriving another individual of the same nutrient pool (Tilman 1982, 1988). Because most resources required by plants are growth-limiting, the deprived plant will express some form of reduced ability, either morphologically or physiologically (Weiner 1990). Two modes of competition are distinguished: asymmetric and symmetric competition. Asymmetric competition occurs when larger individuals acquire a

disproportionate amount of the available resources, thereby exerting a negative effect on neighbouring plants (Schwinning & Weiner 1998), and is often referred to as "dominance and suppression" and "one-sided competition". With symmetric competition, plants share resources equally or proportionally to their size (Weiner 1990; Weiner & Damgaard 2006). It is usually assumed that light competition is size asymmetric whereas below-ground competition is size symmetric (Schwinning & Weiner 1998).

In savannas, it is important to understand the coexistence of two contrasting life-forms viz. grasses and woody plants. In order for stable coexistence of plants of different life forms, Tilman (1982) suggested that competition within life forms should be greater than competition between life forms. In other words, intraspecific competition should be greater than interspecific competition, through differential partitioning of resources by different species (Tilman 1982). In terms of the classic Lotka-Volterra model of competition (Chesson 2000), this translates to the competition coefficient (which is the effect of species "A" on species "A" divided by the effect of species "A" on species "B") being  $< 1$  (Chesson 2000). Under this criterion, one can expect the coexistence of different species, as stronger competition between conspecifics prevents the competitive exclusion of heterospecifics. If stable coexistence theory holds true, competition between trees should be greater than competition between trees and grasses. While there has been considerable evidence supporting this theory, several empirical studies have shown that intraspecific competition was not greater than interspecific competition (see review by Goldberg & Barton 1992).

### **Tree-grass competition**

Important resources such as light, water and soil nutrients play a fundamental role in savanna maintenance, as the delicate balance between grasses and trees largely depends on the ability of each to acquire certain resources more efficiently (Skarpe 1991). One of the first attempts to explain the coexistence of trees and grasses was Walters's two-layer hypothesis, which postulated that trees and grasses are water limited and acquire moisture from different soil depths (Walter 1939).

Grasses, which have shallow roots, rely on water from the topsoil, while trees which have deeper roots, use water from the subsoil. Under these conditions, grasses out-compete seedlings whose rooting depths during the early stages of establishment are equivalent to that of grasses (Walter 1939, 1971). Once tree seedlings are established, their extensive root networks begin to depress grass cover (Walter 1971; Skarpe 1991; Ludwig *et al.* 2003). Through this vertical spatial partitioning of soil water resources, grass and tree cover in savannas is regulated such that trees and grasses are able to co-exist. This model of tree-grass coexistence has received much criticism for over-simplifying the root zone profiles of both trees and grasses (Knoop & Walker 1985; Jeltsch *et al.* 1996; Ward 2005; Kambatuku, Cramer & Ward 2011).

While several studies have found evidence in support of the two-layer hypothesis (Walker *et al.* 1981; Walker & Noy-Meir, 1982; Knoop & Walker 1985), Knoop & Walker (1985) found that in a South African savanna, grasses did have access to subsoil water, contrary to Walter's (1971) models. Grasses are able to suppress tree germination and establishment directly by having higher growth (Poorter & Nagel 2000) and transpiration rates, as well as a fibrous root system that is more efficient at absorbing water and nutrients (Pärtel & Wilson 2002; Bond 2008). Many savanna tree seedlings are shade-intolerant and high grass biomass can suppress their recruitment, by shading the seedlings during the crucial stages of establishment (Higgins, Bond & Trollope 2000). Grasses also indirectly reduce tree growth by providing sufficient fuel loads required for fires (Skarpe 1991). Fire also has a negative effect on tree seedling establishment when saplings are still too small to escape the flame zone (Balfour & Midgley 2008).

### **Tree-tree competition**

Although tree-grass competition is an important feature in savannas, inter and/or intra-specific tree competition may also be a fundamental driver of the savanna ecosystem (Meyer *et al.* 2008). During the early stages of seedling establishment, adult trees may exert a strong asymmetric effect on neighbouring seedlings, via root competition for available soil moisture and nutrients

(Schwinning & Weiner 1998; Calabrese *et al.* 2010). Competitive exclusion of weaker individuals may also occur later on in the life history of trees when extensive root networks are formed, causing an overlap in rooting zones. Two plants compete with each other when their zones of influence overlap. The greater the overlap, the more intense is the competition (Bonan 1991; Meyer *et al.* 2008).

### **Tree spacing**

Competition between trees is important in maintaining a savanna ecosystem, as it affects the spacing of trees, and thus the spatial heterogeneity of the landscape (Meyer *et al.* 2008). Intense density-dependent mortality can convert a savanna into a grassland, whereas weak competitive interactions (or facilitation) may in fact promote tree aggregation (which can be considered as woody plant encroachment) (Jeltsch *et al.* 1996; Meyer *et al.* 2008).

Tree spacing can be random, clumped or regular. Random tree spacing is an indication either that there are no significant spatial interactions, or that the pattern represents a transitional state in a population shifting from an aggregated distributional pattern to a regular pattern (Skarpe 1991). Trees that display a clumped distribution may be facilitating the growth of one another. In this case, plants growing at high densities create ‘islands of fertility’ (Ravi *et al.* 2010). The formation of islands of fertility is attributed to both abiotic and biotic processes such as local-scale variations in soil erosion and deposition, plant uptake of water and nutrients by lateral roots spreading into the surrounding soils, nitrogen fixation by shrubs, and activities of soil micro and macro-organisms (Pugnaire, Haase & Puigdefábregas 1996; Ravi *et al.* 2010). This facilitative interaction improves the living conditions of surrounding plants, and is a common phenomenon in arid areas (Schleicher *et al.* 2011a; Schleicher, Wiegand & Ward 2011 b). Facilitation may also promote the shrub encroachment process (Ravi *et al.* 2010), especially in arid areas with a patchy landscape, where aggregated trees form nutrient-rich shrub patches. These “resource islands” are scattered among patches of grasses and nutrient-depleted bare soil interspaces (Schlesinger *et al.*

1990). Directed seed dispersal, may also lead to a clumped distribution of trees, for example, when animal-dispersed seeds of savanna trees are preferentially defaecated beneath other plant species (Milton & Dean 1995). Alternatively, patchy heterogeneous environments may also lead to a clumped tree distribution, where trees aggregate around favourable areas, leaving other less favourable areas bare (Getzin *et al.* 2006). A regular pattern is usually the result of density-dependent mortality, and occurs when trees experience competition for a limited resource. Intense competition leads to mortality of clumped individuals, resulting in a regular spacing of trees. This is the premise of the honeycomb rippling model (Fig 1).

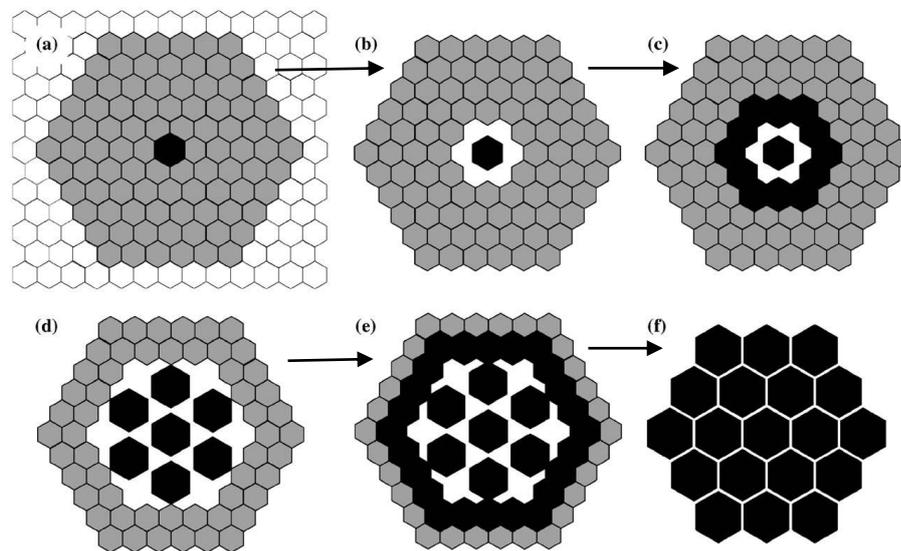


Fig 1. Honeycomb rippling model Figures show a time series (A-F) of hexagonal subsets of a larger patch. Trees get larger from time series A to F, in sequence as indicated by arrows. Each (small) hexagon represents a bush or shrub; the relative sizes of the hexagons represent relative plant sizes. Black filling of the hexagon indicates highly competitive bushes/trees acquiring sufficient resources to survive the competition with their neighbors (from Ward 2005; Wiegand *et al.* 2008).

According to this model, if one of the seedlings is stronger than all the others (Figure 1A), this seedling is able to acquire more resources (water and nutrients) than its immediate neighbours

and thereby outcompetes and ultimately kills these neighbours. This seedling is now able to grow in size (Figure 1B). Since more resources are now available, this gives seedlings in the second circle around the central seedling the opportunity to access more resources, to grow and to use even more water and nutrients (Figure 1C). Distances from the focal seedling to the seedlings in the circle of surviving plants are not identical. Therefore, every second plant has a disadvantage, which, with time, leads to mortality of every second seedling in the ring (Figure 1C). Furthermore, the increased size of the surviving seedlings leads to suppression and finally the death of the seedlings in the third row (Figure 1D). The death of these seedlings gives seedlings in the fourth row access to more water and nutrients, leading to their growth (Figure 1E) and the death of the next ring and so on. Therefore, in a patch of closely aggregated tree seedlings, if one of the seedlings happens to be competitively superior to the others, this model predicts that a ‘honeycomb-rippling effect’ of mortality and growth of individuals will occur. As seedlings continue to grow, they reach a regular, dense hexagonal pattern (Figure 1F) (Ward 2005; Wiegand, Saltz & Ward 2006; Wiegand *et al.* 2008).

### **Evidence for tree-tree competition**

Few studies have tested competition between savanna trees, as opposed to the “savanna question” of tree-grass coexistence. In addition, evidence for the importance of tree-tree interactions in savannas is sparse and indirect (Scholes & Archer 1997), providing largely inferential evidence for competition. However, over the last three decades, there has been an increase in empirical studies testing this type of interaction in savanna ecosystems across a wide range of sites (Table 1). Several features such as fire frequency, herbivory and soil nutrient status affect the establishment and subsequent survival of savanna tree seedlings. However, rainfall is viewed as the main driver of woody plant cover in savanna ecosystems, especially in areas receiving less than 650 mm mean annual rainfall (Sankaran *et al.* 2005). As a result, few studies have empirically tested the effects of competition in humid savannas (Table 1).

Table 1. Empirical studies of tree on tree competition, ranked according to mean annual rainfall  
(Adapted from Calabrese *et al.* 2010).

Location	Mean annual rainfall (mm)	Researchers
Namibia	150	Wiegand, Saltz & Ward 2005
South Africa	210	Jeltsch, Moloney & Milton 1999
Botswana	300	Skarpe 1991
South Africa	377	Meyer <i>et al.</i> 2008
South Africa	377	Schleicher, Wiegand & Ward 2011b
South Africa	388	Kambatuku, Cramer & Ward 2011
Chile	403	Gutierrez & Fuentes 1979
South Africa	411	Moustakas <i>et al.</i> 2008; 2006
South Africa	610	Smith & Goodman 1986
South Africa	630	Smith & Grant 1986
Portugal	685	Gouveia & Freitas 2008
Ivory Coast	1300	Barot <i>et al.</i> 1999
Australia	1584	Lehmann, Prior & Bowman 2009

Studying competitive interactions between savanna trees may be difficult for various reasons, such as long lifespans, during which competitive ability of an individual plant may fluctuate. Perennial savanna trees typically reach reproductive maturity at around 10 years old (Rohner & Ward 1999). Therefore, while reproductive fitness is the most relevant measure of the importance of competition (Goldberg *et al.* 1999), it is not always possible to measure a metric such as fecundity in savanna trees. Also, the overlap of rooting zones is difficult to determine. Root systems of a single tree may span tens of metres, such that competing trees may in fact be far apart (Casper, Schenk & Jackson 2003). Nevertheless, several studies have inferred the presence of competitive interactions between trees through both direct and indirect methods. Direct methods include neighbour removal experiments (Smith 1986; Wiegand, Saltz & Ward 2006; Meyer *et al.* 2008; Kambatuku, Cramer & Ward 2011) and indirect methods involve nearest neighbour analysis (Smith 1986; Grundy, Campbell & Frost 1994) and spatial pattern analysis (Wiegand & Moloney

2004; Getzin *et al.* 2006). While there are other methods of quantifying tree-on-tree competition, such as canopy symmetry and tree morphology (Iponga, Milton & Richardson 2008), only the aforementioned techniques will be described here.

### **Importance of competition in humid savanna**

While it is widely agreed that competition is an important factor structuring plant communities, there is little agreement on the presence of competitive interactions along productivity gradients (Grime 1979; Tilman 1982; Grace 1995; Craine 2005), i.e. is competition more intense under high or low productivity, or are competitive interactions present at all levels of productivity? This disagreement forms the basis of the prolonged “Grime-Tilman” debate (Grime 1979; Tilman 1982), which is still in need of resolution (Grace 1995; Goldberg & Novoplansky 1997; Craine 2005).

Grime (1979) asserted that competition is a predominant force within plant communities in productive environments, but as productivity decreases and abiotic environmental stress increases, the role of competition in plant communities decreases. According to Grime’s R-C-S (Ruderal-Competitor-Stress tolerator) model (also known as “Grime’s triangle”), competition intensity is presumed to increase with increasing habitat productivity, based on the corresponding increase in plant biomass (Grime 1979; Reader *et al.* 1994). While this theory is primarily concerned with three major syndromes of life-history traits, 'Ruderal', 'Stress-tolerator', and 'Competitor', an integral part is its assumptions/predictions about the relationship between plant traits and competitive success (Grace 1991). Conversely, the resource ratio model (Tilman 1982) argues that competition is equally significant in plant communities irrespective of system productivity, but that the mechanisms by which plants compete change along productivity gradients (Newman 1973; Tilman 1982, 1988). Tilman (1982) stated that in highly productive environments plants attain high biomass, and therefore compete strongly for light or space. Likewise, in unproductive environments, plants compete just as strongly, but for different resources, viz. soil water or nutrients (Tilman 1982). Tilman's theory is based on an analytical model consisting of a pair of equations that

describe the dynamics of populations as a function of resource concentration and the concentration of resource as a function of supply rate and uptake rate (Tilman 1982; Grace 1991).

These hypotheses have been tested by comparing the magnitude of competition intensity along productivity gradients (cf. Goldberg & Novoplansky 1997; Craine 2005). However, empirical studies supporting each hypothesis have been inconsistent, leaving the debate unresolved (Goldberg & Barton 1992). Upon analysis of the Grime-Tilman debate, several reviews have concluded that the two authors employed different definitions of competition (Grace 1991, 1995; Goldberg & Novoplansky 1997; Craine 2005). Grace (1991) suggested that debate over the models of Grime and Tilman can be resolved by clearly distinguishing between two key components of competition, the intensity of competition and the importance of competition. The intensity of competition is a reduction in the growth of species A as a consequence of the presence of species B. The importance of competition is the impact of B on A expressed as a proportion of the impact of the whole environment on A (Brooker *et al.* 2005). Grime's theory postulates that the *importance* of competition in structuring plant communities increases along a productivity gradient, while Tilman's theory, on the other hand, postulates that the *intensity* of competition is constant along a productivity gradient. As a possible resolution, Goldberg & Novoplansky (1997) have developed a two-phase resource dynamics hypothesis of plant competition along productivity gradients, which is based on the fact that water and nutrient resources are usually supplied in pulses rather than continuously, as assumed by most theories. Craine (2005) has reconciled ideas of Grime and Tilman, and has suggested a number of scenarios of competition based on the supply of resources and the relative abilities of plants to pre-empt these resources. Nevertheless, general theory on the mechanisms and outcomes of resource competition along productivity gradients and our ability to resolve key questions about the role interactions may play in plant communities are still lacking.

A recent meta-analysis of African savanna field sites showed a strong positive relationship between mean annual rainfall (MAR) and woody plant cover (Sankaran *et al.* 2005). Below

650 mm MAR, common in arid and semi-arid savannas, herbivory, fire, and soil properties can only reduce woody cover below its maximum, which depends linearly on MAR (Meyer *et al.* 2007). Above this threshold, savannas are unstable and disturbances such as fire or herbivory are necessary to prevent bush encroachment or canopy closure (Sankaran *et al.* 2005). The presence of competitive interactions in arid and semi-arid savannas has been well documented (Schleicher *et al.* 2011a; Schleicher, Wiegand & Ward 2011b). However, it is still unclear as to whether competition plays a vital role in regulating woody plant biomass in humid savannas receiving around 1000 mm MAR (Bond 2008).

## **Field methods of detecting competition**

### **Neighbour removal**

Detecting patterns of competition can be very difficult, especially under field conditions where many other environmental variables have to be taken into account. Some of the earliest field experiments in ecology showed that removal of competitors allowed species to grow outside their usual range (Tansley 1917). Reductions in allocations to biomass may be attributed to trade-offs related to neighbourhood competition. For example, thinning of *Colophospermum mopane* stands has been shown to stimulate vegetative growth, flowering and seed production in the remaining trees (Smit 1994). Smith & Goodman (1986) found a significant increase in both stem diameter and shoot extension of *Acacia nilotica* trees whose neighbours were removed within a radius of 5 m. Schleicher, Wiegand & Ward (2011b) have shown that when *Acacia mellifera* was removed from ten 1 ha plots in an arid area of South Africa, then neighbouring *Tarchonanthus camphoratus* recruited more and invested more in biomass. A recent study by Kambatuku, Cramer & Ward (2011) has shown that when all neighbouring woody competitors were removed from a semi-arid savanna in South Africa, the remaining target shrubs displayed greater growth, less water stress, and a relatively small degree of canopy dieback.

### **Nearest neighbour analysis**

The most common method of inferring competitive interactions between plants is nearest neighbour analysis (Yeaton & Cody 1976; Shackleton 2002). This method assumes that competitive interference between neighbouring plants, if present, will be manifest through a reduction in the size of one or both of the competing neighbours. If there is a significant correlation between the distance separating the two neighbouring plants and the sum of their sizes (usually canopy cover or diameter at breast height), then competition is inferred (Pielou 1962). Significant positive correlations between the size of a tree and the distance to its nearest neighbour, indicating competitive interactions, have been reported for *Burkea africana*-*Terminalia sericea* savanna in southern Africa (Smith & Grant 1986) and for large individuals of *Brachystegia spiciformis* and *Julbernardia globiflora* in Zimbabwe (Grundey, Campbell & Frost 1994).

### **Point pattern analysis**

While nearest neighbour analysis and removal experiments are useful in inferring underlying processes, they have been criticised (cf. Campbell *et al.* 1991). In terms of nearest neighbour analysis, differences in size attributes of neighbours may be due to variable growth rates and modular plasticity, rather than purely a result of competitive interactions (Shi & Zang 2003; Getzin *et al.* 2006). Neighbour removal experiments are often complicated to perform as whole-plant excavations, especially root profiles, are difficult to identify (Casper, Schenk & Jackson 2003). Over the last decade, there has been an increasing interest in the study of spatial patterns in ecology (e.g., Turner 1989; Levin 1992; Gustafson 1998; Liebhold & Gurevitch 2002; Wiegand & Moloney 2004; Fortin, Dale & ver Hoef 2006; Getzin *et al.* 2006). The origin of spatial-pattern analysis is linked to plant community research (Watt 1947), but has also been applied in numerous studies of different animal taxa, such as birds, slugs, insects and spiders (Birkhofer, Henschel & Scheu 2006). Ecologists study spatial pattern to infer the existence of underlying processes (Perry *et al.* 2002).

For example, spatial patterns of plants may result from different processes and forces such as seed dispersal, intraspecific competition, interspecific competition, disturbance, herbivory, or environmental heterogeneity (Schleicher *et al.* 2011a).

When using spatial statistics, the position of a plant in a plot is represented by a point and the analysis of the spatial point pattern exhibits whether the distribution of the points are random, clumped, or regular by comparing the distribution to a null model of random distribution (Schleicher *et al.* 2011a). First-order statistics describe the large-scale variation in the intensity of the points in the study region. In contrast, second-order statistics are based on the distribution of distances of pairs of points (Ripley 1981) and they describe the small-scale spatial correlation structure of the point pattern. Some of the second-order statistics, such as the commonly used Ripley's  $K$ -function or the pair-correlation function  $g$ , use the information on all inter-point distances (Ripley 1981; Bailey & Gatrell 1995) and provide more information on the scale of the pattern than do statistics that use nearest-neighbour distances only. Significance is usually evaluated by comparing the observed data with Monte Carlo envelopes from the analysis of multiple simulations of a null model (Wiegand & Moloney 2004). Using the confidence envelopes, one can derive the underlying pattern; if the function exceeds the upper confidence envelope it indicates a spatial aggregation (facilitation) of the species. However, if the function is below the lower confidence envelope, it indicates a spatial regularity (competition) of the plants (Wiegand & Moloney 2004). The common null model is complete spatial randomness (CSR), but other null models may be appropriate depending on the density of plants in an area and the biological question asked. Hence, the major challenge for plant ecologists when using spatial statistics is to apply the correct null model, suitable to answer the appropriate biological questions (Wiegand & Moloney 2004; Lancaster 2006).

## Greenhouse methods of studying competition

### Competitive effect and response

The inference of competition under field conditions, as discussed above, may be reinforced with greenhouse studies. While greenhouse studies are often criticized as being artificial representatives of natural processes (Cousens 2000), it is often necessary to manipulate certain variables while excluding other confounding factors. This is rarely achievable in the field. Quantifying the competitive ability of a plant requires a statistically sound experimental design that allows for the measurement of plant performance along a gradient of disturbance (Gibson *et al.* 1999). There is much debate surrounding the constituents of a good experimental design, and the methods of analysis and interpretation (Gibson *et al.* 1999; Freckleton & Watkinson 2000). Several experimental designs have been employed over the years to investigate plant interactions. Among these are simple pairwise experiments, replacement series and target-neighbour / additive designs, as well as numerous variations of each. Simple pairwise experiments usually have a 1:1 ratio of a two-species combination. In a replacement series design, the density of both competing species is varied while the overall density is maintained. The target-neighbour design is one in which the density of the target species is maintained throughout the experiment, and the density of the neighbour species is varied (Gibson *et al.* 1999).

Using a target-neighbour design, two aspects of competitive ability viz. *competitive effect* and *competitive response* can easily be quantified. *Competitive effect* and *response* are useful measures of evaluating competition between species (Goldberg & Landa 1991). *Competitive effect* can be described as the ability of a plant to constrain the growth and performance of neighbours, while *competitive response* is the ability of a plant to tolerate competition from neighbouring plants (Goldberg & Landa 1991; Keddy *et al.* 2002). Numerous studies have quantified the *competitive effect* and *response* of plants (Goldberg & Landa 1991; Keddy *et al.* 2002; Hager 2004; Violle *et al.* 2009), usually employing short-lived annual plants, and have shown the effects of neighbourhood

competition on the survival, growth rate and biomass of target individuals. These studies focus not only on co-occurring indigenous plants, but also on the interactions between native and non-native invasive plants that have an apparently higher competitive ability (Hager 2004). Competition between plants result in trade-offs between growth, defence and reproduction (Suding, Goldberg & Hartman 2003). In plants growing in highly competitive environments, growth will be limited firstly through exploitation competition, where resources are depleted by neighbouring plants (Tilman 1982), or secondly by interference competition where neighbouring plants make resources inaccessible (Aarssen & Keogh 2002). Therefore, reductions in allocations to biomass may be attributed to trade-offs related to neighbourhood competition (White & Harper 1970). Hence, the performance of an individual plant will be determined by its ability to tolerate neighbour competition, as well as its ability to suppress neighbouring plants through resource acquisition.

A survey of the literature by Goldberg & Barton (1992) revealed that in many cases, competition experiments measured either competitive effect or response, when the experimental design allowed them to measure both aspects. Wang *et al.* (2010) posed the question as to whether effect and response are two sides of the same coin; i.e. whether these two forms of competition were functionally linked, and which plant traits are associated with effect and response competitive abilities? In addition, competitive effect and response are not always correlated, i.e. a good effect competitor may not be a good response competitor. Goldberg & Landa (1991) found that there was no significant correlation between the competitive effect and response of seven species of herbaceous plants. Keddy, Twolan-Strutt & Wisheu (1994) also found that competitive effect and response were not correlated, while Goldberg & Fleetwood (1987) found a positive relationship between competitive effect and response. This means that in order to fully understand the dynamics of species competitive interactions, both aspects of competitive ability need to be measured (Goldberg & Landa 1991; Goldberg & Barton 1992).

## **Competitive hierarchies and trait-based frameworks**

Competitive effect and response quantification allows for the ranking of a species based on the relative ability to acquire resources or to tolerate resource depletion by neighbours. These species rankings are termed “competition hierarchies” and have been constructed for many biological systems (Perkins, Holmes & Weltzin 2007), ranging from sessile invertebrate communities in artificial reefs to ant communities as well as many types of plant communities (Panetta & Randall 1993; Goldberg & Landa 1991; Howard & Goldberg 2001; Fynn *et al.* 2011). Species at the top of hierarchies are characterized as being competitively superior to the remaining species, based on either competitive effect or response ability. Competitive hierarchies are an effective way of using species rankings as a predictive tool of species abundance and distribution in natural communities (Keddy & Shipley 1989; Silvertown & Dale 1991; Keddy, Gaudet & Fraser 2000; Fynn *et al.* 2011). For example, Miller & Werner (1987) reported a correlation between the abundance of six species in an old field community and their competitive ability in additive field experiments. They concluded that the competitive hierarchy explained relative species abundance in the field.

## **Linking species traits to abundance/performance**

The most common method of assessing the importance of various types of biotic interactions, such as competition and facilitation, has been a species-based approach (Gross *et al.* 2009). While species-based approaches are useful in highlighting the main drivers of species interactions, they are often difficult to generalize across communities and habitats of different productivities (Goldberg *et al.* 1999; Gross *et al.* 2009). In order to fully conceptualize the role of biotic interactions on a community level and the effects at the community level, more generalized principles are needed. Statements about functional traits give generality and predictability, whereas nomenclatural ecology tends towards highly contingent rules and special cases (McGill *et al.* 2006). Cornelissen *et al.* (2003) also state that it is widely recognized that species should be classified into functional trait

groups, rather than higher taxonomic identities because it does not allow for easy ecological interpretation.

A number of authors have suggested that competitive ability may be related to simple ecological traits such as seed size (Rees & Westoby 1997), seedling size (Schwinning & Fox 1995), emergence time (Cousens *et al.* 1987), plant size (Goldberg & Landa 1991) and population productivity (Gaudet & Keddy 1988). Violle *et al.* (2009) have shown that instantaneous measurements of certain plant traits, such as specific leaf area, can provide information on how plants perceive competitive environments. To be useful to community ecology, traits should vary more between than within species and preferably be measured on continuous scales. As environmental problems such as global climate change increase, the need for general predictive models in ecology become more crucial. A functional trait-based framework of assessing biotic interactions should therefore be the main focus of future competition studies (Cornelissen *et al.* 2003).

### **Woody plant encroachment**

Savanna ecosystems are driven by resource and disturbance mediated patterns, with competitive interactions playing a vital role. Although coexistence of species may occur through resource partitioning, often one life form may dominate another. Woody plant encroachment (often known as bush or shrub encroachment) refers to the increasing prevalence of woody vegetation, which subsequently suppresses the palatable grass layer, resulting in substantial economic and biodiversity losses. The causes of woody plant encroachment have been debated: chronic cattle grazing and fire suppression are important drivers (Archer, Schimel & Holland 1995; Hudak 1999). In savannas, rainfall events are usually patchy, both on spatial and temporal scales (Wiegand, Saltz & Ward 2006). Sparse and often low amounts of precipitation are only sufficient to infiltrate the uppermost soil layers, which are often only available to the shallow root profiles of grasses. However, when grasses are heavily grazed, the competitive effect of grasses is greatly reduced, and soil moisture

usually intercepted by the grass layer is, is now able to seep down to the subsoil layers, which is then used by trees (Walter 1939, 1971). This allows for the proliferation of woody plant biomass. However, rooting niche separation cannot be an exclusive explanation for the initiation of woody plant encroachment because young trees use the same subsurface soil layer as grasses in the sensitive early stages of growth (Ward 2005). For example, Kraaij & Ward (2006) found that germination of the heavily encroaching species *Acacia mellifera* is much more sensitive to rainfall supplementation than to grazing.

Woody plant encroachment results in closed-canopy environments, which reduce the grazing capacity of savanna rangelands (Archer, Schimel & Holland 1995; Ward 2005; Wiegand, Saltz & Ward 2006). In addition, the species diversity of encroached areas is greatly reduced (Archer, Schimel & Holland 1995). Woody plant encroachment has become an increasingly destructive force over the last fifty years, and still is a poorly understood phenomenon, lacking in clear explanations and predictive tools (Scholes & Archer 1997). It is therefore of great importance that all factors related to woody plant establishment and survival are clearly tested, so that more insight can be gained, and hopefully applied to the problem of woody plant encroachment.

### **Research gaps, problem statement and justification**

Woody plant encroachment, coupled with increasing global climate change poses a major threat to maintenance of the savanna biome. Comprehensive knowledge on the interactions between savanna woody plants is necessary to implement correct land-use practices and conservation efforts. In addition, our knowledge of the impacts of competition in humid savannas is lacking.

Based on this justification, I aim to investigate the competitive interactions between humid and mesic savanna tree species experimentally in the greenhouse and in the field.

## Species notes

Four dominant tree species (*Acacia nigrescens*, *Acacia tortilis*, *Colophospermum mopane*, *Combretum apiculatum*) were chosen from a mesic savanna (receiving about 650 mm of annual rainfall), and four dominant tree species (*Acacia sieberiana*, *Acacia karroo*, *Acacia robusta*, *Schotia brachypetala*) were selected from a humid savanna (receiving about 1000 mm of annual rainfall). We focused primarily on the genus *Acacia*, because it is widely distributed in southern Africa, with the highest concentration of *Acacia* species found in the savanna biome (Smit 1999).

1. *Acacia karroo* (sweet thorn) is the most widely distributed *Acacia* species in southern Africa, occurring in Zimbabwe, Botswana, Swaziland, Lesotho, Namibia, South Africa, Mozambique, and Zambia. This species has oblong leaflets (6 x 2.5mm long), and is capable of nodulating with *Rhizobium* (Coates Palgrave 2005). This deciduous tree is a highly polymorphic species, ranging in height from 1 m to more than 30 m, and with enormous variation in the architecture of adults (Archibald & Bond 2003; Ward 2011). This is the coastal form that occurs from the mouth of the Tugela River to Mozambique and is otherwise known as *A. kosiensis* (Coates Palgrave 2005). Ward (2011) has found that the *A. kosiensis* epithet is inappropriate and prefers the retention of *A. karroo* for this widespread and variable species. I used plants from Richards Bay in the first experiment (Chapter 2).
2. *Acacia nigrescens* (knobthorn) is a small to medium-sized tree (5-18 m) with a broad distribution, occurring from Tanzania southwards to KwaZulu-Natal (Van Wyk & Van Wyk 2007). *A. nigrescens* has nearly circular leaflets (0.7 x 2.2 mm long), and is capable of forming root nodules (Coates Palgrave 2005).
3. *Acacia robusta* subsp. *robusta* (ankle thorn) is a deciduous, medium to large tree (7-15 m), with leaflets around 2.5-7.5 mm in size, found across the Northern Cape, Gauteng, North West province, Mpumalanga and Limpopo (Smit 1999). *Acacia robusta* is nodulated by nitrogen-fixing *Rhizobium* bacteria

4. *Acacia sieberiana* (paperbark thorn) is a medium-sized (7-15 m), deciduous, flat-topped tree, found in South Africa, Swaziland, Zimbabwe, northern and eastern Botswana, northern Namibia and tropical Africa north to Ethiopia, and is capable of nodulating with *Rhizobium* strains (Smit 1999). Leaflets of this species are narrowly oblong (2 – 6.5 x 0.8 mm in size) (Coates Palgrave 2005) .
5. *Acacia tortilis* subsp. *heteracantha* (umbrella thorn) is a small to medium-sized, deciduous , nodulating tree (5 -15 m), flat-crowned, and is mostly single-stemmed (Van Wyk & Van Wyk 2007). The subspecies *A. tortilis heteracantha* is the only subspecies represented in South Africa (Smit 1999). Leaflets occur in pairs of 6 – 9, and are usually very small (0.3- 3 mm long) (Coates Palgrave 2005).
6. *Colophospermum mopane* (mopane) grows in hot, dry, low-lying areas, in the far northern parts of South Africa, into Zimbabwe, Mozambique, Botswana, Zambia, Namibia, Angola and Malawi. It is a non-nodulating, deciduous shrub or a tall tree up to 30 m in the northern part of its range, depending on soil conditions and water availability (Van Wyk & Van Wyk 2007). Leaves are bifoliolate, with two leaflets (10 x 1.5 mm in size) (Coates Palgrave 2005).
7. *Combretum apiculatum* subsp. *apiculatum* (red bushwillow) is a non-nodulating, deciduous, small to medium-sized tree (3 - 10 m), widespread in Africa, growing from KwaZulu-Natal and Mpumalanga and Limpopo (South Africa) to Botswana, Mozambique, Namibia, Zimbabwe and other parts of tropical Africa. Leaves are usually 7 x 4 cm in size (Coates Palgrave 2005).
8. *Schotia brachypetala* (weeping boer-bean) is a medium to large, non-nodulating tree (10 - 16 m) with a broadly-spreading, densely branched, rounded crown, and oblong leaflets (2.5 – 8.5 x 1.2 – 4.5 mm in size) (Coates Palgrave 2005). This deciduous tree is found from the northern parts of the Eastern Cape, through KwaZulu-Natal, Swaziland, Mpumalanga, Northern Province and into Mozambique and Zimbabwe (Van Wyk & Van Wyk 2007).

## Structure of the thesis

This thesis has been written and compiled as a series of papers for publication. This necessarily results in some overlap among the chapters. The aim of this study was to determine the effects of competitive interactions between savanna tree species, and to detect patterns of competition in the field.

Chapter 1 is a literature review. Chapter 2 represents a greenhouse study in which I tested all pair-wise combinations of four humid and four mesic savanna tree species, at varying neighbour densities. I investigated the effect of neighbourhood competition on the growth, survival, biomass and functional traits of savanna tree species. I also quantified two aspects of competitive ability for each species; *competitive effect* and *response*, and correlated these to several plant functional traits. I contrasted the differences in effects and responses between tree species from humid and mesic savannas, and commented on the relevance of competition in humid savannas. Chapter 2 is formatted for *Journal of Vegetation Science*.

Chapter 3 is a field survey of *Acacia karroo* trees from three humid savannas in KwaZulu-Natal. Spatial statistics and nearest neighbour analysis were used to assess the distribution of the trees, and to identify underlying mechanisms such as competition or facilitation. I examined the overall spatial pattern of *A. karroo* trees, as well as the relative distributions of adult and juvenile trees. In this chapter, I discuss the efficacy of spatial statistics and nearest neighbour analysis in detecting competitive interactions, as well as alternative explanations for clumped or aggregated tree patterns. Chapter 3 is formatted for *Ecography*.

Finally, in Chapter 4, I summarize the overall findings with regard to competitive interactions between savanna tree species. I also provide recommendations for future studies.

## References

- Aarssen, L.W. & Keogh, T. (2002) Conundrums of competitive ability in plants: what to measure? *Oikos*, **96**, 531-542.
- Archer, S., Schimel, D.S. & Holland, E.A. (1995) Mechanisms of shrubland expansion: land use, climate or CO<sub>2</sub>? *Climatic Change*, **29**, 91-99.
- Archibald, S. & Bond, W.J. (2003) Growing tall vs growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos*, **102**, 3-14.
- Bailey, T.C. & Gatrell, A.C. (1995) *Interactive Spatial Data Analysis*. Longman Scientific and Technical, Harlow, UK.
- Balfour, D.A. & Midgley, J.J. (2008) A demographic perspective on bush encroachment by *Acacia karroo* in Hluluwe-Imfolozi Park, South Africa. *African Journal of Range and Forage Science*, **23**, 147-155.
- Barot, S., Gignoux, J. & Menaut, J.C. (1999) Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology*, **80**, 1987-2005.
- Birkhofer, K., Henschel, J. & Scheu, S. (2006) Spatial-pattern analysis in a territorial spider: evidence for multi-scale effects. *Ecography*, **29**, 641-648.
- Bonan, G.B. (1991) Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. *Annals of Botany*, **68**, 341-347.
- Bond, W.J. (2008) What limits trees in C<sub>4</sub> grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*, **39**, 641-659.
- Brooker, R., Kikvidze, Z., Pugnaire, F.I., Callaway, R.M., Choler, P., Lortie, C.J. & Michalet, R. (2005) The importance of importance. *Oikos*, **109**, 63-70.
- Calabrese, J.M., Vazquez, F., Lopez, C., San Miguel, M. & Grimm, V. (2010) The independent and interactive effects of tree-tree establishment competition and fire on savanna structure and dynamics. *American Naturalist*, **175**, 44-65.

- Campbell, B.D., Grime, J.P., Mackey, J.M.L. & Jalili, A. (1991) The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. *Functional Ecology*, **5**, 241-253.
- Casper, B.B., Schenk, H.J. & Jackson, R.B. (2003) Defining a plant's belowground zone of influence. *Ecology*, **84**, 2313-2321.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343-366.
- Coates Palgrave, M. (2005) *Keith Coates Palgrave's Trees of Southern Africa*. Struik Publishers, Cape Town.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335-380.
- Cousens, R. (2000) Greenhouse studies of interactions between plants: the flaws are in interpretation rather than design. *Journal of Ecology*, **88**, 352-353.
- Cousens, R., Brain, P., O'Donovan, J.T. & O'Sullivan, P.A. (1987) The use of biologically realistic equations to describe the effects of weed density and relative time of emergence on crop yield. *Weed Science*, **35**, 720-725.
- Craine, J.M. (2005) Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology*, **93**, 1041-1052.
- Fortin, M.J., Dale, M.R.T. & ver Hoef, J. (2006) Spatial analysis in ecology. *Encyclopedia of Environmetrics* (eds A. H. El-Shaarawi & W.W Piegorsch), pp. 2051-2058. John Wiley & Sons, Ltd, New York, USA.
- Freckleton, R.P. & Watkinson, A.R. (2000) Designs for greenhouse studies of interactions between plants: an analytical perspective. *Journal of Ecology*, **88**, 386-391.

- Fynn, R.W.S., Morris, C., Ward, D. & Kirkman, K. (2011) Trait–environment relations for dominant grasses in South African mesic grassland support a general leaf economic model. *Journal of Vegetation Science*, **22**, 528-540.
- Gaudet, C.L. & Keddy, P.A. (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242-243.
- Getzin, S., Dean, C., He, F., A. Trofymow, J., Wiegand, K. & Wiegand, T. (2006) Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, **29**, 671-682.
- Gibson, D.J., Connolly, J., Hartnett, D.C. & Weidenhamer, J.D. (1999) Designs for greenhouse studies of interactions between plants. *Journal of Ecology*, **87**, 1-16.
- Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist*, **139**, 771-801.
- Goldberg, D.E. & Fleetwood, L. (1987) Competitive effect and response in four annual plants. *Journal of Ecology*, **75**, 1131-1143.
- Goldberg, D.E. & Landa, K. (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013-1030.
- Goldberg, D.E. & Novoplansky, A. (1997) On the relative importance of competition in unproductive environments. *Journal of Ecology*, **85**, 409-418.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118-1131.
- Gouveia, A. & Freitas, H. (2008) Intraspecific competition and water use efficiency in *Quercus suber*: evidence of an optimum tree density? *Trees - Structure and Function*, **22**, 521-530.
- Grace, J.B. (1991) A clarification of the debate between Grime and Tilman. *Functional Ecology*, **5**, 583-587.

- Grace, J.B. (1995) On the measurement of plant competition intensity. *Ecology*, **76**, 305–308.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, Chichester, UK.
- Gross, N., Kunstler, G., Liancourt, P., De Bello, F., Suding, K.N. & Lavorel, S. (2009) Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology*, **23**, 1167-1178.
- Grundy, I.M., Campbell, B.M. & Frost, P.G.H. (1994) Spatial pattern, regeneration and growth rates of *Brachystegia spiciformis* and *Julbernardia globiflora*. *Plant Ecology*, **115**, 101-107.
- Gustafson, E.J. (1998) Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems*, **1**, 143-156.
- Hager, H.A. (2004) Competitive effect versus competitive response of invasive and native wetland plant species. *Oecologia*, **139**, 140-149.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, **88**, 213-229.
- Howard, T.G. & Goldberg, D.E. (2001) Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology*, **82**, 979-990.
- Hudak, A. (1999) Rangeland mismanagement in South Africa: failure to apply ecological knowledge. *Human Ecology*, **27**, 55-78.
- Iponga, D.M., Milton, S.J. & Richardson, D.M. (2008) Superiority in competition for light: A crucial attribute defining the impact of the invasive alien tree *Schinus molle* (Anacardiaceae) in South African savanna. *Journal of Arid Environments*, **72**, 612-623.
- Jeltsch, F., Milton, S.J., Dean, W.R.J. & Rooyen, N.V. (1996) Tree spacing and coexistence in semiarid savannas. *Journal of Ecology*, **84**, 583-595.
- Jeltsch, F., Moloney, K. & Milton, S.J. (1999) Detecting process from snapshot pattern: lessons from tree spacing in the southern Kalahari. *Oikos*, **85**, 451-466.

- Jeltsch, F., Weber, G.E. & Grimm, V. (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, **150**, 161-171.
- Kambatuku, J., Cramer, M. & Ward, D. (2011) Intraspecific competition between shrubs in a semi-arid savanna. *Plant Ecology*, **212**, 701-713.
- Keddy, P., Nielsen, K., Weiher, E. & Lawson, R. (2002) Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science*, **13**, 5-16.
- Keddy, P.A. & Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos*, **54**, 234-241.
- Keddy, P.A., Gaudet, C. & Fraser, L.H. (2000) Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *Journal of Ecology*, **88**, 413-423.
- Keddy, P.A., Twolan-Strutt, L. & Wisheu, I.C. (1994) Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? *Journal of Ecology*, **82**, 635-643.
- Knoop, W.T. & Walker, B.H. (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology*, **73**, 235-253.
- Kraaij, T. & Ward, D. (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, **186**, 235-246.
- Lancaster, J. (2006) Using neutral landscapes to identify patterns of aggregation across resource points. *Ecography*, **29**, 385-395.
- Lehmann, C., Prior, L. & Bowman, D. (2009) Fire controls population structure in four dominant tree species in a tropical savanna. *Oecologia*, **161**, 505-515.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943-1967.
- Liebhold, A.M. & Gurevitch, J. (2002) Integrating the statistical analysis of spatial data in ecology. *Ecography*, **25**, 553-557.
- Ludwig, F., Dawson, T.E., Kroon, H., Berendse, F. & Prins, H.H. (2003) Hydraulic lift in *Acacia tortilis* trees on an East African savanna. *Oecologia*, **134**, 293-300.

- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- Meyer, K.M., Ward, D., Wiegand, K. & Moustakas, A. (2008) Multi-proxy evidence for competition between savanna woody species. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 63–72.
- Meyer, K.M., Wiegand, K., Ward, D. & Moustakas, A. (2007) SATCHMO: A spatial simulation model of growth, competition, and mortality in cycling savanna patches. *Ecological Modelling*, **209**, 377-391.
- Miller, T.E. & Werner, P.A. (1987) Competitive effects and responses between plant species in a first-year old-field community. *Ecology*, **68**, 1201-1210.
- Milton, S.J. and Dean, W.R.J. 1995. How useful is the keystone species concept, and can it be applied to *Acacia erioloba* in the Kalahari Desert? *Zeitschrift für Ökologie und Naturschutz*, **4**, 147-156.
- Moustakas, A., Guenther, M., Wiegand, K., Mueller, K.-H., Ward, D., Meyer, K.M. & Jeltsch, F. (2006) Long-term mortality patterns of the deep-rooted *Acacia erioloba*: The middle class shall die! *Journal of Vegetation Science*, **17**, 473-480.
- Moustakas, A., Wiegand, K., Getzin, S., Ward, D., Meyer, K.M., Guenther, M. & Mueller, K.H. (2008) Spacing patterns of an *Acacia* tree in the Kalahari over a 61-year period: How clumped becomes regular and *vice versa*. *Acta Oecologica*, **33**, 355-364.
- Newman, E.I. (1973) Competition and diversity in herbaceous vegetation. *Nature*, **244**, 310.
- Panetta, F.D. & Randall, R.P. (1993) *Emex australis* and the competitive hierarchy of a grazed annual pasture. *Journal of Applied Ecology*, **30**, 373-379.
- Pärtel, M. & Wilson, S.D. (2002) Root dynamics and spatial pattern in prairie and forest. *Ecology*, **83**, 1199-1203.
- Perkins, T.A., Holmes, W.R. & Weltzin, J.F. (2007). Multi-species interactions in competitive hierarchies: New methods and empirical test. *Journal of Vegetation Science*, **18**, 685 - 692.

- Perry, J.N., Liebhold, A.M., Rosenberg, M.S., Dungan, J., Miriti, M., Jakomulska, A. & Citron-Pousty, S. (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography*, **25**, 578-600.
- Pielou, E.C. (1962) The use of plant-to-neighbour distances for the detection of competition. *Journal of Ecology*, **50**, 357-367.
- Poorter, H. & Nagel, O. (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO<sub>2</sub>, nutrients and water: A quantitative review. *Functional Plant Biology*, **27**, 1191-1191.
- Pugnaire, F.I., Haase, P. & Puigdefábregas, J. (1996) Facilitation between higher plant species in a semiarid environment. *Ecology*, **77**, 1420-1426.
- Ravi, S., D'Odorico, P., Huxman, T.E. & Collins, S.L. (2010) Interactions between soil erosion processes and fires: Implications for the dynamics of fertility islands. *Rangeland Ecology and Management*, **63**, 267-274.
- Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, I., Keddy, P.A., Tilman, D., Morris, E.C., Grace, J.B., McGraw, J.B., Olff, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., Hulst, R.v., Johansson, M.E., Nilsson, C., Gurevitch, J., Grigulis, K. & Beisner, B.E. (1994) Plant competition in relation to neighbor biomass: An intercontinental study with *Poa pratensis*. *Ecology*, **75**, 1753-1760.
- Rees, M. & Westoby, M. (1997) Game-theoretical evolution of seed mass in multi-species ecological models. *Oikos*, **78**, 116-126.
- Ripley, B.D. (1981) *Spatial Statistics*. John Wiley and Sons, New York, USA.
- Rohner, C. & Ward, D. (1999) Large mammalian herbivores and the conservation of arid *Acacia* stands in the Middle East. *Conservation Biology*, **13**, 1162-1171.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost,

- P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846-849.
- Sankaran, M., Ratnam, J. & Hanan, N.P. (2004) Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480-490.
- Schleicher, J., Meyer, K.M., Wiegand, K., Schurr, F.M. & Ward, D. (2011a) Disentangling facilitation and seed dispersal from environmental heterogeneity as mechanisms generating associations between savanna plants. *Journal of Vegetation Science*, **22**, 1038-1048.
- Schleicher, J., Wiegand, K. & Ward, D. (2011b) Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. *Journal of Arid Environments*, **75**, 270-278.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990) Biological feedbacks in global desertification. *Science*, **247**, 1043-1048.
- Scholes, R.J. & Archer, S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517-544.
- Schwinning, S. & Fox, D.A. (1995) Population dynamic consequences of competitive symmetry in annual plants. *Oikos*, **72**, 422–432.
- Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, **113**, 447-455.
- Shackleton, C. (2002) Nearest-neighbour analysis and the prevalence of woody plant competition in South African savannas. *Plant Ecology*, **158**, 65-76.
- Silvertown, J. & Dale, P. (1991) Competitive hierarchies and the structure of herbaceous plant communities. *Oikos*, **61**, 441-444.

- Skarpe, C. (1991) Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science*, **2**, 565-572.
- Smit, G.N. (1994) The influence of intensity of tree thinning on Mopani veld. Ph.D thesis, University of Pretoria, Pretoria, South Africa.
- Smit, N., 1999. *Guide to the Acacias of South Africa*. Briza Press, Pretoria, South Africa.
- Smith, T.M. & Goodman, P.S. (1986) The effect of competition on the structure and dynamics of *Acacia* savannas in southern Africa. *Journal of Ecology*, **74**, 1031-1044.
- Smith, T.M. & Grant, K. (1986) The role of competition in the spacing of trees in a *Burkea africana*- *Terminalia sericea* savanna. *Biotropica*, **18**, 219-223.
- Suding, K.N., Goldberg, D.E. & Hartman, K.M. (2003) Relationships among species traits, separating levels of response and identifying linkages to abundance. *Ecology*, **84**, 1–16.
- Tansley, A. G. (1917) On competition between *Gallium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. *Journal of Ecology*, **5**, 173-179.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey, USA.
- Turner, M.G., O'Neill, R.V., Gardner, R.H. & Milne, B.T. (1989) Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology*, **3**, 153-162.
- Van Wyk, B. & Van Wyk, P. (1997) *Field Guide to Trees of Southern Africa*. Struik Publishers, Cape Town, South Africa.
- Violle, C., Garnier, E., Lecoœur, J., Roumet, C., Pouteau, C., Blanchard, A. & Navas, M.L. (2009) Competition, traits and resource depletion in plant communities. *Oecologia*, **160**, 747–755.
- Walker, B.H. (1987) *Determinants of Tropical Savannas*. IRL Press Ltd, Oxford, UK.

- Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.M. (1981) Stability of semi-arid savanna grazing systems. *Journal of Ecology*, **69**, 473-498.
- Walter, H. (1939) Grasland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. *Jahrbücher für Wissenschaftliche Botanik*, **87**, 750–860.
- Walter, H. (1971) *Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd, Edinburgh, UK.
- Wang, P., Stieglitz, T., Zhou, D.W. & Cahill Jr, J.F. (2010) Are competitive effect and response two sides of the same coin, or fundamentally different? *Functional Ecology*, **24**, 196-207.
- Ward, D. (2005) Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science*, **22**, 101-105.
- Ward, D. (2011) Population differentiation in a purported ring species, *Acacia karroo* (Mimosoideae). *Biological Journal of the Linnean Society*, **104**, 748-755.
- Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology*, **35**, 1–22.
- Weiner, J. & Damgaard, C. (2006) Size-asymmetric competition and size-asymmetric growth in a spatially explicit zone-of-influence model of plant competition. *Ecological Research*, **21**, 707-712.
- Weiner, J. (1990) Asymmetric competition in plant populations. *Trends in Ecology and Evolution*, **5**, 360-364.
- White, J. & Harper, J.L. (1970) Correlated changes in plant size and number in plant populations. *Journal of Ecology*, **58**, 467-485.
- Wiegand, K., Saltz, D. & Ward, D. (2006) A patch-dynamics approach to savanna dynamics and woody plant encroachment - Insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 229-242.
- Wiegand, K., Saltz, D., Ward, D. & Levin, S.A. (2008) The role of size inequality in self-thinning: A pattern-oriented simulation model for arid savannas. *Ecological Modelling*, **210**, 431-445.

- Wiegand, K., Ward, D. & Saltz, D. (2005) Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. *Journal of Vegetation Science*, **16**, 311-320.
- Wiegand, T. & Moloney, K.A. (2004) Rings, circles, and null models for point pattern analysis in ecology. *Oikos*, **104**, 209–229.
- Yeaton, R.I. & Cody, M.L. (1976) Competition and spacing in plant communities: The northern Mohave Desert. *Journal of Ecology*, **64**, 689-696.
- Young, M.D. & Solbrig, O.T. (1993) *The World's Savannas: Economic Driving Forces, Ecological Constraints and Policy Options for Sustainable Land Use*. Parthenon Publishing Group, Carnforth, UK.

## Chapter 2

### **Competitive *effect* and *response* of savanna tree seedlings: Comparison of survival, growth and associated functional traits**

Tiffany Pillay and David Ward

Running title: Competition between savanna tree seedlings.

Ward, D. (Corresponding author, [ward@ukzn.ac.za](mailto:ward@ukzn.ac.za)) : School of Biological & Conservation Sciences, University of KwaZulu-Natal, P. Bag X01, Scottsville 3209, South Africa.

Pillay, T. ( [Tifpillay@gmail.com](mailto:Tifpillay@gmail.com) ) : School of Biological & Conservation Sciences, University of KwaZulu-Natal, P. Bag X01, Scottsville 3209, South Africa.

This chapter has been written following the format of the *Journal of Vegetation Science*.

## **Abstract**

**Questions:** What is the effect of neighbour competition on the survival, growth and biomass of mesic and humid savanna tree species? Can competitive *effect* and *response* be linked to plant functional traits?

**Location:** Neil Tainton Arboretum at the University of KwaZulu-Natal, Pietermaritzburg.

**Methods:** Using a target-neighbour design, all combinations of four humid and four mesic savanna tree seedlings were tested in a greenhouse experiment, to establish the effects of neighbourhood competition on target performance. The competitive *response* and *effect* of each species was quantified, and regressed against several functional traits to determine which traits are predictive of competitive ability. We also compared the competitive *response* of species growing with conspecifics to species grown with heterospecifics to test whether intraspecific competition is stronger than interspecific competition.

**Results:** We found that neighbour density negatively affected the initial *survival* of tree seedlings, with a stronger negative effect in mesic species. However, mesic plants were able to maintain their *relative growth rates* despite increasing neighbourhood competition, while the *relative growth rates* of humid species significantly decreased as the density of neighbours increased indicating that competition may be a factor affecting plants in savannas receiving more than 650 mm mean annual rainfall. We used the upper boundary regression method to show that the biomass of humid and mesic tree seedlings decreased with increased neighbour biomass, when considering competitive *response* only. We found that intraspecific competition is rarely greater than interspecific competition for both humid and mesic species. We also found that several different plant traits were

related to competitive *response* and *effect*, indicating that both aspects of competitive ability should be measured.

**Conclusions:** Competitive interactions between savanna tree seedlings affect the survival, growth and biomass of individual seedlings, although the competitive *effect* or *response* of a species depends on its adaptation to either high- or low-resource environments. Our results reiterate the usefulness of functional trait-based approaches to interpreting competitive interactions between plants, as we found that traits such as specific leaf area and above-ground features (e.g. shoot biomass and leaf number) were significantly related to the competitive *response* or *effect* of savanna tree seedlings.

#### **Key-words**

Competitive hierarchy; interspecific competition; intraspecific competition; neighbour density; specific leaf area; tree seedling mortality; upper boundary regression.

## Introduction

Savannas are dynamic on both temporal and spatial scales, and vary with changes in climate (primarily rainfall), soil nutrient content, fire regime and herbivory (Walker et al. 1981; Sankaran et al. 2004; Wiegand et al. 2006). The most important feature of savannas is the co-existence of grasses and woody plants. Many studies have focused on the factors that influence the relative abundance of the grass and woody components (Sankaran et al. 2004; Kraaij & Ward 2006). Although tree-grass competition is an important feature in savannas (Skarpe 1991), inter- and/or intra-specific tree competition may also be a fundamental driver of savanna ecosystems (Calabrese et al. 2010). Competition between trees affects the spacing of trees, and thus the spatial heterogeneity of the landscape (Meyer et al. 2008). Intense density-dependent mortality can drive a savanna to grassland (Jeltsch et al. 2000), whereas weak competitive interactions (or facilitation) may promote tree aggregation (woody plant encroachment) (Wiegand et al. 2006; Meyer et al. 2008). Woody plant encroachment has become an increasingly negative force over the last fifty years, and still is a poorly understood phenomenon, lacking clear explanations and predictive tools (Ward 2005). While competition between trees and grasses has been widely tested (Walter 1971; Walker et al. 1981; Kraaij & Ward 2006), considerably fewer studies have tested competition between savanna trees. In addition, evidence for the importance of tree-tree interactions in savannas is sparse and indirect (Scholes & Archer 1997), providing largely inferential evidence for competition.

Competitive interactions between plants shape the abundance, distribution and patterns of succession in communities (Rösch et al. 1997). Quantifying the competitive ability of a plant has long been of interest to researchers (e.g. Goldberg & Fleetwood 1987; Goldberg & Landa 1991), and the importance of different indices of competition has been widely debated (Gibson et al. 1999; Freckleton & Watkinson 2000; Armas et al. 2004; Oksanen et al. 2006). A useful method of evaluating competition between species is to determine the competitive *effect* and *response* of a particular species when grown in the presence of competitors (Goldberg & Landa 1991).

Competitive *effect* can be described as the ability of a plant to constrain the growth and performance of neighbours, while competitive *response* is the ability of a plant to tolerate competition from neighbouring plants (Goldberg & Landa 1991; Keddy et al. 2002). Numerous studies have quantified the competitive *effect* and *response* of plants (Goldberg & Landa 1991; Keddy et al. 2002; Hager 2004; Violle et al. 2009), usually employing short-lived annual plants, and have shown the effects of neighbourhood competition on the survival, growth rate and biomass of target individuals.

While studies of annual plants have been useful at ascertaining the effects of competition on several aspects of fitness such as fecundity, germination and survival, few studies have focused on the competitive interactions between perennial plants (Goldberg & Landa 1991; Howard & Goldberg 2001). Reproductive fitness is directly related to the population dynamics of a plant and is the most relevant measure of the importance of competition (Goldberg et al. 1999). However, it is not always possible to measure a metric such as fecundity in perennial savanna trees that typically reach reproductive maturity at around 10 years old (Rohner & Ward 1999). Nevertheless, because a number of studies have asserted that recruitment is the most vital stage of savanna tree life history (Higgins et al. 2000; Jeltsch et al. 2000; Wiegand et al. 2006), studying the initial stages of plant development is both crucial and informative.

Violle et al. (2009) have emphasized the importance of using a trait-based approach to interpret resource competition between plants. In this pioneer study, Violle et al. (2009) showed that plant traits can be useful indicators of resource depletion or acquisition in a target-neighbourhood design. Cornelissen et al. (2003) also state that it is widely recognized (e.g. Keddy 1992) that species should be classified into functional trait groups, rather than higher taxonomic identities because it does not allow for easy ecological interpretation. Plant traits at the individual level can often be used to make predictions about community-level outcomes because trade-offs between traits affect the ways in which plants interact with other plants, as well as with the environment (Suding et al. 2003; Fynn et al. 2011).

The aim of this study was to investigate tree seedling competition in a greenhouse experiment. We used a target-neighbour design (Gibson et al. 1999; Freckleton & Watkinson 2000) to determine the effects of neighbour density on the survival and growth rate of tree seedlings from humid (> 1000 mm mean annual rainfall (MAR)) and mesic savanna (<650 mm MAR). Sankaran et al. (2005) have shown in a meta-analysis that, in African savannas, there is a strong effect of abiotic factors when MAR is less than 650 mm. They found that there was a positive relationship between tree density and annual rainfall up to 650 mm MAR, while tree density asymptoted at higher MAR, indicating that fire and biotic factors such as herbivory were important. We wished to assess whether an additional biotic factor affecting humid savanna (but not mesic) species was intra- and inter-specific competition. We quantified the competitive *response* and *effect* of each species. We compared differences in competitive *response* under intraspecific and interspecific competition to determine if competition is stronger between conspecifics as predicted by stable coexistence theory (Tilman 1982; Abrams 1983). We predicted that:

1. The mortality of target plants would increase with increased neighbour density and that the relative growth rate of target species growing alone would be higher than that of targets grown with neighbours. Furthermore, target biomass should decrease as the biomass of neighbours increases.
2. The competitive *response* of target plants under intraspecific competition would be greater than those under interspecific competition.
3. The competitive *response* and *effect* of target species will be correlated with plant traits such as relative growth rate and specific leaf area.
4. Humid species would be more adversely affected by neighbourhood competition, and should show more profound decreases in growth rate and biomass than mesic species which are more adapted to low water-resource environments.

## Materials and Methods

### STUDY SPECIES

Four dominant tree species (*Acacia nigrescens*, *Acacia tortilis*, *Colophospermum mopane*, *Combretum apiculatum*) were chosen from a mesic savanna (receiving about 650 mm of annual rainfall), and four dominant tree species (*Acacia sieberiana*, *Acacia karroo*, *Acacia robusta*, *Schotia brachypetala*) were selected from a humid savanna (receiving about 1000 mm of annual rainfall). All species are indigenous to South Africa and were selected based on their relative abundance in mesic and humid savannas. *Acacia karroo* is highly phenotypically plastic and occurs in many habitats (Ward 2011); we selected a population of the humid savanna type from Richards Bay (28°48'0" S, 32°6'0" E) in KwaZulu-Natal, South Africa.

### EXPERIMENTAL SETUP

The experiment was carried out at the Neil Tainton Arboretum at the University of KwaZulu-Natal, Pietermaritzburg. All tree species used in the study were germinated from seed, during August 2010. One thousand seeds of each species were pre-treated with fungicide and germinated on agar plates. Four hundred seedlings per species were used for the experiment.

A target-neighbour design (Gibson et al. 1999) was used to test the competitive *effect* and *response* of each of the four species in the mesic and humid groups. The target-neighbour design is one in which the density of the target species is maintained throughout the experiment, and the density of the neighbour species is varied (Gibson et al. 1999; Freckleton & Watkinson 2000), in order to assess the response of a target plant to increasing density of a particular neighbour. All pairwise combinations of each species were tested, including intraspecific combinations. Due to spatial separation of mesic and humid savannas in nature, there is little likelihood that mesic species will compete with humid species. Therefore, competition was tested among species within the mesic and humid groups only.

One individual of a particular target species was placed in a potting bag with one of five possible competition levels, i.e. either a control treatment with no competitor or with one, two, four or eight individuals of the competitor species. All individuals of the competitor species were the same species (i.e. no mixing of more than two species occurred). Each target individual occupied the centre of the potting bag (180 L), with neighbours being equidistant from other neighbours, as well as from the target plant. Potting bags contained alluvial sand from the Umgeni River, near Pietermaritzburg, and received a standard, recommended amount of fertilizer (2 g fertilizer per litre), and 1250 mm of regular watering for the humid species and 650 mm of watering for the mesic species, over a period of 24 weeks. Each of these neighbour density treatments was replicated five times.

## DATA COLLECTION

At the start of the experiment, the initial biomass of 10 randomly selected individuals of each species was recorded, and used in relative growth rate calculations; calculated as  $[(\ln(\text{actual final biomass}) - \ln(\text{initial biomass})) / \text{time in days from initial to final measurements}]$  (Grime & Hunt 1975). The highest RGR of each species was considered its  $\text{RGR}_{\text{max}}$ . Data were collected and plants harvested after 24 weeks of growth. Plant morphological parameters were recorded for target plants only. We measured stem height and basal diameter, and recorded the number of leaves, as well as dry biomass of roots, shoots and leaves for each target plant. In addition, we determined the specific leaf area of each target plant, calculated as the total one-sided area of a fresh leaf divided by its oven-dried mass (Cornelissen et al. 2003). The above- and below- ground biomasses of all neighbours in a particular potting bag were recorded as the neighbour biomass for that treatment. The mortality of target plants in each treatment was also recorded.

## STATISTICAL ANALYSIS

All statistical analyses were conducted in SPSS. Differences in mortality of target plants were assessed using pairwise  $\chi^2$  analysis of contingency tables. The relative growth rates of target plants were compared using a one-way ANOVA. To account for inherent differences in the sizes of different species, the target biomass was standardized by dividing by the highest observed target biomass for that species, to yield the proportion of maximum target biomass (Goldberg & Landa 1991; Lessin et al. 2001).

An upper boundary regression technique was used to determine if plant performance was constrained by the biomass of neighbouring plants (Lessin et al. 2001). This was done to eliminate the excessive variance encountered when correlating ecological data, so that competitive interactions are easily detectable (Goldberg & Scheiner 2001; Thompson et al. 1996; Ward & Ngairorue 2000; Lessin et al. 2001). That is, there is a maximal (theoretical) relationship between a dependent variable such as  $RGR_{max}$  and an independent variable such as neighbour density. However, a plethora of factors may skew this relationship upwards at low neighbour densities. No downward skew can occur because there is a constraint placed by neighbour density on  $RGR_{max}$  below which additional  $RGR_{max}$  cannot be produced. We therefore expect an 'envelope' that describes a triangular cluster of data points below the regression line. Such a relationship violates the assumption of conventional least-squares regression that there is homogeneity of variance (by definition, an 'envelope' results in lower variance at higher values of the independent variable)(Ward & Ngairorue 2000). Neighbour biomass was clustered into 60 g width classes for the humid species, and 30 g for the mesic species. Regressions of proportion of maximum target biomass against neighbour biomass were conducted for each species. Slopes of the regressions of all neighbours against a particular target give the competitive *response*, and slopes of the regression of a single neighbour against all possible targets gives the competitive *effect*.

We then ranked each species according to the competitive *response* and *effect* ability (i.e. the ability to tolerate neighbour competition and the ability to suppress neighbour performance, respectively). For competitive *response*, species with steeper slopes are weaker competitors. For competitive *effect*, species with shallower slopes are less effective competitors (Goldberg & Landa 1991). Concordance among species rankings from competitive *response* and *effect* hierarchies was tested using Kendall's test of concordance, following Goldberg & Landa (1991). Differences in interspecific and intraspecific competition were determined by comparing the competitive *response* slopes for species grown with conspecific neighbours, to the competitive *response* slope of species grown with neighbours of different species. Lastly, we plotted the competitive *response* and *effect* slopes of humid and mesic species against several plant traits to check which traits were related to competitive *response* and *effect* ability.

## Results

### MORTALITY

The percentage mortality of target plants was higher in mesic species (32%) than in humid species (6%) ( $\chi^2_{1,400} = 154.2$ ,  $p = 0.0001$ ). Chi-square analysis showed that there were no significant differences ( $\chi^2_{1,400} = 0.1 - 1$ ,  $p > 0.05$ ) in the mortality of target plants at varying neighbour densities for all humid species, except *Acacia robusta* ( $\chi^2_{1,100} = 5$ ,  $p = 0.02$ , Fig 1a). Conversely, three out of four mesic species showed significant differences in mortality across the treatments (range in  $\chi^2_{1,100} = 5.5 - 13$ ,  $p < 0.05$ , Fig 1). *Combretum apiculatum* was the only mesic species that showed no significant difference in mortality among neighbour densities (range in  $\chi^2_{1,100} = 0.1-0.5$ ,  $p > 0.05$ ). A general trend of increasing mortality with increased neighbour density can be observed in Fig. 1, with the exception of *Acacia tortilis* which showed zero mortality at both the lowest and highest neighbour densities.

## RELATIVE GROWTH RATE (RGR)

*Acacia karroo* maintained its relative growth rate (RGR) among treatments ( $F_{(4,81)} = 2.39$ ,  $p > 0.05$ , Fig 2a). A general trend of decreasing RGR with increasing neighbour density can be observed for the other three humid species (range in  $F_{(4,83)} = 3.41-12.42$ ,  $p < 0.05$ , Fig 2b, c, d); with significant differences occurring between controls (no neighbours) and the highest neighbour density (eight neighbours) in all three species. Three out of the four mesic species showed no significant differences (range in  $F_{(4,66)} = 2.12 - 2.18$ ,  $p > 0.05$ ) in RGR at varying neighbour densities, except for *C.mopane* which showed an increase in RGR at a neighbour density of 2 ( $F_{(4,66)} = 4.65$ ,  $p = 0.003$ ).

## TARGET AND NEIGHBOUR BIOMASS

For competitive *response*, when employing the upper boundary regression method, three out of four humid species showed a significant decline in the proportion of maximum target biomass with increasing neighbour biomass (range in  $r^2 = 0.63-0.86$ , range in  $F_{(1,5)} = 10.08 - 25.04$ , range in  $p = 0.01- <0.05$ , Fig. 3a, b, d). *Acacia robusta* was the only humid species that did not have a significant relationship between RGR and neighbour density ( $r^2 = 0.48$ ,  $F_{(1,5)} = 4.62$ ,  $p = 0.08$ ). A similar trend was observed for the mesic species. *Acacia tortilis*, *C. apiculatum* and *C. mopane* showed a significant decline in the proportion of maximum target biomass when neighbour biomass increased (range in  $r^2 = 0.53-0.81$ , range in  $F_{(1,6)} = 6.85- 29.23$ , range in  $p = 0.001-0.03$ , Fig 4). The proportion of maximum target biomass was not related to neighbour biomass for the mesic species *A. nigrescens* ( $r^2 = 0.24$ ,  $F_{(1,5)} = 1.61$ ,  $p = 0.2$ , Fig 4a). Conversely, for competitive *effect*, the regressions of the proportion of maximum target biomass and neighbour biomass for both humid and mesic species showed no significant relationships (range in  $r^2 = 0.089-0.49$ , range in  $F_{(1,5)} = 2.19- 5.32$ ,  $p = > 0.05$ , Fig 5 a,c,d, Fig 6). However, there was a significant decrease in biomass as neighbour biomass increased for *A. sieberiana* ( $r^2 = 0.89$ ,  $F_{(1,5)} = 44.62$ ,  $p = 0.001$ , Fig 6b).

## COMPETITIVE RESPONSE AND EFFECT HIERARCHIES

*Competitive response*: Higher slopes of the regressions of proportion of maximum target biomass and neighbour biomass indicate decreased ability to tolerate neighbour competition (Goldberg & Landa 1991, Lessin et al. 2001). *Acacia sieberiana* was the weakest competitor (slope = -0.00243) among the humid species, with *S. brachypetala* being the strongest competitor (slope = -0.00114, Table 1). For the mesic species, *C. mopane* showed the highest competitive response (slope = -0.00456), while *A. nigrescens* showed the lowest response to neighbour competition (slope = -0.00136, Table 1).

*Competitive effect*: Species with shallower slopes are less effective competitors (Goldberg & Landa 1991). Here we found that *A. robusta* was the strongest *effect* competitor (slope = -0.00698), while *S. brachypetala* was the weakest *effect* competitor (slope = -0.00146, Table 1). For the mesic species, *A. tortilis* was the weakest *effect* competitor (slope = -0.00154), and *C. mopane* was the species that exerted the greatest effect on neighbouring plants (slope = -0.00433, Table 1). Rankings in *competitive response* and *effect* hierarchies were not concordant (Kendall's tau = 0.667, n = 4, p > 0.05).

## INTRASPECIFIC AND INTERSPECIFIC COMPETITION

For humid species, *competitive response* slopes of intraspecific interactions were not steeper than *response* slopes of interspecific interactions in all cases (Table 2). *Acacia karroo* and *A. sieberiana* showed the least *competitive response* for intraspecific combinations (slopes = -0.00144 and -0.00174, respectively). Among the mesic species, only *A. nigrescens* showed a higher *competitive response* (slope = -0.00087) for intraspecific interactions than interspecific interactions (Table 2).

## COMPETITIVE RESPONSE vs. PLANT TRAITS

Of all plant traits regressed against *competitive response* slopes (Fig 7), only specific leaf area for humid species (Fig 7m) was significantly related to *competitive response* ( $r^2 = 0.83$ ,  $F_{(1,2)} = 12.21$ , p

< 0.02), and increased as competitive *response* increased. Regressions of competitive *effect* slopes against plant traits showed that several plant traits are linked to competitive *effect* (Fig 8).  $RGR_{max}$  ( $r^2 = 0.94$ ,  $F_{(1,2)} = 33.447$ ,  $p = 0.03$ ), shoot biomass ( $r^2 = 0.97$ ,  $F_{(1,2)} = 80.36$ ,  $p = 0.01$ ), root biomass ( $r^2 = 0.97$ ,  $F_{(1,2)} = 90.99$ ,  $p = 0.01$ ), number of leaves ( $r^2 = 0.93$ ,  $F_{(1,2)} = 26.48$ ,  $p = 0.03$ ), stem diameter ( $r^2 = 0.95$ ,  $F_{(1,2)} = 39.94$ ,  $p = 0.02$ ) and stem height ( $r^2 = 0.97$ ,  $F_{(1,2)} = 221.7$ ,  $p = 0.004$ ) all increased significantly as the competitive *effect* of neighbours decreased. Humid species showed no significant relationship between competitive *effect* and plant traits (Fig. 8), with the exception of specific leaf area ( $r^2 = 0.83$ ,  $F_{(1,2)} = 13.87$ ,  $p = 0.04$ , Fig. 8m) which increased as the competitive *effect* of neighbours increased.

## Discussion

### MORTALITY

Overall, tree seedlings were adversely affected by the increasing density of neighbours. This indicates that seedling recruitment of savanna trees is governed by the presence of neighbourhood competition, an idea that has been supported by greenhouse experiments of tree seedling competition (Meiners & Handel 2000), and indirect field experiments of neighbour-removal (Schleicher et al. 2011). We found, as predicted, that mortality of savanna tree seedlings generally increased as the density of neighbour individuals increased. This trend was more evident in mesic species than in humid species, indicating that competition may increase the chances of mortality during the early stages of seedling establishment for species receiving lower mean annual rainfall.

Many studies have postulated that the main limiting factors in arid and semi-arid environments are likely to be density-dependent, intraspecific competition for soil moisture (Smith & Goodman 1987; Skarpe 1991; López et al. 2008). Davis et al. (1999) also found that survival and rate of photosynthesis of woody seedlings were highly correlated with available soil water, when competing with herbaceous vegetation. Chesson et al. (2004) have also stated that in low-resource

environments, seedling establishment of perennial plants is rare (Rohner & Ward 1999), and greatly affected by disturbances such as competition. While humid species in this study showed no significant differences in mortality at varying neighbour densities, effects of competition may in fact be expressed later on in their life histories (Gurevitch 1986; Howard & Goldberg 2001).

#### RELATIVE GROWTH RATE

Although we found that the survival of mesic species was significantly lower than that of humid species, this was only evident during the early phases of seedling establishment. Once seedlings of mesic species were established, they maintained a constant relative growth rate, despite the density of neighbours. This may be due to the array of survival responses that semi-arid and mesic species have acquired, such as minimizing water-loss (via efficient root systems) or setting seed before death (annual plants), to deal with harsh, low-resource environments, thereby allowing these plants to survive the high levels of competition during periods of pulsed resource availability (Chesson et al. 2004). Mesic plants can therefore be described as “stress-tolerant”, and according to Grime (1977) should survive longer because they are more effective in retaining the resources they acquire (McGraw & Chapin 1989). Alternatively, mesic plants may be displaying facilitative interactions, rather than competition. In this case, plants growing at high densities create ‘islands of fertility’, with increased water availability (due to hydraulic lift by larger species) or increased nutrients (due to nitrogen fixation by leguminous plants) (Pugnaire et al. 1996). This facilitative interaction improves the living conditions of surrounding plants, and may be the cause of consistent growth rates at increasing neighbour densities. Humid species showed a reduction in relative growth rate as neighbourhood competition increased. This indicates that humid species are less tolerant of neighbourhood competition, possibly due to reduced competitive interactions in high-resource environments where rainfall and soil nutrients are not limiting factors. This may also indicate that, for woody species from areas receiving more than 650mm MAR, competitive interactions may be as important as fire and herbivory (Sankaran et al. 2005).

## TARGET AND NEIGHBOUR BIOMASS

When considering *competitive response*, the biomass of target plants was shown to decrease with increasing neighbour biomass, for both humid and mesic plants. This result is consistent with several studies (Goldberg & Fleetwood 1987; Goldberg & Landa 1991; Ramseier & Weiner 2006; Violle et al. 2009), all measuring target plant performance against some measure of neighbourhood effect (neighbour height, biomass or density). Competition between plants results in trade-offs between growth, defence and reproduction (Suding et al. 2003). In plants growing in highly competitive environments, growth will be limited initially through exploitation competition, where resources are depleted by neighbouring plants, and possibly secondarily by interference competition where neighbouring plants make resources inaccessible (Aarssen & Keogh 2002). Therefore, reductions in allocations to biomass may be attributed to trade-offs related to neighbourhood competition. For example, Schleicher et al. (2011) showed that when *Acacia mellifera* was removed from ten 1 ha plots in an arid area of South Africa, then neighbouring *Tarchonanthus camphoratus* recruited more and invested more in biomass.

*Competitive effect* slopes revealed no relationship between the biomass of targets and neighbours. This is contrary to the findings of several studies (Goldberg & Landa 1991; Keddy et al. 2000; Hager 2004) that show the effect of neighbour biomass on the biomass of target individuals. This result may be due to the sensitive nature of determining competitive effects, rather than responses of a plant. According to Goldberg & Werner (1983), plants of the same growth form may display equivalence in effects due to similar resource requirements, and the predominance of seedling and adult interactions. This may indicate that *competitive response* should be used instead of *competitive effect* (Goldberg & Werner 1983). However, because *response* and *effect* are not always correlated (as in this study), Goldberg & Landa (1991) have advocated the use of both indices to interpret competitive interactions between plants.

Our study also highlights the efficacy of employing the upper boundary regression method to analyze correlations of ecological data, where standard techniques of analysis may be misleading (Goldberg & Scheiner 2001; Thompson et al. 1996). Lessin et al. (2001) have found, using this technique, that neighbourhood biomass constrained the upper limit of plant performance of annual dicot species in the Negev desert of Israel. Similarly, our study showed that by using the upper limit of target biomass, the effects of neighbour biomass on target performance can be effectively detected.

### COMPETITIVE RESPONSE AND EFFECT HIERARCHIES

A competitive hierarchy is an effective way of using species rankings as a predictive tool of species abundance and distribution in natural communities (Keddy & Shipley 1989; Silvertown & Dale 1991; Keddy et al. 2000). Although extrapolation and transitivity of competitive hierarchies has been a widely debated topic (Keddy & Shipley 1989; Silvertown & Dale 1991), species at the top of competitive hierarchies will be stronger competitors, at least at the seedling stage (Keddy et al. 2002; Fynn et al. 2011).

Goldberg (1990) postulated that good *effect* competitors are early successional species, while good *response* competitors may be later successional species. These hierarchies may be useful in determining patterns of succession, and therefore mechanisms of woody plant encroachment, a phenomenon that poses a severe threat to agricultural lands, as well as the maintenance of biodiverse savanna ecosystems (Ward 2005). We used the slopes of regressions of target biomass against neighbour biomass to quantify the competitive *response* and *effect* of a particular species, as suggested by Goldberg & Landa (1991), Goldberg & Fleetwood (1987) and Lessin et al. (2001), and developed a competitive hierarchy for humid and mesic species. In terms of competitive *response* ability, we found that *Schotia brachypetala* had the highest competitive ability, while for the mesic species *Acacia nigrescens* had the strongest competitive *response* ability. The hierarchy for competitive *effect* ranked species differently to that of competitive

*response*, again indicating the importance of both measures when quantifying competitive interactions. The competitive *effect* hierarchy showed that for humid species *A. robusta* was the strongest *effect* competitor, and that *C. mopane* exerted the strongest competitive *effect* on neighbouring plants. While these hierarchies may only be applicable at the early stages of seedling establishment (Goldberg & Landa 1991), they do provide useful information on the relative abundance of these woody species, and so may also provide insights on the process of woody plant encroachment.

#### INTERSPECIFIC AND INTRASPECIFIC COMPETITION

In order for stable coexistence of plants of different life forms, Tilman (1982) suggested that competition within life forms should be greater than competition between life forms. In other words, intraspecific competition should be greater than interspecific competition, through differential partitioning of resources by different species (Tilman 1982). In terms of the classic Lotka-Volterra model of competition, this translates to the competition coefficient,  $\alpha$ , being less than 1 (which is the effect of intraspecific competition divided by the effect of interspecific competition) (Chesson 2000). However, many ecological studies have shown that intraspecific effects did not differ from interspecific effects (cf. Goldberg & Barton 1992; Gurevitch et al. 1992). Similarly, our study was unable to detect consistent patterns of greater intraspecific than interspecific interactions between savanna tree seedlings.

#### COMPETITIVE RESPONSE AND EFFECT vs. PLANT TRAITS

Correlations of *competitive response* and *effect* with plants traits provide insights into the morphological characteristics that confer competitive ability. Violle et al. (2009) have shown that instantaneous measurements of certain plant traits, such as specific leaf area, can provide information on how plants perceive competitive environments. We found competitive *response* to

be unrelated to several plant traits such as stem height, basal diameter, number of leaves and secondary stem recruitment of target plants. However, we found that competitive *response* of humid plants was related to specific leaf area. High specific leaf area translates into high mass-based photosynthetic rate (Cornelissen et al. 2003), but also to low stress tolerance (Grime 1979; Dahlgren et al. 2006). This may also explain why the relative growth rate of humid species declined with increasing neighbour density. On the other hand, several plant traits such as  $RGR_{max}$ , stem height and diameter, as well as shoot and root biomass, increased significantly as the *competitive effect* of neighbours increased. This may be due to size-asymmetric competition, where larger individuals acquire a disproportionate amount of the available resources, thereby decreasing the negative effect of neighbour competition on their own growth (Schwinning & Weiner 1998).

## Conclusions

Competitive interactions are evident between savanna tree seedlings in our study as neighbourhood competition decreased the survival, growth rate and biomass of seedlings. Humid and mesic tree seedlings showed differential responses to neighbour competition, possibly based on adaptations to high or low-resource environments. We recognise that both mesic and humid species may require similarly moist conditions for germination and establishment, but our results showed that there were consistent differences in their responses. We also note that soil substrate may have resulted in changes in experimental outcomes (e.g. *Colophospermum mopane* typically grows on clay soils) but we wished to standardise our protocols to avoid these additional, possibly confounding, interactions.

Tree seedlings from humid areas showed decreased relative growth rate, indicating that competition may be as important as fire and herbivory in savannas receiving more than 650 mm mean annual rainfall (cf. Sankaran et al. 2005). Competitive hierarchies may be a useful predictive tool to deal with woody plant encroachment, although more rigorous hierarchies are needed,

focusing on a wider range of savanna species. We found that both competitive *response* and *effect* indices should be measured because they yielded different information on the mechanisms of competition. Here, we showed that several plant traits are related to the competitive *response* and *effect* of savanna tree seedlings, and that a trait-based framework is a useful when trying to disentangle ecological interactions (Cornelissen et al. 2003). Clearly, not all trees respond uniformly to neighbourhood competition. Tree-tree interactions should be investigated further, and treated as an important factor in the dynamics of savanna ecosystems.

### **Acknowledgments**

We would like to thank the National Research Foundation for supporting this study, and the technical staff (especially Andile Shange, Freedom Linda, Welcome Ncgobo, Alison Young, Vanessa Stuart and Stephne' Stuart) at the University of KwaZulu-Natal for help with plant harvesting and data collection. We are also grateful to Desale Y. Okubamichael for his valuable contributions to this manuscript.

## References

- Aarssen, L.W. & Keogh, T. 2002. Conundrums of competitive ability in plants: what to measure? *Oikos* 96: 531-542.
- Abrams, P. 1983. The theory of limiting similarity. *Annual Review of Ecology and Systematics* 14: 359-376.
- Armas, C., Ordiiales, R. & Pugnaire, F.I. 2004. Measuring plant interactions: a new comparative index. *Ecology* 85: 2682-2686.
- Calabrese, J.M., Vazquez, F., Lopez, C., Miguel M.S. & Grimm, V. 2010. The independent and interactive effects of tree-tree establishment, competition and fire on savanna structure and dynamics. *American Naturalist* 175: 44-65.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A. & Weltzin, J.F. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141: 236–253.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- Dahlgren, J.P., Eriksson, O., Bolmgren, K., Strindell, M. & Ehrlén, J. 2006. Specific leaf area as a superior predictor of changes in field layer abundance during forest succession. *Journal of Vegetation Science* 17: 577–582.
- Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T. & Muermann, C. 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecology* 145: 341-350.

- Freckleton, R.P. & Watkinson, A.R. 2000. Designs for greenhouse studies of interactions among plants: an analytical perspective. *Journal of Ecology* 88: 386-391.
- Fynn, R.W.S., Morris, C., Ward, D. & Kirkman, K. 2011. Trait–environment relations for dominant grasses in South African mesic grassland support a general leaf economic model. *Journal of Vegetation Science* 22: 528-540.
- Gibson, D., Connolly, J., Hartnett, D.C. & Weidenhamer, J.D. 1999. Designs for greenhouse studies of interactions between plants. *Journal of Ecology* 87: 1-16.
- Goldberg, D. E. 1990. Components of resource competition in plant communities. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 27-49. Academic Press, San Diego.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. 1999. Empirical approaches to quantifying interaction intensity: Competition and facilitation along productivity gradients. *Ecology* 80: 1118-1131.
- Goldberg, D.E. & Barton, A.M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* 139: 771-801.
- Goldberg, D.E. & Landa, K. 1991. Competitive effects and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79: 1013–1030.
- Goldberg, D.E. & Fleetwood, L. 1987. Competitive effect and response in four annual plants. *Journal of Ecology* 75: 1131–1143.
- Goldberg, D.E. & Scheiner, S.M. 2001. ANOVA and ANCOVA. Field competition experiments. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 69-93. Oxford University Press, New York.
- Goldberg, D.E. & Werner, P.A. 1983. Equivalence of competitors in plant communities: A null hypothesis and a field experimental approach. *American Journal of Botany* 70: 1098-1104.

- Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169-1194.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, Chichester, UK.
- Grime, J.P. & Hunt, R. 1975. Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology* 63: 393-422.
- Gurevitch, J. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology* 67: 46-57.
- Gurevitch, J., Morrow, L.L., Alison, W. & Walsh, J.S. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140: 539-572.
- Hager, H.A. 2004. Competitive effect versus competitive response of invasive and native wetland plant species. *Oecologia* 139: 140-149.
- Higgins, S. I., Bond, W.J. & Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213-229.
- Howard, T. G., & Goldberg, D.E. 2001. Competitive response hierarchies for germination, growth, and survival and their influence on abundance. *Ecology* 82: 979-990.
- Jeltsch, F., Weber, G.E. & Grimm, V. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology* 150: 161-171.
- Keddy, P.A. 1992. A pragmatic approach to functional ecology. *Functional Ecology* 6: 621-626.
- Keddy, P.A. & Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54: 234-241.
- Keddy, P.A., Gaudet, C. & Fraser, L.H. 2000. Effects of low and high nutrients on the competitive hierarchy of 26 shoreline plants. *Journal of Ecology* 88: 413-423.
- Keddy, P.A., Nielsen, K., Weiher, E. & Lawson, R. 2002. Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science* 13: 5-16.

- Kraaij, T. & Ward, D. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna. *Plant Ecology* 186: 235-246.
- Lessin, L.M., Dyer, A.R. & Goldberg, D.E. 2001. Using upper boundary constraints to quantify competitive response of desert annuals. *Oikos* 92: 153-159.
- López, B.C., Holmgren, M., Sabaté, S. & Gracia, C.A. 2008. Estimating annual rainfall threshold for establishment of tree species in water-limited ecosystems using tree-ring data. *Journal of Arid Environments* 72: 602–611.
- McGraw, J.B. & Chapin, F.S. 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology* 70: 736-749.
- Meiners, S.J. & Handel, S.N. 2000. Additive and nonadditive effects of herbivory and competition on tree seedling mortality, growth, and allocation. *American Journal of Botany* 87: 1821-1826.
- Meyer, K.M., Ward, D., Wiegand, K. & Moustakas, A. 2008. Multi-proxy evidence for competition between savanna woody species. *Perspectives in Plant Ecology, Evolution and Systematics* 10: 63–72.
- Oksanen, L., Sammuli, M. & Magi, M. 2006. On the indices of plant-plant competition and their pitfalls. *Oikos* 112: 149–155.
- Pugnaire, F.I., Haase, P. & Puigdefábregas, J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77: 1420–1426.
- Ramseier, D. & Weiner, J. 2006. Competitive effect is a linear function of neighbour biomass in experimental populations of *Kochia scoparia*. *Journal of Ecology* 94: 305–309.
- Rohner, C. & Ward, D. 1999. Large mammalian herbivores and the conservation of arid *Acacia* stands in the Middle East. *Conservation Biology* 13: 1162-1171.
- Rösch, H., Van Rooyen, M.W. & Theron, G.K. 1997. Predicting competitive interactions between pioneer plant species by using plant traits. *Journal of Vegetation Science* 8: 489-494.

- Sankaran, M., Ratnam, J. & Hanan, N.P. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7: 480-490.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. 2005. Determinants of woody cover in African savannas. *Nature* 438: 846-849.
- Schleicher, J., Wiegand, K. & Ward, D. 2011. Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. *Journal of Arid Environments* 75: 270-278.
- Scholes, R.J. & Archer, S.R. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28: 517-544.
- Schwinning, S. & Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447-455.
- Silvertown, J. & Dale, P. 1991. Competitive hierarchies and the structure of herbaceous plant communities. *Oikos* 61: 441-444.
- Skarpe, C. 1991. Impact of grazing in savanna ecosystems. *Ambio* 20: 351-356.
- Smith, T. M. & Goodman, P.S. 1987. Successional dynamics in an *Acacia nilotica-Euclea divinorum* savannah in southern Africa. *Journal of Ecology* 75: 603-610.
- Suding, K.N., Goldberg, D.E. & Hartman, K.M. 2003. Relationships among species traits, separating levels of response and identifying linkages to abundance. *Ecology* 84: 1–16.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey, USA.

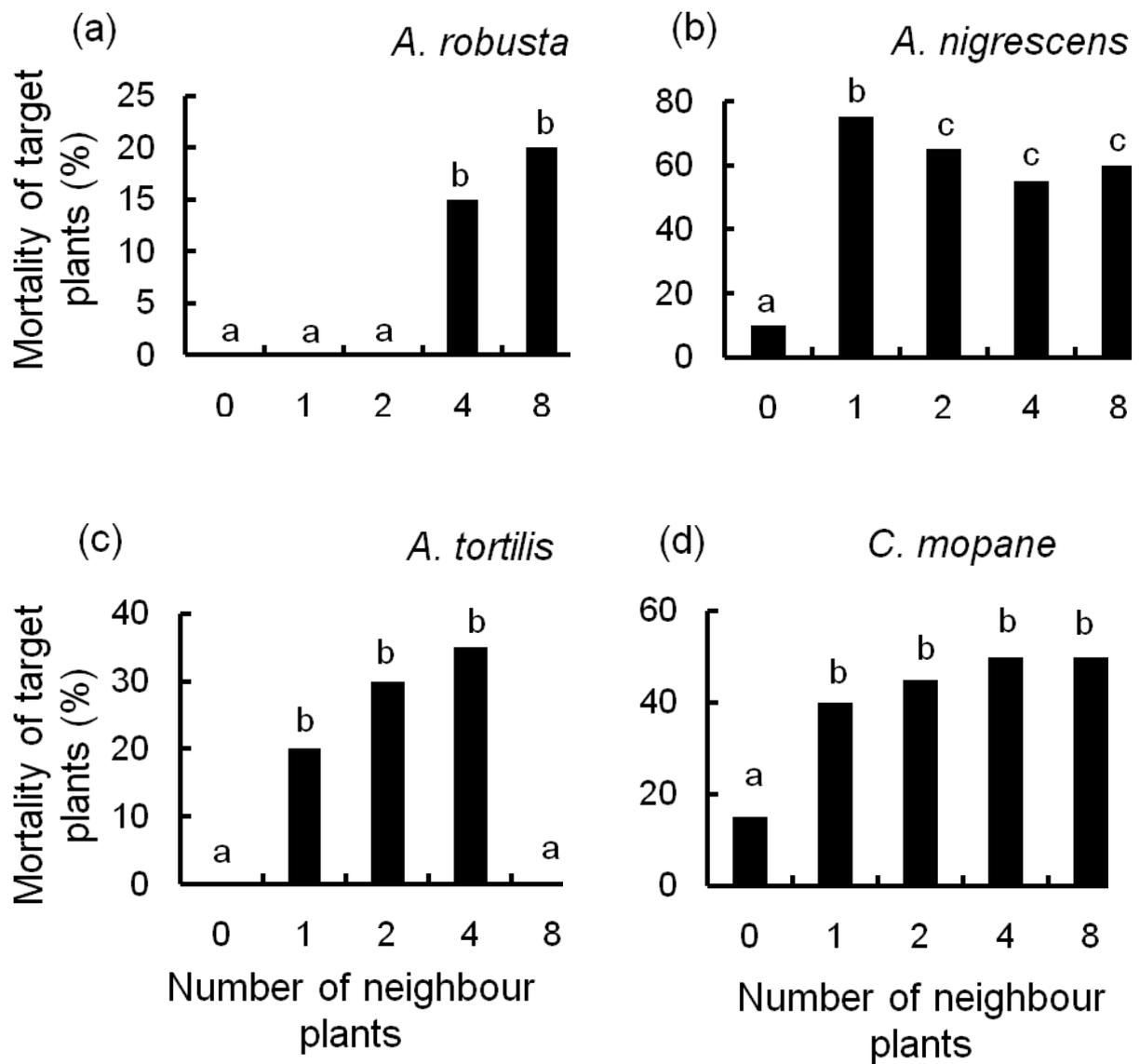
- Violle, C., Garnier, E., Lecoœur, J., Roumet, C., Podgeur, C., Blanchard, A. & Navas, M.L. 2009. Competition, traits and resource depletion in plant communities. *Oecologia* 160: 747–755.
- Walker, B.H., Ludwig, D., Holling, C. S. & Peterman, R. M. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* 69: 473-498.
- Walker, B.H. & Noy-Meir, I. 1982. Aspects of the stability and resilience of savanna ecosystems. *Ecology of Tropical Savannas* (eds B. J. Huntley & B. H. Walker), pp. 556-590. Springer-Verlag, Berlin.
- Walter, H. 1971. *Ecology of Tropical and Subtropical Vegetation*. Oliver and Boyd, Edinburgh, UK.
- Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science* 22: 101-105.
- Ward, D. 2011. Population differentiation in a purported ring species, *Acacia karroo* (Mimosoideae). *Biological Journal of the Linnean Society* 104: 748-755.
- Ward, D. & Ngairorue, B.T. 2000. Are Namibia's grasslands desertifying? *Journal of Range Management* 53: 138-144.
- Wiegand, K., Saltz, D. & Ward, D. 2006. A patch dynamics approach to savanna dynamics and bush encroachment – insights from an arid savanna. *Perspectives in Plant Ecology, Evolution and Systematics* 7: 229-242.

**Table 1.** Species rankings of competitive response and competitive effect for humid and mesic savanna tree species based on the regression slopes of target and neighbour biomass. Species are ranked from lowest to highest competitive ability. For competitive response, species with steeper slopes are weaker competitors. For competitive effect, species with shallower slopes are less effective competitors. Species rankings are not concordant (Kendall's tau = 0.667, n = 4, p > 0.05).

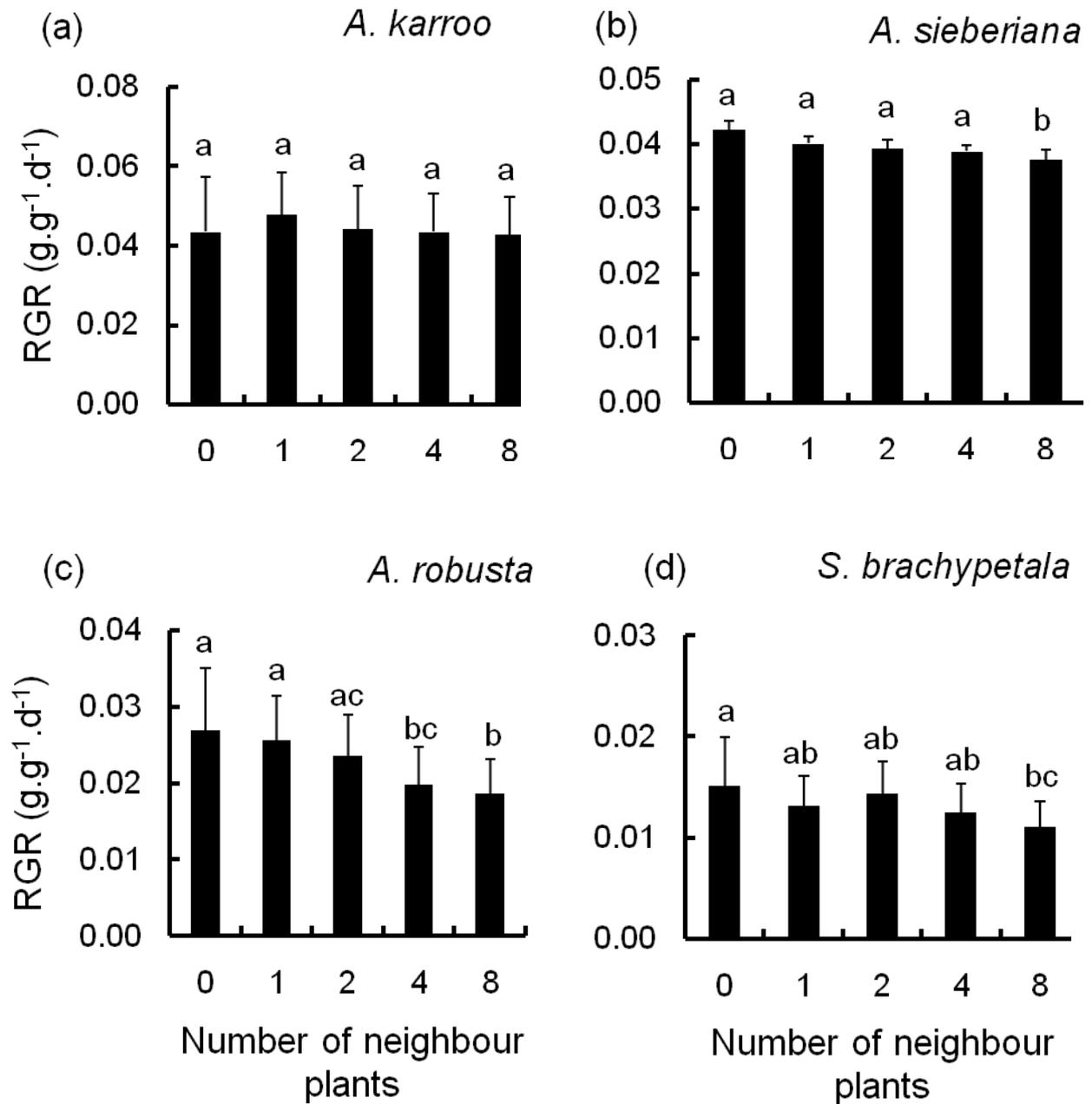
Regression slopes			
(Proportion target biomass vs. neighbour biomass)			
Species ranking	Competitive response	Species ranking	Competitive effect
<b>Humid</b>		<b>Humid</b>	
<i>Acacia sieberiana</i>	-0.00243	<i>Schotia brachypetala</i>	-0.00146
<i>Acacia robusta</i>	-0.00192	<i>Acacia karroo</i>	-0.00152
<i>Acacia karroo</i>	-0.00159	<i>Acacia sieberiana</i>	-0.00265
<i>Schotia brachypetala</i>	-0.00114	<i>Acacia robusta</i>	-0.00698
<b>Mesic</b>		<b>Mesic</b>	
<i>Colophospermum mopane</i>	-0.00456	<i>Acacia tortilis</i>	-0.00154
<i>Acacia tortilis</i>	-0.00380	<i>Acacia nigrescens</i>	-0.00274
<i>Combretum apiculatum</i>	-0.00328	<i>Combretum apiculatum</i>	-0.00344
<i>Acacia nigrescens</i>	-0.00136	<i>Colophospermum mopane</i>	-0.00433

**Table 2.** Competitive response slopes for interspecific and intraspecific species combinations, for humid and mesic savanna tree species. Combinations with steeper slopes indicate strong competitive interactions. Intraspecific combinations are indicated in bold. The upper matrix cells (above the bold numbers) represent the targets while the lower matrix cells represent the neighbours. Note: \* = Intraspecific interaction was greater than interspecific interaction for *A. nigrescens* only.

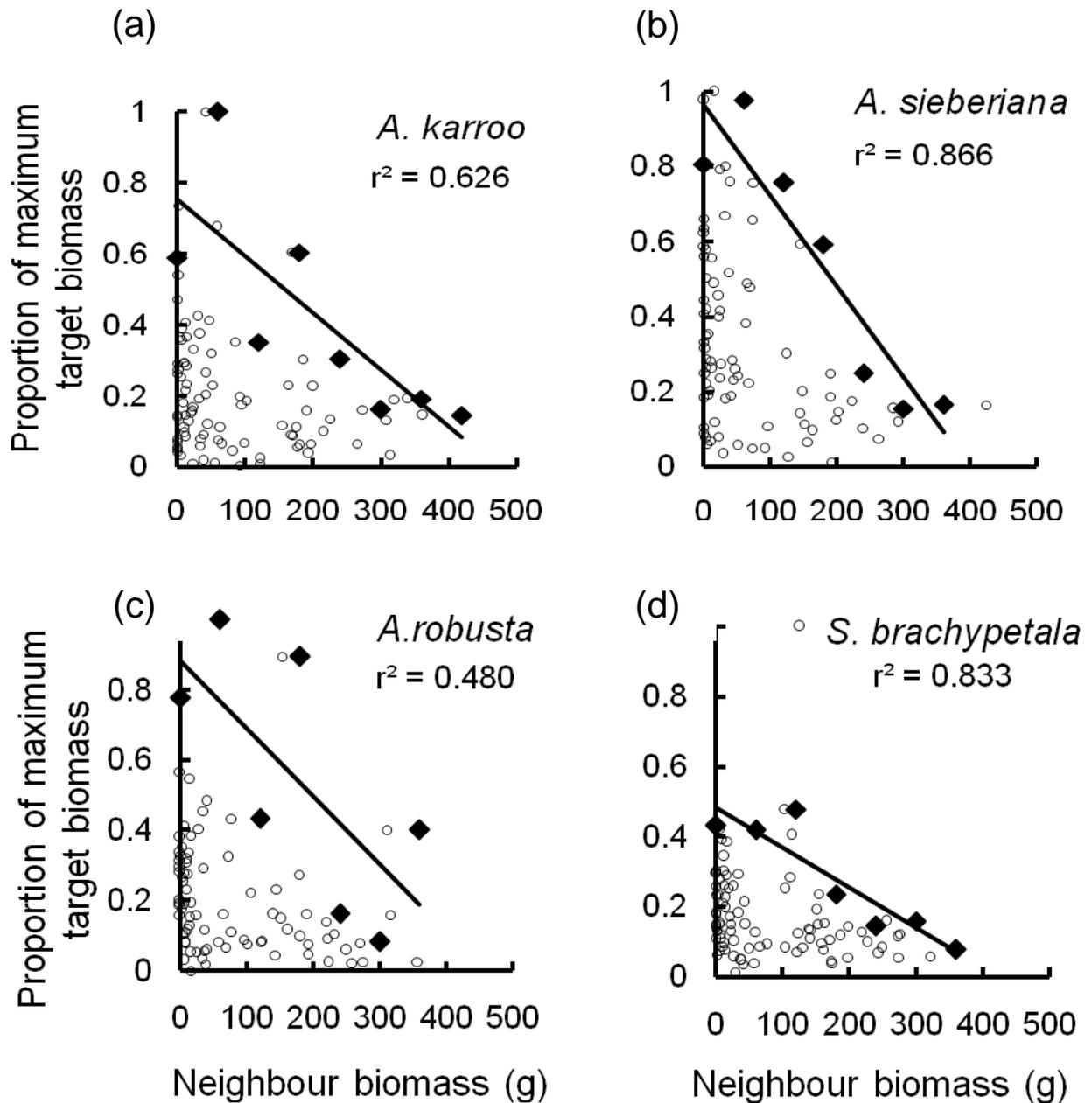
Competitive response slopes				
Humid				
	<i>A.karroo</i>	<i>A. sieberiana</i>	<i>A. robusta</i>	<i>S. brachypetala</i>
<i>A. karroo</i>	<b>-0.00144</b>	-0.00068	-0.00016	-0.00096
<i>A.sieberiana</i>	-0.00043	<b>-0.00174</b>	-0.00323	-0.00045
<i>A. robusta</i>	-0.00071	-0.00457	<b>-0.00541</b>	-0.00579
<i>S. brachypetala</i>	-0.00056	0.00311	-0.00065	<b>-0.00619</b>
Mesic				
	<i>A. nigrescens</i>	<i>A. tortilis</i>	<i>C. apiculatum</i>	<i>C. mopane</i>
<i>A. nigrescens</i>	<b>-0.00087*</b>	-0.00442	-0.00841	-0.00332
<i>A. tortilis</i>	-0.00372	<b>-0.00185</b>	-0.00064	-0.00224
<i>C. apiculatum</i>	-0.00528	-0.00301	<b>-0.00353</b>	-0.10134
<i>C. mopane</i>	-0.00133	-0.00253	-0.00204	<b>-0.00166</b>



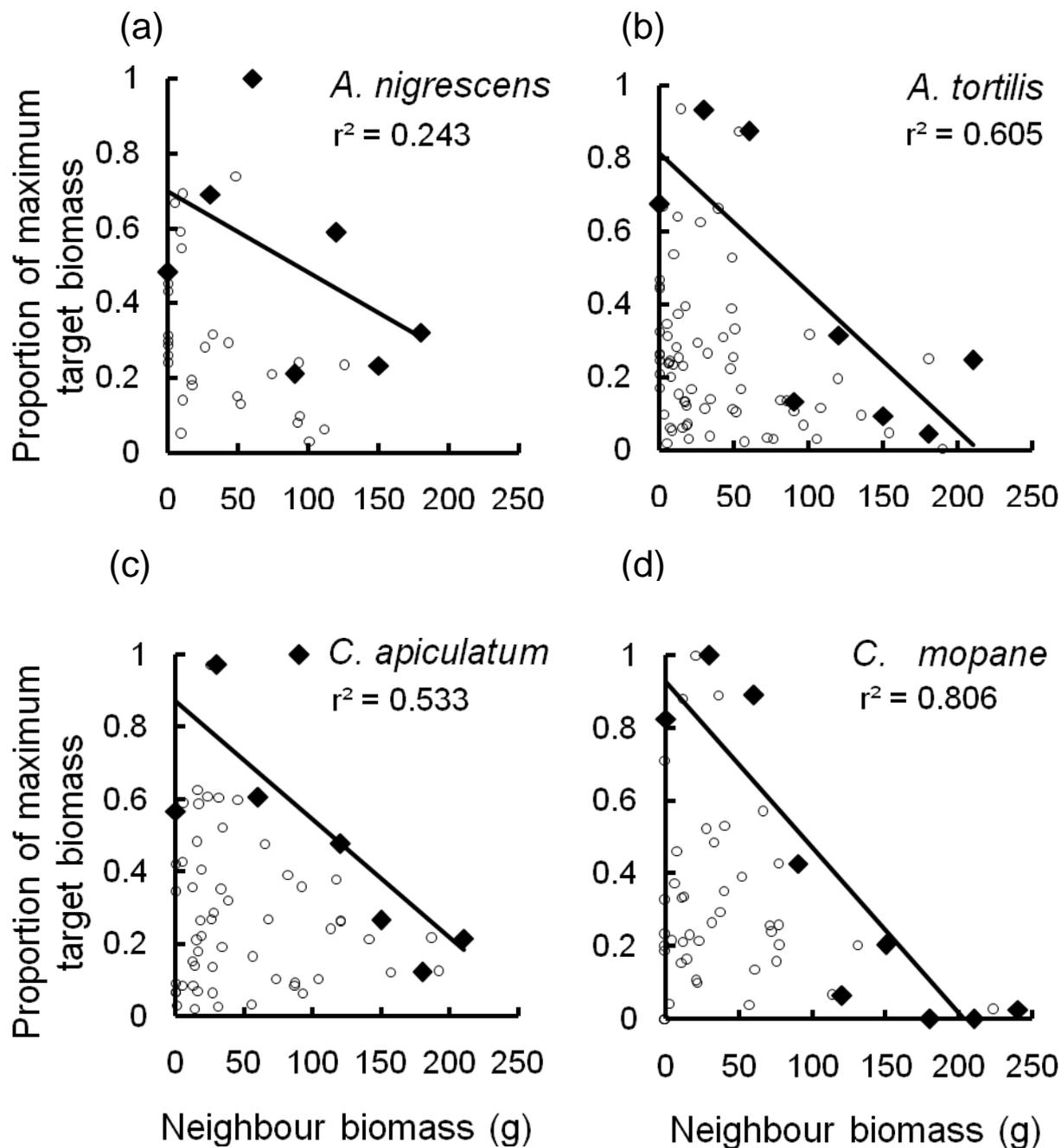
**Fig. 1.** Percentage mortality of humid and mesic target plants at varying neighbour densities (range in  $\chi^2 = 17.29-4.44$ ;  $p = <0.005-0.03$ ). Similar letters denote non-significant differences in mortality. (a) *A. robusta*, (b) *A. nigrescens*, (c) *A. tortilis*, (d) *C. mopane*. The only humid species that showed significant differences in mortality was *Acacia robusta* (a).



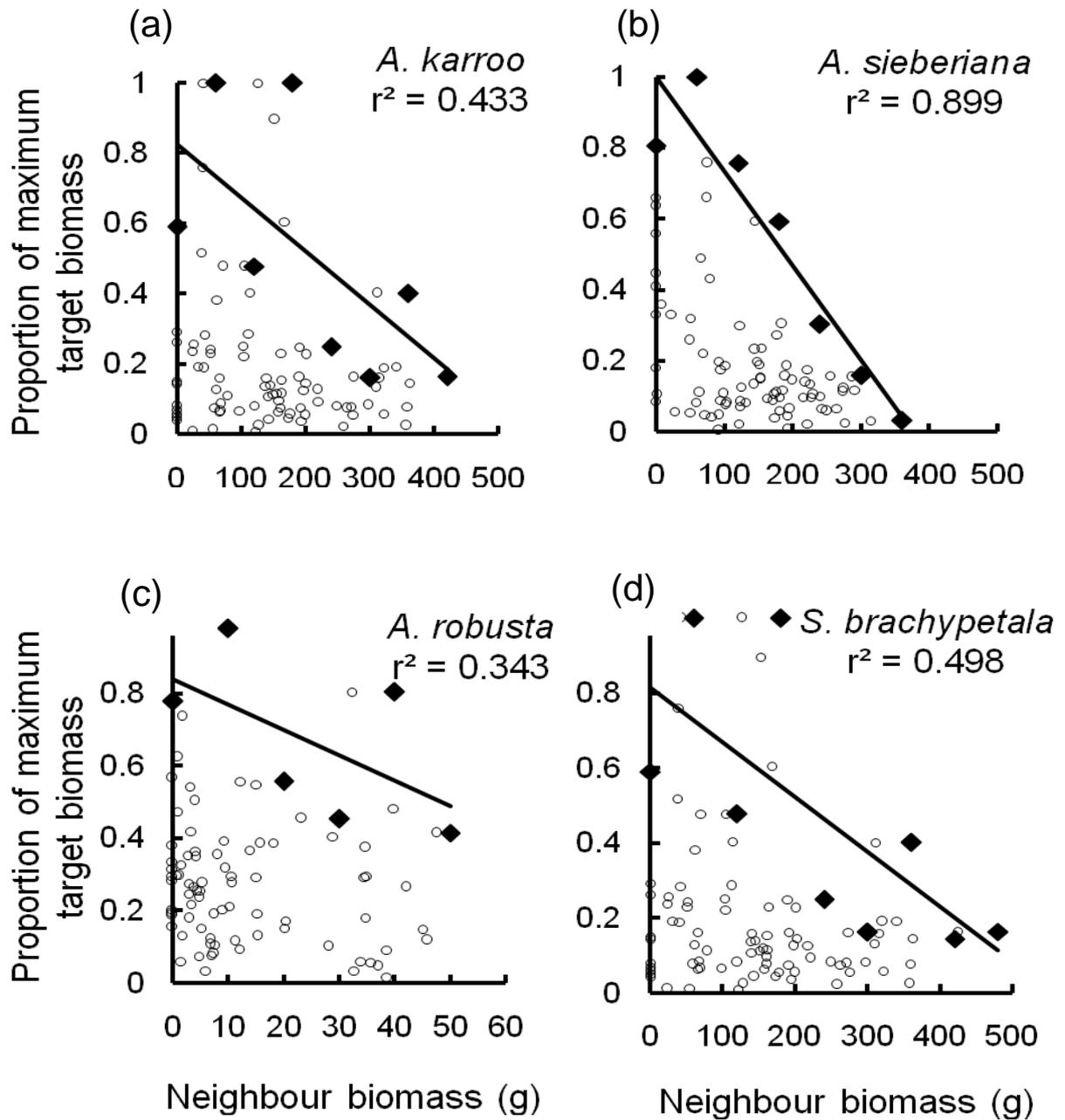
**Fig. 2.** Mean + SE relative growth rate ( $\text{g.g}^{-1}.\text{d}^{-1}$ , calculated as  $[(\ln(\text{actual final biomass}) - \ln(\text{initial biomass})) / \text{time in days from initial to final measurements}]$ ) for the four humid savanna target plants: (a) *A. karroo*, (b) *A. sieberiana*, (c) *A. robusta*, (d) *S. brachypetala*, at varying neighbour densities. Similar letters denote non-significant differences in relative growth rate. Note that the y-axis is not the same.



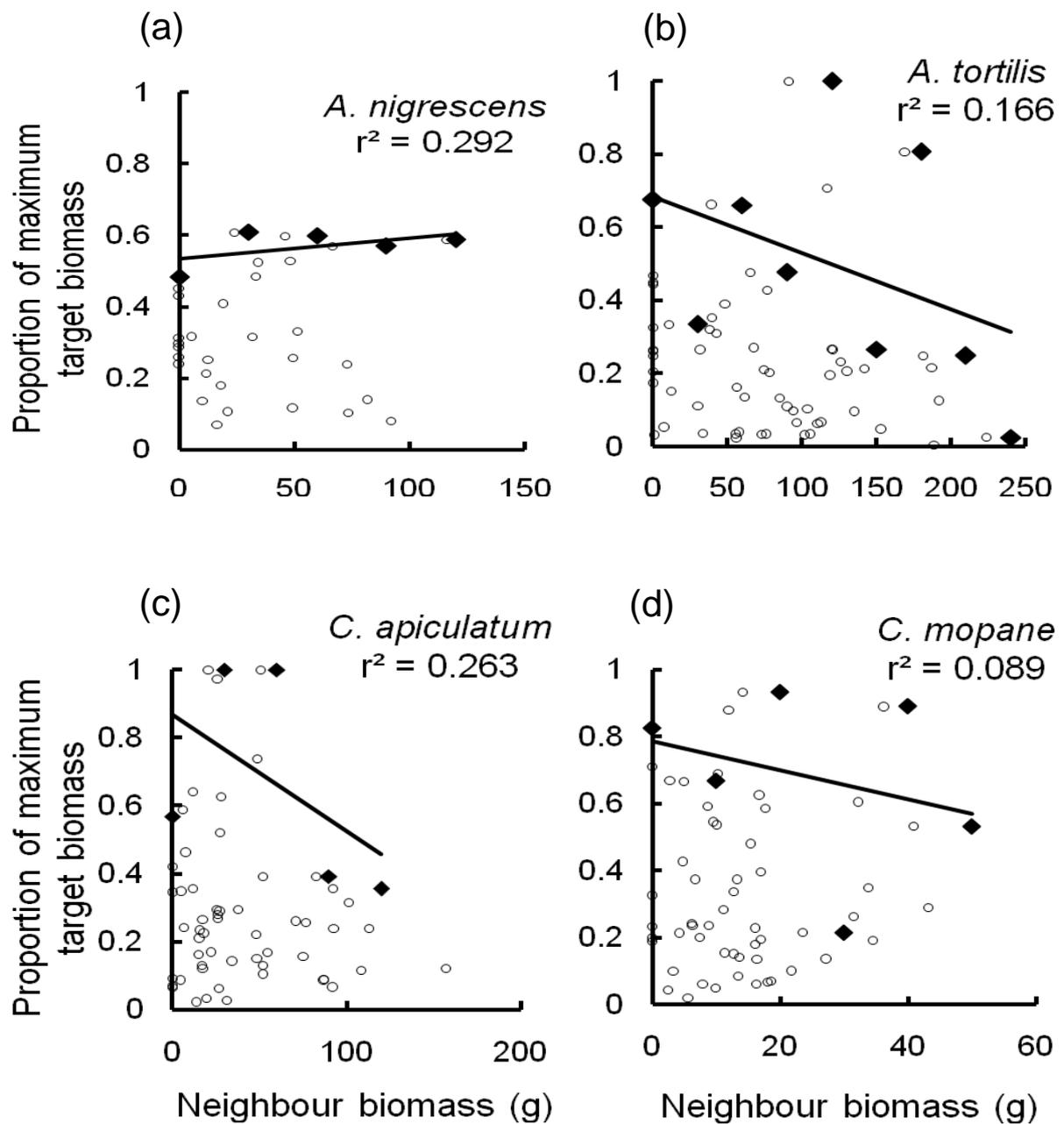
**Fig. 3.** Proportion of maximum target biomass against neighbour biomass for humid savanna species, showing coefficients of determination ( $r^2$ ). The slope indicates the competitive *response*. (○) indicates the regression of target biomass against unclustered neighbour biomass. (◆) indicates the regression using the maximum target biomass against neighbour biomass clustered into width classes of 60g. All regressions are significant except for *A. robusta* (c).



**Fig. 4.** Proportion of maximum target biomass against neighbour biomass for mesic savanna species, showing coefficients of determination ( $r^2$ ). Slope indicates the competitive response. ( $\circ$ ) indicates the regression of target biomass against unclustered neighbour biomass. ( $\blacklozenge$ ) indicates the regression using the maximum target biomass against neighbour biomass clustered into width classes of 30 g. All regressions are significant except for *A. nigrescens* (a).



**Fig. 5.** Proportion of maximum target biomass against neighbour biomass for humid savanna species, showing coefficients of determination ( $r^2$ ). The slope indicates the competitive effect. (○) indicates the regression of target biomass against unclustered neighbour biomass. (◆) indicates the regression using the maximum target biomass against neighbour biomass clustered into width classes of 60 g. All regressions are non-significant except for *A. sieberiana* (b).



**Fig. 6.** Proportion of maximum target biomass against neighbour biomass for mesic savanna species, showing coefficients of determination ( $r^2$ ). Slope indicates the competitive effect. (○) indicates the regression of target biomass against unclustered neighbour biomass. (◆) indicates the regression using the maximum target biomass against neighbour biomass clustered into width classes of 30 g. All regressions are non-significant.

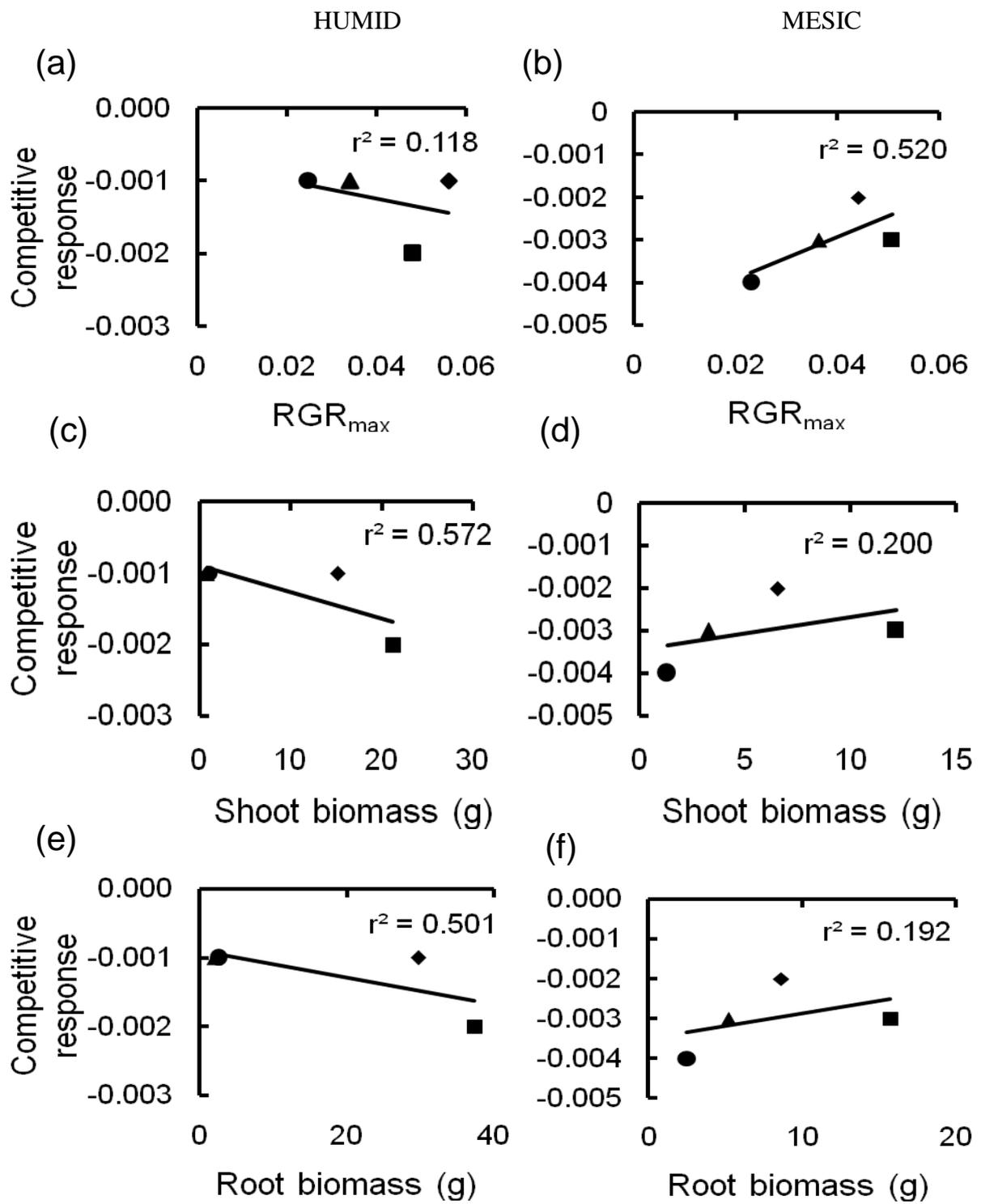


Fig. 7

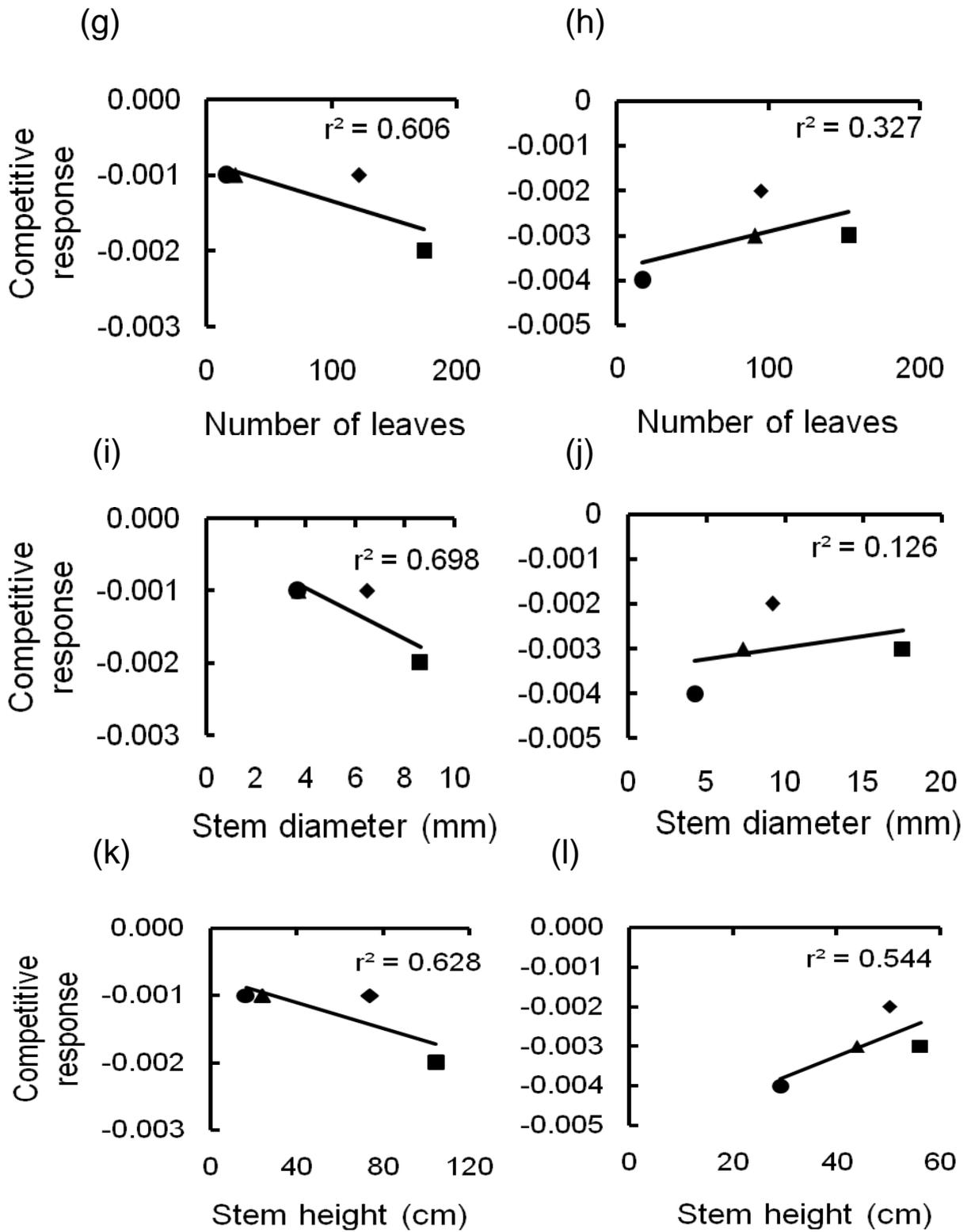
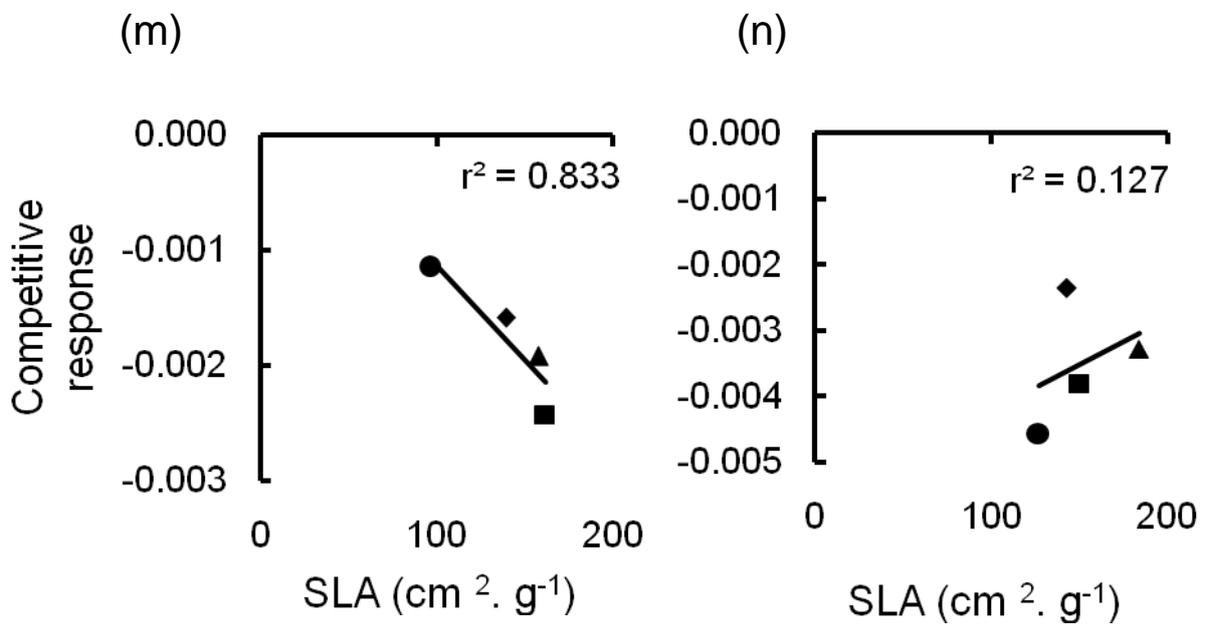


Fig 7.



**Fig. 7.** Plots of species competitive response against plant functional traits. (a)  $RGR_{max}$  for humid species. (b)  $RGR_{max}$  for mesic species. (c) Shoot biomass for humid species. (d) Shoot biomass for mesic species. (e) Root biomass for humid species. (f) Root biomass for mesic species. (g) Number of leaves for humid species. (h) Number of leaves for mesic species. (i) Stem diameter for humid species. (j) Stem diameter for mesic species. (k) Stem height for humid species. (l) Stem height for mesic species. (m) Specific leaf area (SLA) for humid species. (n) Specific leaf area for mesic species. All regressions were non-significant with the exception of SLA for humid species (m) ( $p = 0.02$ ). Symbols indicate different species. For humid: ● = *S. brachypetala*, ◆ = *A. karroo*, ▲ = *A. robusta*, ■ = *A. sieberiana*. For mesic: ● = *C. mopane*, ◆ = *A. nigrescens*, ▲ = *C. apiculatum*, ■ = *A. tortilis*.

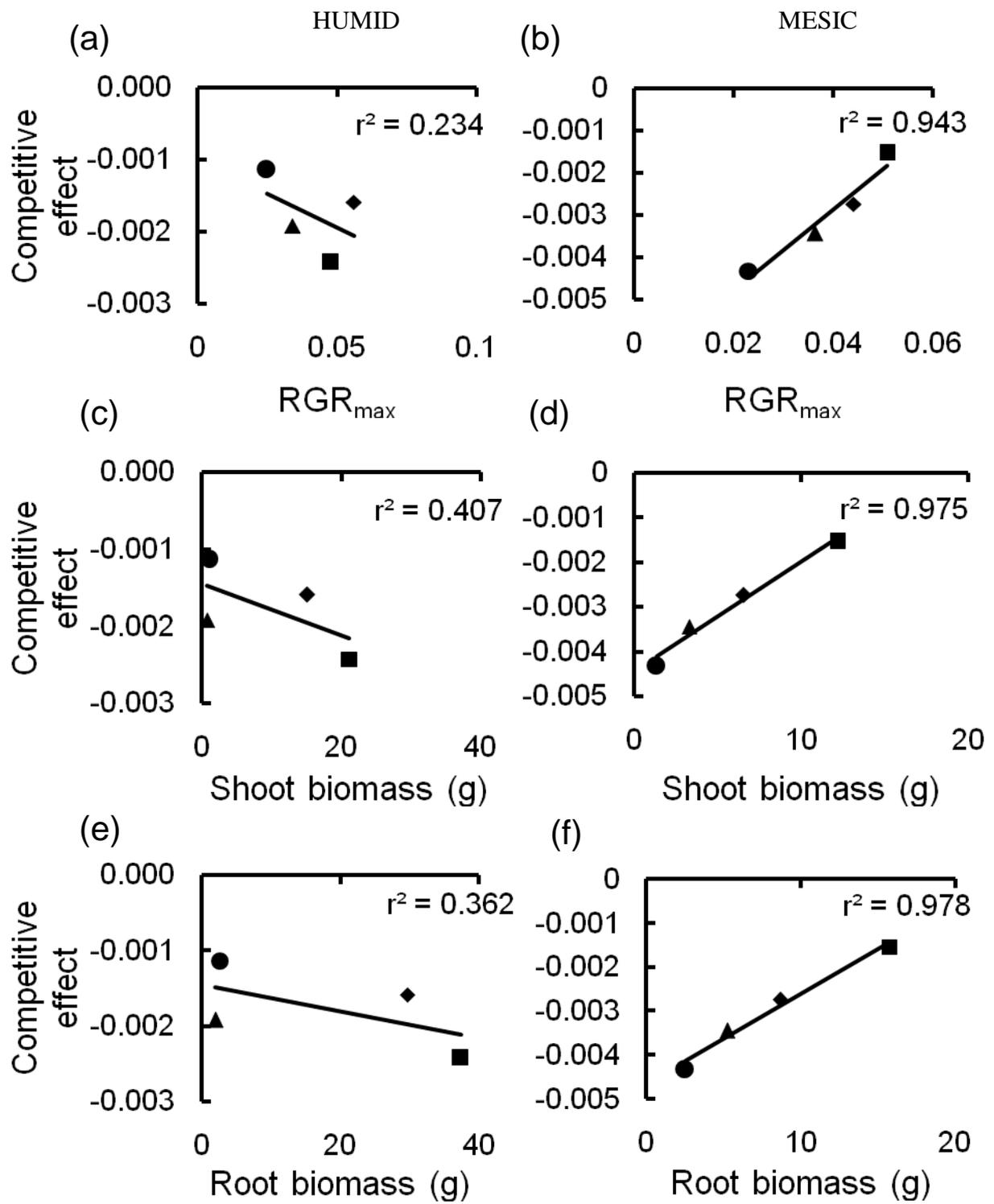


Fig 8.

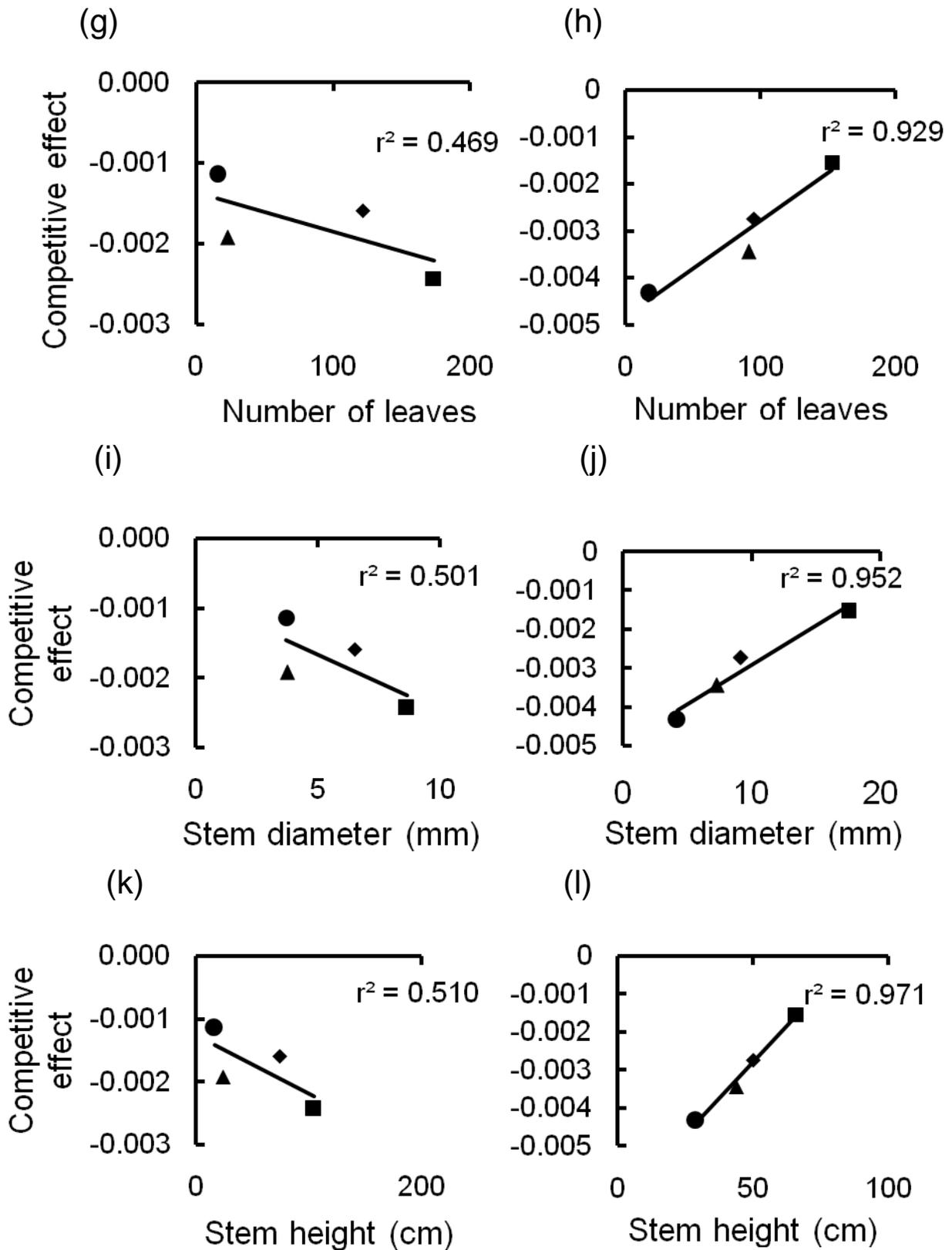
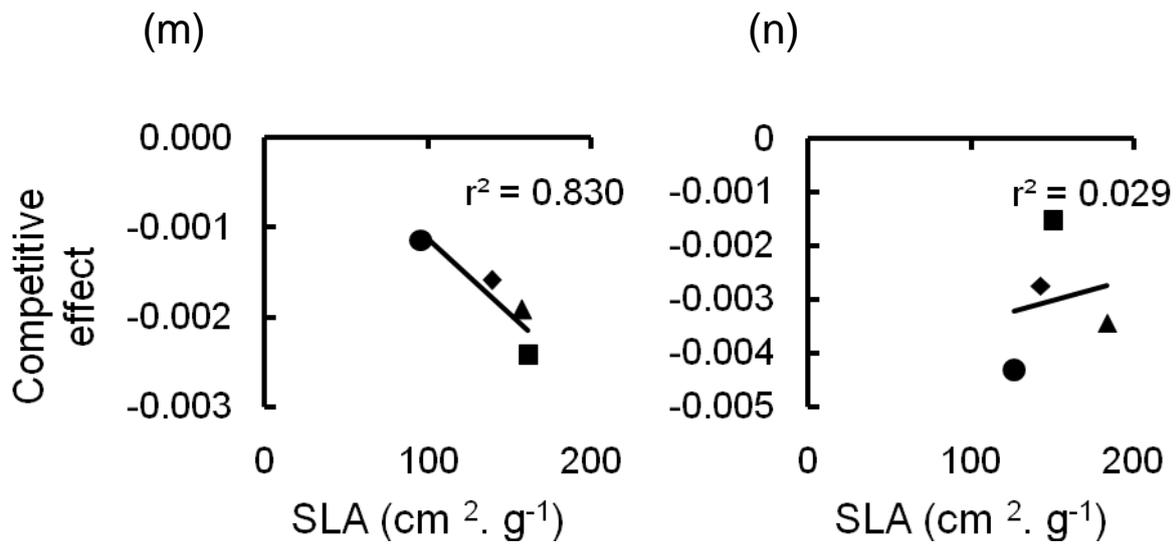


Fig 8.



**Fig. 8.** Plots of species competitive effect against plant functional traits. (a)  $RGR_{max}$  for humid species. (b)  $RGR_{max}$  for mesic species. (c) Shoot biomass for humid species. (d) Shoot biomass for mesic species. (e) Root biomass for humid species. (f) Root biomass for mesic species. (g) Number of leaves for humid species. (h) Number of leaves for mesic species. (i) Stem diameter for humid species. (j) Stem diameter for mesic species. (k) Stem height for humid species. (l) Stem height for mesic species. (m) Specific leaf area (SLA) for humid species. (n) Specific leaf area for mesic species. For humid: ● = *S. brachypetala*, ◆ = *A. karroo*, ▲ = *A. robusta*, ■ = *A. sieberiana*. For mesic: ● = *C. mopane*, ◆ = *A. nigrescens*, ▲ = *C. apiculatum*, ■ = *A. tortilis*. Note: Varying scales.

## Chapter 3

# Spatial pattern analysis and competition between *Acacia karroo* trees in humid savannas

**Tiffany Pillay and David Ward\***

*School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, Pietermaritzburg, South Africa*

---

Ward, D. (Corresponding author, [ward@ukzn.ac.za](mailto:ward@ukzn.ac.za)): School of Biological & Conservation Sciences, University of KwaZulu-Natal, P. Bag X01, Scottsville 3209, South Africa.

Pillay, T. ( [Tifpillay@gmail.com](mailto:Tifpillay@gmail.com)): School of Biological & Conservation Sciences, University of KwaZulu-Natal, P. Bag X01, Scottsville 3209, South Africa.

## Abstract

While tree-grass interactions in savannas have been widely documented, competition between trees has received considerably less attention, and it is still unclear whether competition plays a role in determining the woody plant cover of humid savannas. Nearest neighbour analysis and spatial point pattern analysis can give insights to the underlying processes affecting the individuals in a population, and is often used to detect competition between plants. We assessed the spatial patterns of *Acacia karroo* trees from savannas in KwaZulu-Natal, using Ripley's L and K statistics, as well as the univariate and bivariate O-ring statistics. We predicted that juvenile trees would be more spatially aggregated, due to facilitation between shrubs when zones of overlap are relatively small, while adult trees would be regularly spaced due to the effects of density-dependent mortality (i.e. consistent with the honeycomb rippling model). We found that juvenile trees were more aggregated than expected by chance, and the overall spatial distribution of all trees was also found to be aggregated, with no evidence of spatial evenness among large individuals. Nearest neighbour analysis, however, revealed significant positive correlations between the sum of the distances to the four nearest neighbours and the sum of the canopy diameters of the target tree and its four nearest neighbours in most cases, indicating the presence of competition. In sum, these results suggest that competitive interactions between *A. karroo* trees at these sites are relatively weak, and result in decreased performance (smaller canopy diameters) rather than mortality, thus preventing a regular pattern of tree distribution. We advocate the use of both methods of detecting competitive interactions in the field, especially if the effects of competition are too subtle to result in differential mortality.

## Introduction

The coexistence of two contrasting life forms, grasses and woody plants, has been of interest to savanna ecologists for many years (e.g. Walter 1971, Walker et al. 1981, Kraaij and Ward 2006). Numerous empirical studies have shown the competitive effect of grasses on trees, and *vice versa* (Walker et al. 1981, Sankaran et al. 2004, Kraaij and Ward 2006, Wiegand et al. 2006). On the basis of Lotka-Volterra stable coexistence theory, competition within life forms should be of greater importance than interspecific competition between life forms (Tilman 1982). Consequently, competition between trees should be a significant feature of savanna dynamics. However, the effects of tree-on-tree competition have been largely overlooked (Scholes and Archer 1997, Calabrese et al. 2010).

Interestingly, competition between trees affects the spacing of trees, and thus the spatial heterogeneity of the landscape (Wiegand et al. 2006, Meyer et al. 2008). Intense density-dependent mortality can convert a savanna into a grassland (Jeltsch et al. 2000), whereas weak competitive interactions (or facilitation) may promote tree aggregation (woody plant encroachment), turning savannas into woodlands (Wiegand et al. 2006, Meyer et al. 2008). The importance of competitive interactions between woody plants in savannas is the basis of the honeycomb rippling model (Ward 2005, Wiegand et al. 2005), which states that trees become more evenly spaced with increasing size, as weaker trees that are too close to others are eliminated.

Competition between trees has been inferred by the use of nearest neighbour analysis and neighbour removal experiments (Shackleton 2002, Meyer et al. 2008, Schleicher et al. 2011a). Both of these analyses are based on the idea that if competitive interactions are present, there will be a marked reduction in the size of one or both of the competing neighbours, or a substantial increase in the size of plants when neighbours are removed (Pielou 1962, Schleicher et al. 2011a). Nearest neighbour analysis, in particular, is the most common method of inferring competitive interactions in southern African savannas (Shackleton 2002). This analysis is based on the premise that the combined size of a plant and its nearest neighbour is generally positively correlated with the

distance between them (Gutierrez and Fuentes, 1979, Smith and Walker, 1983, Wiegand et al. 2005), indicating that larger plants have smaller neighbours due to their competitive effect. Nearest-neighbour analysis has been criticized for underestimating the prevalence of competition because the nearest neighbour may not have the greatest competitive impact on a target plant if the nearest neighbour is very small compared to other plants in the vicinity (Shackleton 2002). This limitation can be overcome by using more than one nearest neighbour (Shackleton 2002).

Ecologists may also detect the existence of underlying processes by studying the spatial structure of populations, which may elucidate intraspecific and inter-specific interactions such as competition, predation, and reproduction (Dale 1999, Perry et al. 2002). Spatial point pattern statistics can be used to infer the presence of competition by assessing the spatial distribution of trees and determine the scales at which a spatial pattern is significantly clustered or regular (Wiegand and Moloney 2004). First-order statistics describe large-scale variation in the intensity of points in a study region, whereas second-order characteristics are summary statistics of all point-to-point distances in a mapped area and offer the potential for detecting both different types and scales of patterns (Ripley 1981). Second-order analysis based on Ripley's *K*-function is increasingly used in ecology to characterize spatial patterns and to develop hypotheses on underlying processes (Getzin et al. 2006, Meyer et al. 2008, Schleicher et al. 2011a).

When using spatial statistics, the position of a plant in a plot is represented by a point and the analysis of the spatial point pattern exhibits whether the distribution of the points are random, clumped, or regular by comparing the distribution to a null model of random distribution (Schleicher et al. 2011b). Significance is usually evaluated by comparing the observed data with Monte Carlo envelopes from the analysis of multiple simulations of a null model (Wiegand and Moloney 2004). The common null model is complete spatial randomness (CSR), but other null models may be appropriate depending on the point pattern of plants in an area and the biological question asked. Hence, the major challenge for plant ecologists when using spatial statistics is to

apply the proper null model and fit to answer ecological questions (Wiegand and Moloney 2004, Lancaster 2006).

Competitive interactions have been detected in arid environments using both nearest neighbour analysis and spatial statistics (Meyer et al. 2008, Schleicher et al. 2011a). While we have found, using a target-neighbour greenhouse experiment, that there was a strong effect of competition on the growth of seedlings/saplings from humid savannas (receiving about 1000 mm of annual rainfall) (Pillay and Ward, submitted) it is still unclear as to whether competitive interactions play an important role in regulating woody plant biomass in humid savannas. Sankaran et al. (2005) have shown in a meta-analysis that, in African savannas, there was a positive relationship between tree density and annual rainfall up to 650 mm MAR, while tree density asymptoted at higher MAR, indicating that fire and biotic factors such as herbivory were important. We wished to assess whether an additional biotic factor affecting humid species was intra-specific tree competition.

The aim of this study was to detect the presence of inter-tree competition, and to assess the spatial distribution of *Acacia karroo* in several sites of humid savanna in KwaZulu-Natal, South Africa. We employed nearest neighbour analysis to determine intraspecific tree competition by examining the neighbourhood effects on plant performance, measured by canopy diameter. We also used spatial statistics to determine the overall pattern of *A. karroo* trees and the difference in spatial structure of adult and juvenile trees. We predicted that:

1. There will be a positive relationship between distance and canopy diameter, indicating competition between individuals, and a negative relationship between the coefficient of variation in nearest neighbour distance and canopy diameter, if older trees are more evenly spaced (i.e. consistent with the honeycomb rippling model).
2. The overall spatial pattern of *Acacia karroo* trees will be regular, indicating the presence of density-dependent mortality (competition).
3. Juvenile *A. karroo* plants will be more aggregated than larger trees, either due to facilitation, directed seed dispersal or environmental heterogeneity. With growth of

the juvenile plants, competition increases between juvenile and mature plants (Wiegand et al. 2006), so that the association disappears in the larger size classes.

## **Materials and methods**

### **Study species**

The species selected for this study was *Acacia karroo* Hayne (Mimosoideae; Fabaceae). This species is the most widely distributed *Acacia* species in southern Africa, occurring in Zimbabwe, Botswana, Swaziland, Lesotho, Namibia, South Africa, Mozambique, and Zambia. *Acacia karroo* is also the most abundantly available *Acacia* species in southern Africa with a mean density of between 400 and 800 plants/ha (O'Connor 1995). It is deciduous, but may be evergreen under favourable conditions (Pooley 1998, Ward 2011).

### **Study sites and data collection**

Three humid savannas, defined as receiving at least 1000 mm of annual rainfall, were surveyed along the east coast of South Africa. The first site was situated at Empangeni (28°34'20" S, 31°57'22" E), and receives 1300 mm of mean annual rainfall (MAR). The second site was located at Kwambonambi (28° 36' 0" S, 32° 5' 0" E), receiving 1400 mm of MAR. Lastly, we surveyed *A. karroo* trees at Richards Bay (28°48'0" S, 32°6'0" E), where MAR is 1200 mm.

At each site, we surveyed 50 m by 50 m plots of pure stands of *Acacia karroo*, in order to eliminate the confounding effects of interspecific tree competition. At Kwambonambi and Richards Bay, three replicate plots were surveyed, while at Empangeni only two replicate plots were surveyed. For each tree we recorded the geographic co-ordinates, tree height, diameter at breast height of 1.3 m (DBH) and the canopy diameter (Table 1). We classified trees into adults (> 15 cm DBH) and juveniles (< 15 cm DBH) for the trees present at Kwambonambi and Empangeni. However, the trees at Richards Bay belonged to a large variant with enormous variation in the

architecture of adults (Mboumba and Ward 2008, Ward 2011) and adults were classified as having a DBH > 30 cm (Table 1).

## **Data analysis**

### *Nearest neighbour analysis*

For all trees in each plot, we examined whether trees were directly competing with their nearest neighbouring trees. If this is valid then the mean distance to the nearest neighbouring trees should be smaller for smaller trees than for larger trees. We measured the distance from the focal tree to the four nearest neighbours. We then investigated the relationship between the sum of the distances to the four nearest neighbours and the sum of the canopy diameters of the target tree and its four nearest neighbours. Significant positive slopes indicate competition between individuals. We also examined the relationship between the coefficient of variation in nearest neighbour distances and canopy diameter, to determine whether larger (and presumably, older) trees were more evenly spaced than smaller trees, indicating density-dependent mortality. These analyses were performed using regression in SPSS (version 18).

### *Spatial pattern analysis*

All spatial analyses were conducted using the software *Progamita* (Wiegand and Moloney 2004). We determined the intensity  $\lambda$  (the number of plants per unit area) of each plot. The intensity was assessed using Ripley's L-function, a modification of Ripley's K, which applies a transformation that removes the scale dependence of  $K$  for independent patterns and stabilizes the variance (Ripley 1981). Any spatial dependence that is indicated by the estimated  $K$  function of a heterogeneous pattern could be due more to first-order effects rather than to interactions between the points themselves (Wiegand and Moloney 2004). In this case, a null model that acknowledges the overall first order heterogeneity has to be adopted to examine possible second-order effects. When the intensity of plants in a plot was homogeneous the usual null model of complete spatial randomness

(CSR) was applied to ascertain second-order effects. However, when the intensity was heterogeneous, alternate null models were applied (e.g. heterogeneous Poisson process).

### *O-ring statistic*

Wiegand and Moloney (2004) developed a multi-scale method called the O-ring statistic that is based on Ripley's L-function (Ripley 1981). The O-ring statistic is similar to Ripley's (1981) K-statistic, but uses annuli instead of circles, so that the spatial relation between points can be related to a certain scale (Wiegand and Moloney, 2004). The accumulative K-function can detect aggregation or dispersion *up to* a given distance  $r$  and is therefore appropriate if the process in question (e.g. the negative effect of competition) may work only up to a certain distance, whereas the O-ring statistic can detect aggregation or dispersion *at* a given distance  $r$ . The O-ring statistic has the additional advantage that it is a probability density function with the interpretation of a neighborhood density, which is more intuitive than an accumulative measure (Stoyan and Pettingen 2000).

The O-ring statistic of a univariate point pattern counts the number of points in a ring around an arbitrarily chosen point at a specific distance and width. This is done for all points in the pattern. The  $O_{12}$ -ring statistic for a bivariate analysis is similar to the univariate function but counts the number of points of pattern 2 in a ring of distance  $h$  from an arbitrary point of pattern 1. Confidence envelopes for the O-ring statistic were estimated from 999 Monte-Carlo simulations of the point patterns using an appropriate null model (Bailey and Gatrell 1995). In each simulation, the points were redistributed according to the null model and the O-ring statistic was calculated for the simulated point pattern. From all simulations, the upper and lower confidence envelopes were estimated using the 5th lowest and 5th highest value for each distance  $h$ , representing a significant level of approximately  $p = 0.01$ .

### *Univariate O-ring analysis*

Using the univariate O-ring statistic, we assessed the overall spatial pattern of *Acacia karroo* trees in each plot. In the univariate case, if the O-ring function exceeds the upper confidence envelope it indicates a spatial aggregation of the species. However, if the function is below the lower confidence envelope, it indicates a spatial regularity of the plants. If the function is between both limits, the distribution of plants does not deviate from the assumption of the chosen null model.

We also tested for the presence of cohorts. If cohorts are present, one would expect more intense competition between individuals of the same cohort, which may be hard to detect when looking at the overall patterns of competition (Wiegand et al. 2005). As a non-parametric measure of variability (or inequality) in tree size, we used the Gini coefficient (Glasser 1962), which equals 0 when all trees are equal in size and approaches unity when the tree size hierarchy is strongly unequal (Wiegand et al. 2005).

### *Bivariate O-ring statistics*

We then tested the independence of adult and juvenile *A.karroo* trees in each plot, using a null model under antecedent conditions for investigating the relationship between adult trees (pattern 1) and seedlings (pattern 2); an appropriate null model to test for repulsion or attraction would be to randomize the locations of the seedlings (because they could potentially be found in the entire study region) and to keep the locations of the trees fixed. Randomizing the locations of the trees would be inappropriate because they did not change their position during the development of the seedlings. Moreover, possible repulsion or attraction between seedlings and trees might be obscured by randomizing the locations of the trees (Wiegand and Moloney 2004). In the bivariate analysis, values above the upper confidence envelope indicate significant association between the two point patterns, whereas values below the lower confidence envelope indicate significant repulsion. As in

the univariate case, values within the two confidence envelopes do not differ significantly from the null model.

## **Results**

### **Nearest neighbour analysis**

Significant positive correlations between the sum of the distances to the four nearest neighbours and the sum of the canopy diameters of the target tree and its four nearest neighbours were noted for five out of eight plots (range in  $r = 0.418- 0.716$ ; range in  $p = 0.003 - 0.05$ ; Fig 1 a, b, d, e & f). One of the plots displayed a significant negative relationship between distance to neighbours and canopy diameter ( $r = -0.490$ ;  $p = 0.006$ ; Fig 1 c). Two plots showed no relationship between neighbour distance and canopy diameter ( $r = 0.102, 0.107$ ;  $p > 0.05$ ). We found no significant relationship between the coefficient of variation in nearest neighbour distance and canopy diameter for any of the plots (range in  $r = 0.096 - 0.14$ ;  $p > 0.05$ ).

### **Spatial analysis**

#### **Univariate analysis**

Ripley's L-function revealed that plots 1 and 2 (Empangeni), 3 and 4 (Kwambonambi) and 8 (Richards Bay) had a homogeneous intensity; therefore we applied the null model of CSR (complete spatial randomness). Plots 5 (Kwambonambi), 6 and 7 (Richards Bay) had a heterogeneous intensity, therefore we applied a heterogeneous Poisson process, with a moving window based on the mean canopy diameter for that plot (Table 1) (See Wiegand and Moloney 2004). The univariate spatial analysis of the overall pattern of *A. karroo* trees revealed that all five plots with homogenous intensity displayed aggregated spatial distributions of *A. karroo* trees (Fig 2a-e), while all plots with heterogeneous intensity of plants showed a random spatial distribution of trees (Fig 3. a, b & c). In plot 1 (Empangeni), aggregation was observed from 1 to 9 m, and 14 – 17

m (Fig 2a). In the same plot, we observed that at 23 - 25 m, significant repulsion of *A. karroo* trees occurred. In plots 2 (Empangeni), 3 (Kwambonambi) and 8 (Richards Bay), spatial aggregation of trees was detected at 2 - 3 m, 1 - 7 m and 1 - 6 m, respectively (Fig 2 b, c & e). In plot 4 (Kwambonambi), spatial aggregation of plants was noted at 1-3 m, 11 m and 15 m (Fig 2 d). The size inequalities of trees in all plots were relatively small (range in Gini = 0.04 – 0. 2), indicating the absence of cohorts.

### **Bivariate analysis**

The spatial analysis of mature trees and juveniles with the null model accounting for antecedent conditions showed that five out of eight plots displayed spatial aggregation (Fig 4). In plots 1 and 2 (Empangeni), 3 and 5 (Kwambonambi ) and 8 (Richards Bay) positive association of juveniles was found at 1 - 20 m, 28 m, 6 m, 14 - 15 m and 1 - 10 m, respectively (Fig 4 a, b, c, e and h). In plots 4 (Kwambonambi), 6 and 7 (Richards Bay) there was no observed pattern between juvenile *A. karroo* trees (Fig 4 d, f and g).

### **Discussion**

We have illustrated the use of two different methods of detecting competition in the field, viz. spatial pattern analysis and nearest neighbour analysis. We found that juvenile trees were significantly clustered in relation to adult trees, in most sites, as predicted. Patterns of seedling aggregation have been explained in terms of regeneration ecology, e.g. regeneration close to seed sources, vegetative regeneration, facilitative interactions due to the occurrence of 'safe sites' (Skarpe 1991), and has been found to occur among a variety of species and life forms (Skarpe 1991, Barot et al. 1999, Meyer et al. 2008). The effect of seedling competition may not be strong enough to result in differential mortality and hence result in the regular pattern expected of adult trees. This is because the rooting zones of seedlings may not overlap or the area of influence of seedlings is reduced (Schwinning and Weiner 1998). Two plants compete with each other when their zones of

influence overlap. The greater the overlap, the more intense is the competition (Meyer et al. 2008). In addition, competition between plants increases with the growth of the plants and therefore may lead to a self-thinning process over a period of time (Wiegand et al. 2008). Hence, we can expect aggregation at the seedling stage, and more regular distributions as seedlings mature and begin demanding more resources resulting in increasing competitive interactions.

The overall pattern of *A. karroo* trees also revealed that a majority of the sites displayed aggregation, despite the absence of cohorts. This is contrary to our prediction that the spatial distribution would be regular, indicating competitive interactions. A regular pattern is usually the result of density-dependent mortality, and occurs when trees experience competition for a limited resource. Intense competition may lead to mortality of clumped individuals, resulting in a regular spacing of trees in accordance with the honeycomb rippling model (Ward 2005, Wiegand et al. 2005). Therefore, older trees should be more evenly-spaced than juvenile plants. However, the spatial pattern of a population does not directly identify the processes involved in forming the observed pattern (Coomes et al. 1999). In some cases, competition may not be strong enough to cause mortality but rather reduces growth. Only when competition leads to sufficient mortality within a species, will it cause regular distributions (Stoll and Bergius 2005). While point pattern statistics incorporate more information from a fully mapped spatial pattern than most other spatial methods, it is only particularly effective when the effects of competition are strong enough to result in differential mortality (Ward 2005). However, distances between neighbours may not always be sufficient to detect competitive interactions, as changes in neighbour density may be compensated for by variable growth rates and modular plasticity (Getzin et al. 2006). In such cases, it may be more suitable to employ nearest neighbour analysis, which takes into account inter-neighbour distances as well as plant performance. Getzin et al. (2006) found a lack of evidence of spatial regularity in Douglas fir (*Pseudotsuga menziesii* var. *menziesii*), despite detecting important competitive interactions via size correlations. Hence, spatial aggregation of *A. karroo* may still be present even in the presence of competitive interactions. This idea is supported by our results.

While inter-neighbour distances revealed significant aggregation of individuals, analysis of neighbour distances and tree performance, as given by canopy diameter, revealed that larger *A. karroo* trees had smaller neighbours, or neighbours that were further away. In addition, we found no relationship between the coefficient of variation in nearest neighbour distances and canopy diameter, indicating that spatial evenness was absent, even among the large individuals. This suggests that while competitive interactions are present between *Acacia karroo* trees from humid savannas, the effects are relatively weak, and result in decreased performance rather than mortality, which in turn prevents the regular spacing expected when individuals of a population are competing strongly, as predicted by the honeycomb rippling model (Ward 2005, Wiegand et al. 2005). This result is also supported by a greenhouse study that revealed strong effects of neighbourhood competition on the growth, and not survival, of humid savanna tree species (Pillay and Ward, submitted). Significant positive correlations between the size of a tree and the distance to its nearest neighbour, indicating competitive interactions, have also been reported for *Burkea africana-Terminalia sericea* savanna in southern Africa (Smith and Grant 1986) and for large individuals of *Brachystegia spiciformis* and *Julbernardia globiflora* in Zimbabwe (Grundy et al. 1994).

Interestingly, in our study, nearest neighbour analysis revealed that at one site, there was a significant negative relationship between distance to neighbours and canopy diameter, indicating that larger trees were closer together. Facilitation, seed dispersal and environmental heterogeneity are possible reasons for a clumped distribution (Schleicher et al. 2011b). Trees that display a clumped distribution may be facilitating the growth of one another (Schleicher et al. 2011b). In this case, plants growing at high densities create 'islands of fertility' which favour the growth of surrounding plants (Ravi et al. 2010). Facilitative interactions may be present when water availability increases (due to hydraulic lift by larger species) or nutrient pools are increased (e.g. due to nitrogen fixation by leguminous plants) (Pugnaire et al. 1996). This facilitative interaction improves the living conditions of surrounding plants, and will result in spatially aggregated populations. However, facilitation has frequently been observed in arid and semi-arid environments,

and is regarded as a response to patchy rainfall events in arid savannas (Holmgren et al. 1997; Schleicher et al. 2011 a, b), which is uncommon in humid rainfall areas (Eisinger and Wiegand 2008, Ward 2009). Directed seed dispersal may also be the cause of aggregated spatial distributions (Nathan and Muller-Landau 2000, Schleicher et al. 2011b). Dispersal is often spatially limited, which leads to intraspecific aggregation (Nathan and Muller-Landau 2000). Directed seed dispersal results in spatial plant associations similar to those caused by facilitative interactions (Schleicher et al. 2011b). This may occur when animal-dispersed seeds of savanna trees (such as *A. karroo*) are preferentially defaecated beneath other plant species (Milton and Dean 1995). Directed dispersal can thus generate apparent facilitative patterns (Schleicher et al. 2011 b). A clumped distribution may be the result of environmental heterogeneity which causes uneven distribution of environmental variables both spatially and/or temporally (Schleicher et al. 2011b). If the heterogeneity of the landscape creates favourable conditions in certain areas only, species will tend to co-occur in those areas even in the absence of facilitative interactions (Barot et al. 1999, Schleicher et al. 2011b). Schleicher et al. (2011a) conducted an analysis of the spatial distribution of *Acacia mellifera* and *Tarchonanthus camphoratus* in an arid savanna. They found clear differences in the spatial distribution of *T. camphoratus* with regard to the environmental heterogeneity of soil conditions. In a rocky area, *T. camphoratus* juveniles were positively associated with *A. mellifera* whereas in a sandy area they were positively associated with mature *T. camphoratus* shrubs.

Overall, we found that competitive interactions between *Acacia karroo* are present in humid savanna sites in KwaZulu-Natal. However, the effects of intraspecific competition are relatively weak, and did not cause density-dependent mortality and regular spacing of trees in most cases. This suggests that while competition may be important in structuring humid savanna communities at a small spatial scale, other factors, such as fire or herbivory may be more important at larger spatial scales. Our study highlights the use of spatial statistics for detecting underlying patterns and processes, although future studies aiming to detect competition should incorporate both nearest neighbour analysis as well as spatial statistics if subtle competitive effects are to be detected.

**Acknowledgements** - We would like to thank S. Vadigi, J. Russell, D. Okubamichael and Z.

Tsvuura for field assistance. We thank Owen Sithole Agricultural College for allowing us access to their facilities and Jana Schleicher for help with the spatial analysis.

## References

Bailey, T. C. and Gatrell, A. C. 1995. Interactive spatial data analysis. - Longman Scientific & Technical.

Barot, S., et al. 1999. Demography of a savanna palm tree: Predictions from comprehensive spatial pattern analyses. - Ecology 80: 1987-2005.

Calabrese, J. M., et al. 2010. The independent and interactive effects of tree-tree establishment competition and fire on savanna structure and dynamics. – Am. Nat. 175: E44-65.

Coomes, D. A., et al. 1999. Identifying aggregation and association in fully mapped spatial data. - Ecology 80: 554-565.

Dale, M. R. T. 1999. Spatial pattern analysis in plant ecology - Cambridge University Press.

Eisinger, D. and Wiegand, K. 2008. SERGE: A spatially explicit generator of local rainfall in southern Africa. – S. Afr. J. Sci. 104: 37-42.

Getzin, S., et al. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. - Ecography 29: 671-682.

Glasser, G. J. 1962. Variance formulas for the mean difference and coefficient of concentration. - J. Am. Stat. Ass. 57: 648- 654.

Grundy, I. M., et al. 1994. Spatial pattern, regeneration and growth rates of *Brachystegia spiciformis* and *Julbernardia globifera*. – Vegetatio. 115: 101–107.

Gutierrez, J. R. and Fuentes, E. R. 1979. Evidence for intraspecific competition in the *Acacia caven* (Leguminosae) savanna of Chile. – Oecolog. Plantar. 14: 151–158.

- Holmgren, M., et al. 1997. The interplay of facilitation and competition in plant communities. - Ecology 78: 1966-1975.
- Jeltsch, F., et al. 2000. Ecological buffering mechanisms in savannas: A unifying theory of long-term tree-grass coexistence. - Plant Ecol. 150: 161-171.
- Kraaij, T. and Ward, D. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. - Plant Ecol. 186: 235-246.
- Lancaster, J. 2006. Using neutral landscapes to identify patterns of aggregation across resource points. - Ecography 29: 385-395.
- Meyer, K. M., et al. 2008. Multi-proxy evidence for competition between savanna woody species. – Perspect. Plant. Ecol. Evol. Syst. 10: 63–72.
- Milton, S.J. and Dean, W.R.J. 1995. How useful is the keystone species concept, and can it be applied to *Acacia erioloba* in the Kalahari Desert? - Z. Ökol. Natursch. 4: 147-156.
- Mboumba, G. and Ward, D. 2008. Phenotypic plasticity and local adaptation in two extreme populations of *Acacia karroo*. – Afr. J. Range. For. Sci. 25: 121-130.
- Nathan, R. and Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. – Trends. Ecol. Evol. 15: 278-285.
- O'Connor, T. G. 1995. *Acacia karroo* invasion of grassland: Environmental and biotic effects influencing seedling emergence and establishment. - Oecologia 103: 214-223.
- Perry, J. N., et al. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. - Ecography 25: 578-600.
- Pielou, E.C. 1962. The use of plant-to-neighbour distances for the detection of competition. – J. Ecol. 50: 357-367.
- Pillay T. and Ward D submitted. Competitive response and effect of savanna tree seedlings: Comparison of survival, growth and associated functional traits. J. Veg. Sci.
- Pooley, E. 1998. Trees: Southern African green guide - Southern Book Publishers.

- Pugnaire, F. I., et al. 1996. Facilitation between higher plant species in a semiarid environment. - Ecology 77: 1420-1426.
- Ripley, B. D. 1981. Spatial statistics. - Wiley.
- Sankaran, M., et al. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. – Ecol. Lett. 7: 480-490.
- Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. - Nature 438: 846-849.
- Schleicher, J., et al. 2011a. Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. – J. Arid. Environ. 75: 270-278.
- Schleicher, J., et al. 2011b. Disentangling facilitation and seed dispersal from environmental heterogeneity as mechanisms generating associations between savanna plants. – J. Veg. Sci. 22: 1038-1048.
- Scholes, R. J. and Archer, S. R. 1997. Tree-grass interactions in savannas. – Annu. Rev. Ecol. Syst. 28: 517-544.
- Schwinning, S. and Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. - Oecologia 113: 447-455.
- Shackleton, C. 2002. Nearest-neighbour analysis and the prevalence of woody plant competition in South African savannas. - Plant Ecol. 158: 65-76.
- Smith, T. M. and Grant, K. 1986. The role of competition in the spacing of trees in a *Burkea africana*- *Terminalia sericea* savanna. – Biotrop. 18: 219-223.
- Smith, T. M. and Walker, B. H. 1983. The role of competition in the spacing of savanna trees. - Proc. Grassl. Soc. Sth. Afr. 18: 159–164.
- Stoll, P. and Bergius, E. 2005. Pattern and process: competition causes regular spacing of individuals within plant populations. – J. Ecol. 93: 395-403.

- Stoyan, D. and Penttinen, A. 2000. Recent applications of point process methods in forestry statistics. – Stat. Sci. 15: 61-78.
- Tilman, D. 1982. Resource competition and community structure. - Princeton University Press.
- Walker, B. H., et al. 1981. Stability of semi-arid savanna grazing systems. – J. Ecol. 69: 473-498.
- Walter, H. 1971. Ecology of tropical and subtropical vegetation. - Oliver and Boyd.
- Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? – Afr. J. Range. For. Sci. 22: 101-105.
- Ward, D. 2009. The biology of deserts. – Oxford University Press.
- Ward, D. 2011. Population differentiation in a purported ring species, *Acacia karroo* (Mimosoideae). – Biol. J. Linn. Soc. 104: 748-755.
- Wiegand, K., et al. 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. – J. Veg. Sci. 16: 311-320.
- Wiegand, K., et al. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment - Insights from an arid savanna. – Perspect. Plant. Ecol. Evol. Syst. 7: 229-242.
- Wiegand, K., et al. 2008. The role of size inequality in self-thinning: A pattern-oriented simulation model for arid savannas. – Ecol. Model. 210: 431-445.
- Wiegand, T. and Moloney, K. A. 2004. Rings, circles, and null models for point pattern analysis in ecology. - Oikos 104: 209-229.

Table 1. Morphological features of *Acacia karroo* trees at eight plots of humid savanna (n = 245).

EMP = Empangeni ; KWAM = Kwambonambi; RB = Richards Bay.

Plot #	Location	Mean DBH (cm)	Max DBH (cm)	Mean height (m)	Max height (m)	Mean canopy diameter (m)
1	EMP	24.16	51	3.09	4.4	2.69
2	EMP	23.98	82	2.99	5	2.62
3	KWAM	23.33	62.5	4.90	10.2	3.91
4	KWAM	13.19	54	2.67	6	1.99
5	KWAM	14.23	58	2.74	5.8	1.58
6	RB	48.81	138	10.24	17.2	5.04
7	RB	39.88	92	8.7	14.6	4.45
8	RB	52.81	129	8.39	15.2	4.82

## Figure Legends

Fig. 1. Nearest neighbour analysis showing the relationship between the sum of the canopy diameters of the target tree and its 4 nearest neighbours and the sum of the distances to the 4 nearest neighbours in each of the eight plots. a = plot 1 Empangeni; b= plot 2 Empangeni; c = plot 1 Kwambonambi; d = plot 2 Kwambonambi; e = plot 3 Kwambonambi; f = plot 1 Richards Bay; g = plot 2 Richards Bay; h = plot 3 Richards Bay. (n = 245).

Fig. 2. The univariate O-ring statistic  $O(h)$  at different scales  $h$  with upper and lower confidence envelopes representing the maximum and the minimum value from 999 simulations with the null-hypothesis of Complete Spatial Randomness (CSR) . If  $O(h)$  is above the upper confidence interval, the pattern is significantly clustered, if  $O(h)$  is below the lower confidence interval, the pattern is significantly regular at the considered scale ( $p < 0.01$ ). a = plot 1 Empangeni; b= plot 2 Empangeni; c = plot 1 Kwambonambi; d = plot 2 Kwambonambi; e = plot 3 Richards Bay.

Fig. 3. The univariate O-ring statistic  $O(h)$  at different scales  $h$  with upper and lower confidence envelopes representing the maximum and the minimum value from 999 simulations with the null hypothesis of a heterogeneous Poisson process . If  $O(h)$  is above the upper confidence interval, the pattern is significantly clustered, if  $O(h)$  is below the lower confidence interval, the pattern is significantly regular at the considered scale ( $p < 0.01$ ). a = plot 3 Kwambonambi; b = plot 1 Richards Bay; c = plot 2 Richards Bay.

Fig. 4. The bivariate O-ring function test of spatial dependence between adult and juvenile *A. karroo* trees with the null model accounting for antecedent conditions which randomizes the locations of the seedlings (because they could potentially be found in the entire study region) and keeps the locations of the trees fixed. The 5th lowest and highest values of 999 Monte-Carlo simulations (representing a significant level of approximately  $p = 0.01$ ) were used to estimate the

confidence envelopes. a = plot 1 Empangeni; b= plot 2 Empangeni; c = plot 1 Kwambonambi; d = plot 2 Kwambonambi; e = plot 3 Kwambonambi; f = plot 1 Richards Bay; g = plot 2 Richards Bay; h = plot 3 Richards Bay (n = 245).

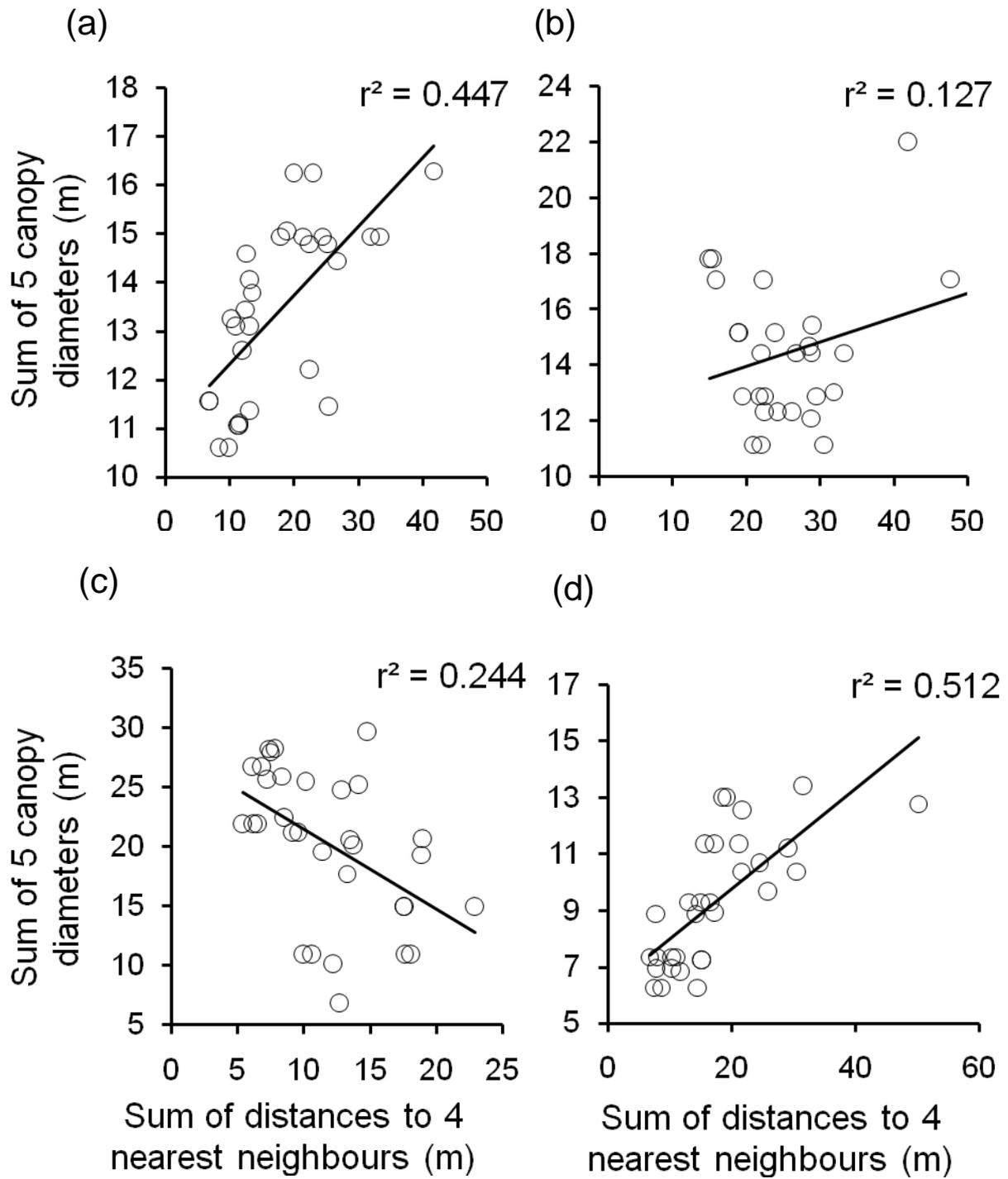


Fig. 1.

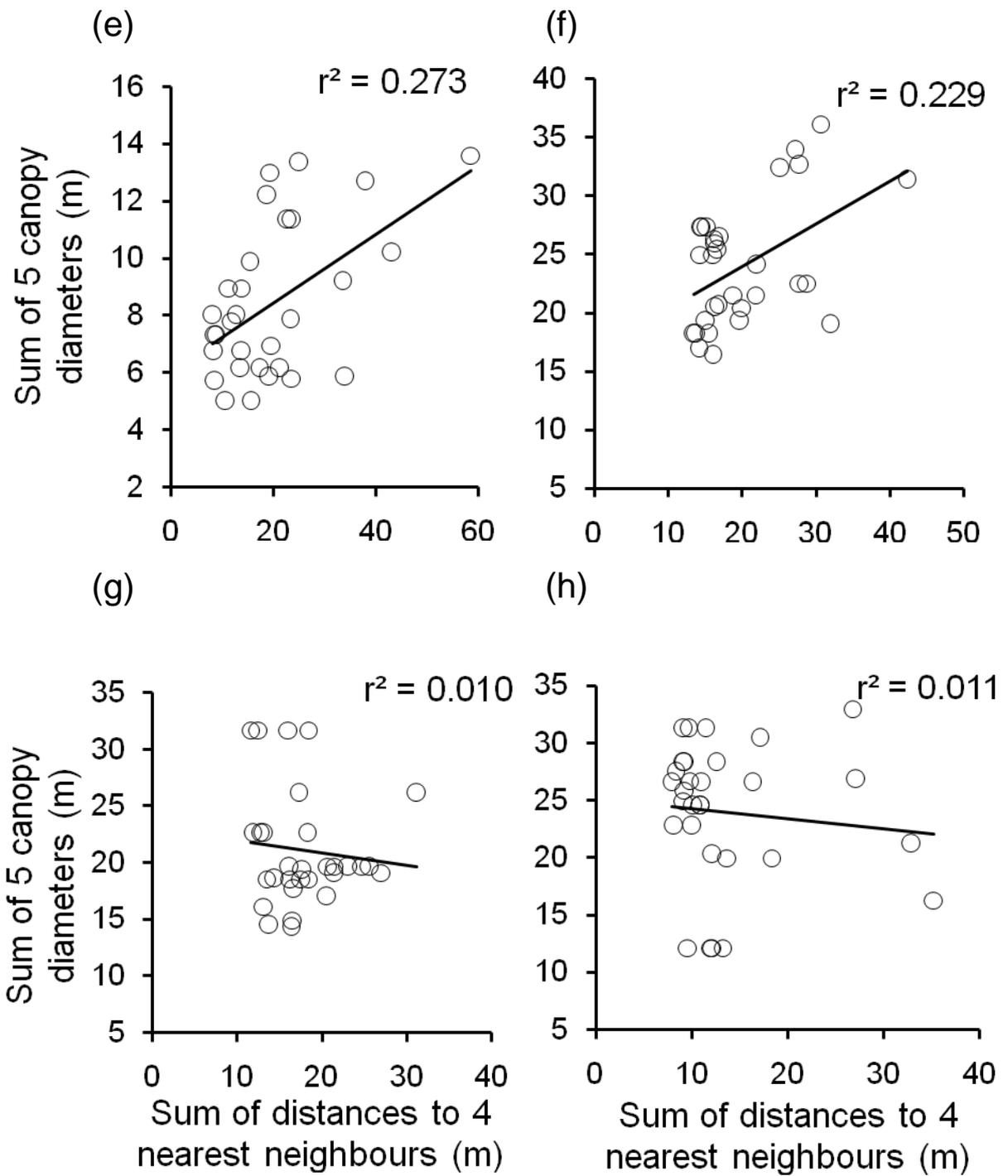


Fig. 1.

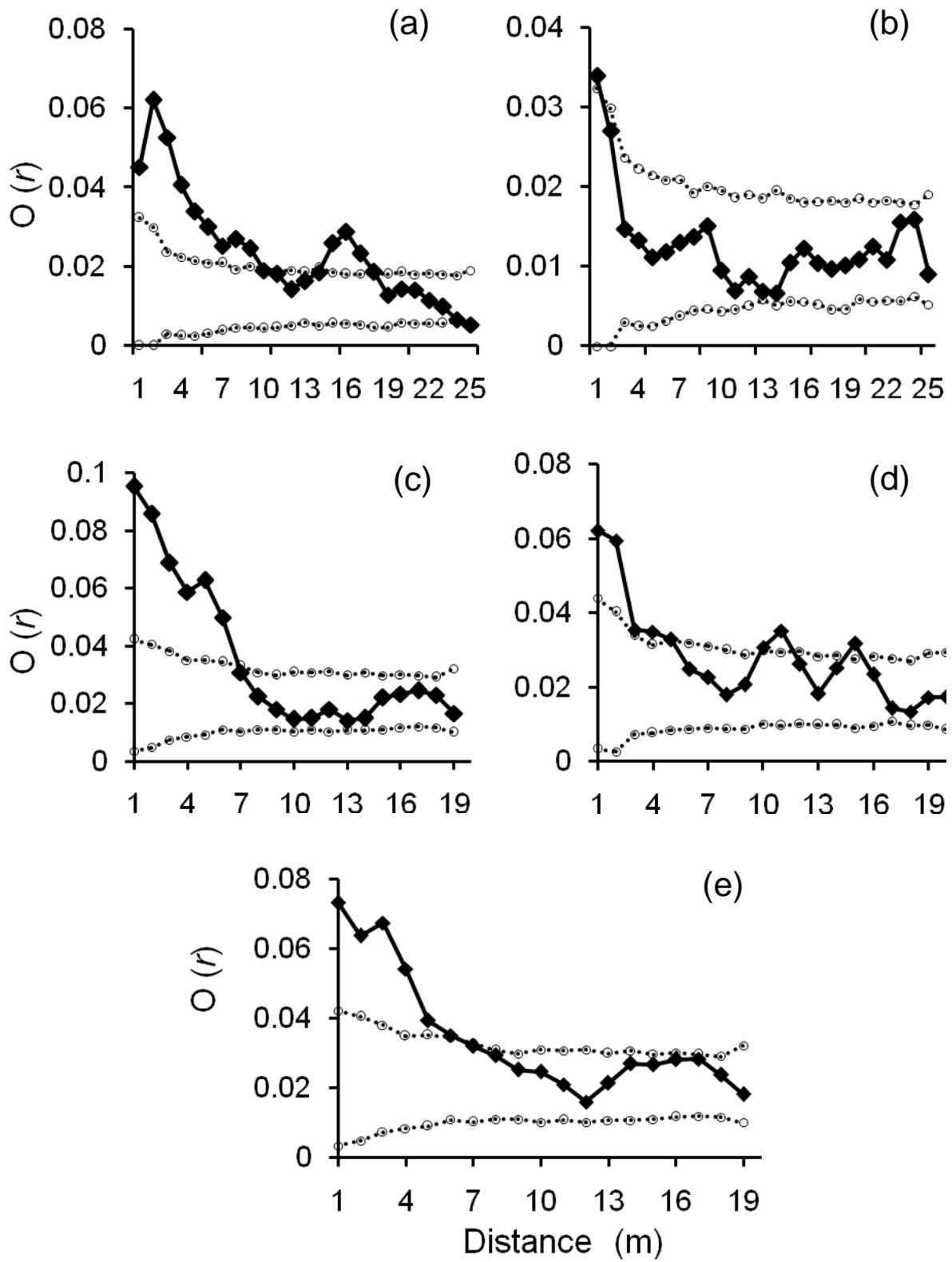


Fig. 2.

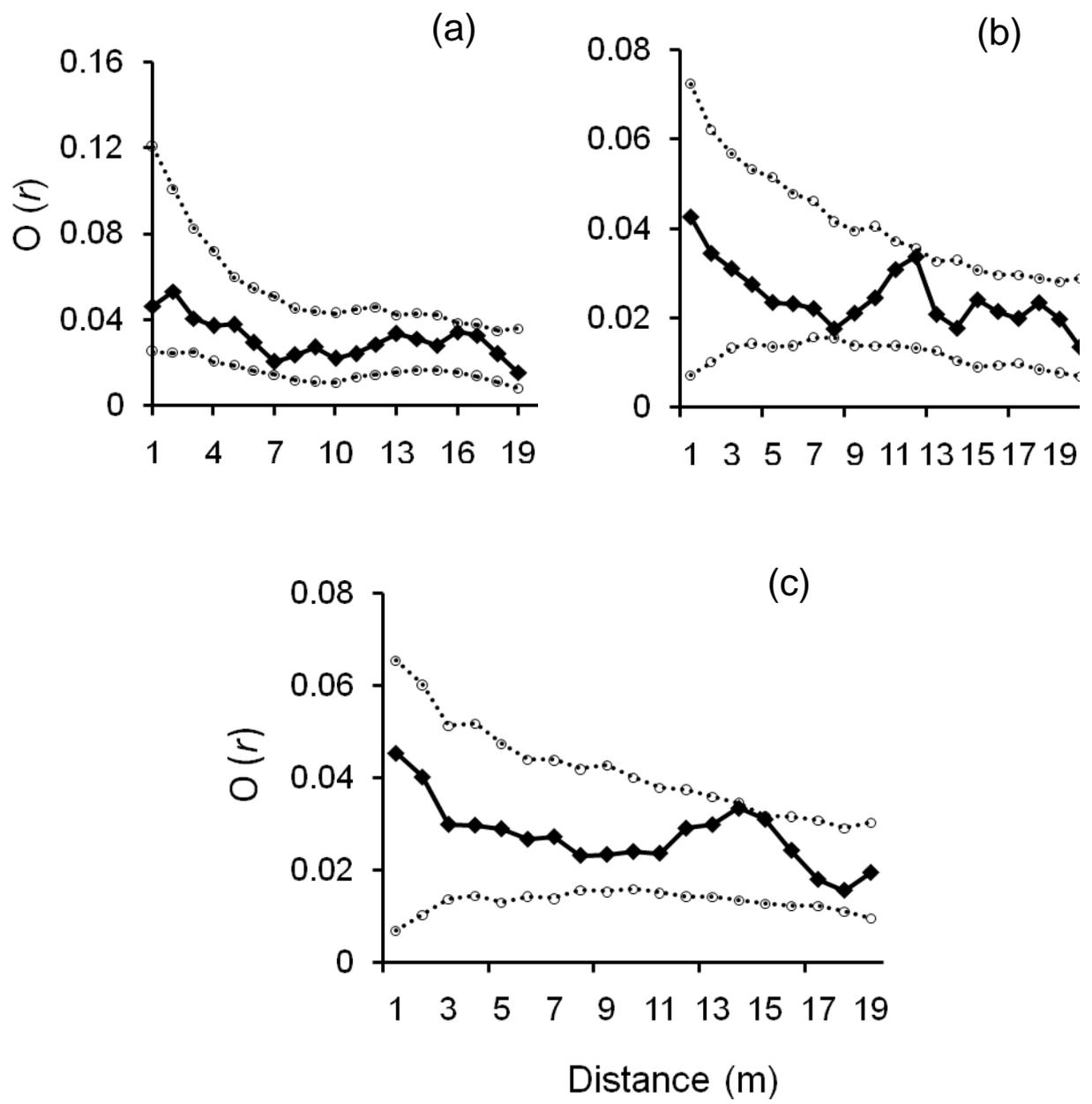


Fig. 3.

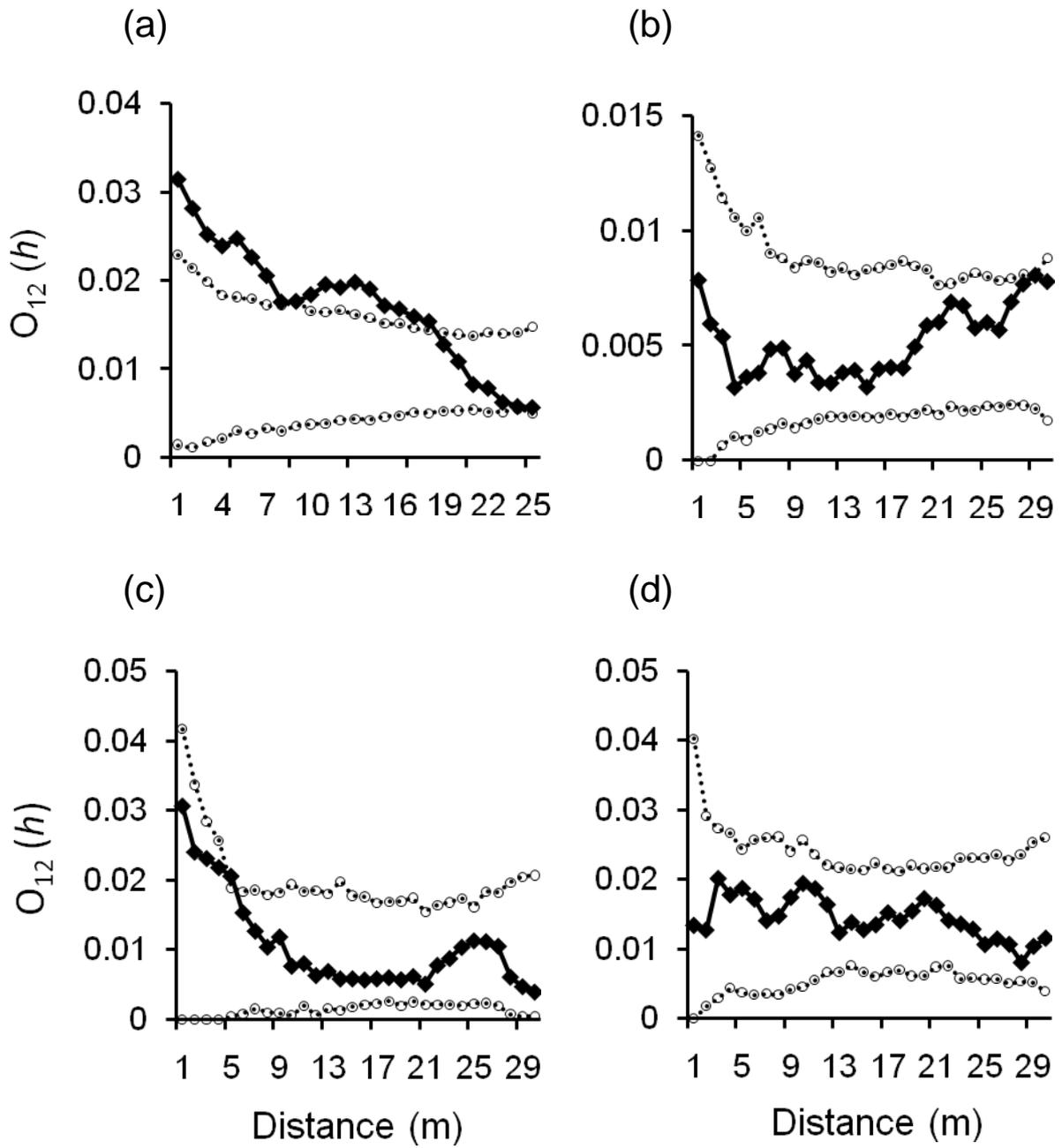


Fig. 4.

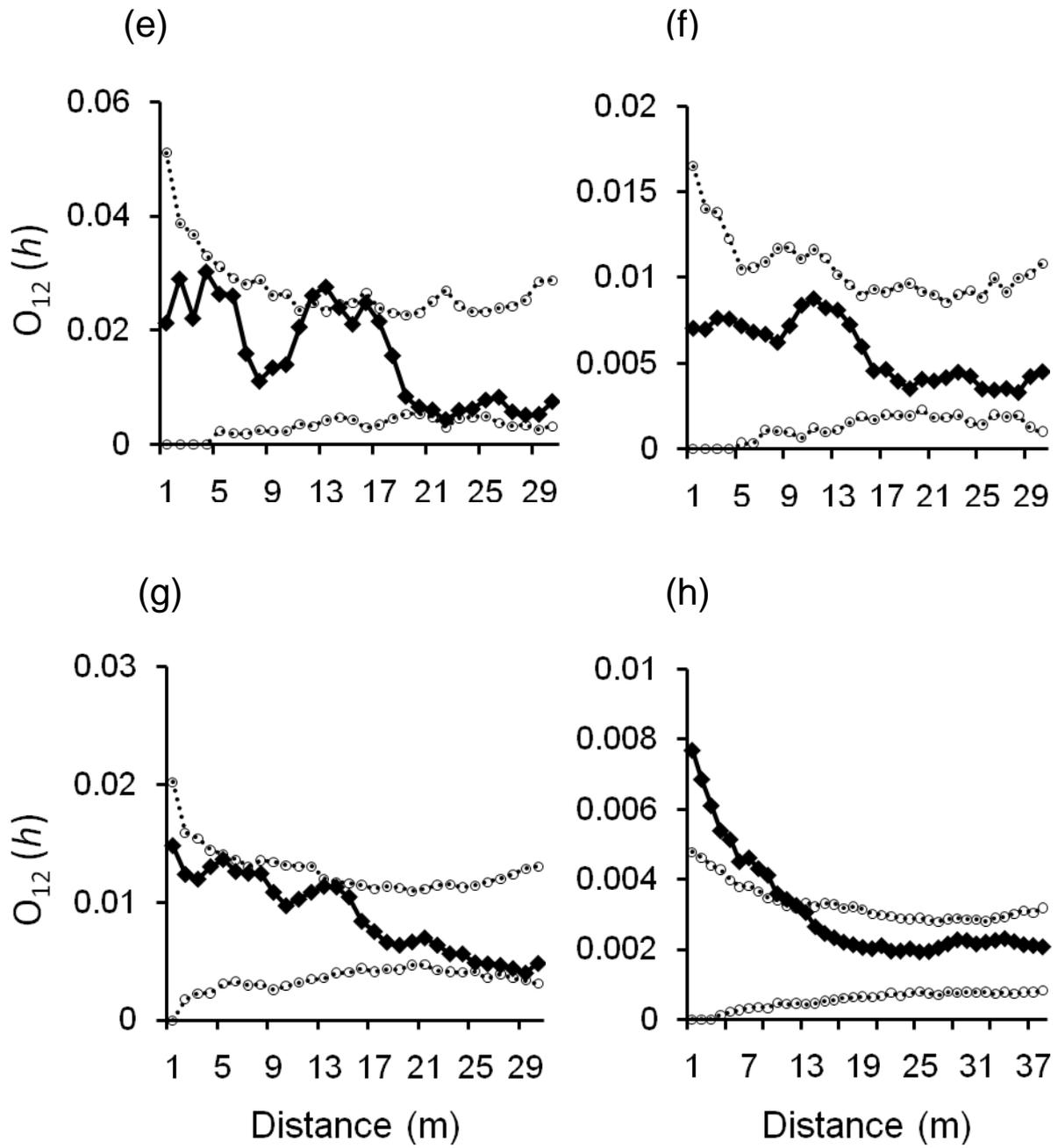


Fig. 4.

## Chapter 4

### Conclusions and future research

#### Conclusions

The dynamic nature of savannas is determined by the balance between grasses and woody plants (Walter 1939; Skarpe 1991; Scholes and Archer 1997; Higgins, Bond & Trollope 2000).

Interactions between the woody components are especially important in structuring the spatial heterogeneity of the savanna landscape, with competition for resources being one of the major processes explaining the local abundance of plant species (e.g. Grime 1979; Tilman 1982).

According to classic Lotka-Volterra models of competition, in order for the stable coexistence of two contrasting life forms, competition within a life form should be greater than competition between life-forms (Chesson 2000). Hence, intraspecific competition between savanna trees should be an important factor in savanna dynamics. However, most empirical studies have focused primarily on tree-grass competition (Skarpe 1991; Higgins, Bond & Trollope 2000; Jeltsch, Weber & Grimm 2000; Sankaran, Ratnam & Hanan 2004; Kraaij & Ward 2006), leaving several unanswered questions pertaining to tree-tree interactions.

One of the main points of contention regarding competition between plants is whether competition is present along productivity gradients (Grime 1979; Tilman 1982; Grace 1995; Craine 2005). In savannas particularly, the importance of competition in highly productive humid areas has been questioned. A meta-analysis of African savanna field sites showed a strong positive relationship between mean annual rainfall (MAR) and woody plant cover (Sankaran *et al.*, 2005), below 650 mm MAR. However, above this threshold, savannas are unstable and disturbances such as fire or herbivory, and possibly competition are necessary to prevent bush encroachment or canopy closure (Sankaran *et al.* 2005).

In this study we examined the effects of neighbourhood competition on humid and mesic savanna tree seedlings. Competition between plants may result in decreased growth, performance or in more severe instances, mortality (Suding, Goldberg & Hartman 2003). We measured the effects of neighbour density on the relative growth rate and survival of tree seedlings. We found that neighbour density negatively affected the initial survival of tree seedlings, with a stronger negative effect in mesic species. However, despite mesic plants experiencing lower survival under high neighbour competition, once mesic plants were established they were able to maintain their relative growth rates. Conversely, while humid species experienced low mortality, the relative growth rates significantly decreased as the density of neighbours increased. This suggests that competition may be a strong factor affecting the recruitment of tree seedlings in mesic areas, while established trees are relatively well-adapted to coping with resource-limitation and competition. However, in humid savannas, competition between tree seedlings did not strongly affect the recruitment of seedlings, but the subsequent growth is greatly reduced.

We also determined the competitive effect and response of humid and mesic savanna tree species, and linked these to plant functional traits to compile a competitive hierarchy for each group. Competitive effect can be described as the ability of a plant to constrain the growth and performance of neighbours, while competitive response is the ability of a plant to tolerate competition from neighbouring plants (Goldberg & Landa 1991; Keddy *et al.* 2002). We found that competitive effect and response hierarchies were not concordant, meaning that good effect competitors were not necessarily good response competitors. Competitive effect and response hierarchies, as well as the linkage with plant functional traits can be useful predictive tools when assessing possible encroaching species (Cornelissen *et al.* 2003), as rankings in hierarchies generally correlate with abundance in the field (Miller & Werner 1987). Hence, one would expect that a good effect and response competitor would have the competitive ability to displace neighbours.

In addition to the experiment with savanna tree seedlings, we conducted a field study investigating the patterns of plant competition in natural stands of the savanna tree, *Acacia karroo*, in humid savannas around KwaZulu-Natal. While greenhouse-based studies are often necessary to manipulate certain variables while excluding other confounding factors, field studies of plants under natural conditions can give insight into long-term processes (Cousens 2000). We surveyed *A. karroo* trees from three humid savanna sites, and detected the presence of competition using spatial statistics and conventional nearest neighbour analysis. We found that juvenile trees were more clustered than expected by chance, as one may expect due to seed dispersal, facilitation or vegetative growth. According to the honeycomb rippling model (Ward 2005; Wiegand *et al.* 2008), trees become more evenly spaced with increasing size, as weaker trees that are too close to others are eliminated through density-dependant competition. However, we found no evidence in support of the honeycomb rippling model. Rather, we detected subtle competitive interactions which resulted in reduced growth (expressed as smaller canopy diameter), rather than mortality.

Overall, we found that at the seedling stage, both humid and mesic savannas are negatively affected by neighbourhood competition. For mesic species, high neighbour densities greatly reduce the survival of seedlings, while for humid species mortality is rare but growth rates decline. This result is reinforced by the results of our field study. In humid savannas, *A. karroo* trees also showed rare mortality and reduced growth. Hence, we conclude that while competition is more important for mesic savannas as recruitment is strongly affected, competitive interactions are also present between humid savanna species, albeit relatively weak and resulting in decreased growth, rather than mortality. Our results also emphasize the importance of studying multiple stages when studying competition (Getzin *et al.* 2006), as well as taking multiple approaches to studying the role of competition in communities (Meyer *et al.* 2008). We showed how spatial point pattern analyses detect processes determining the spatial distribution of woody plants, and how these results can be further understood by means of conventional field methods, such as nearest neighbour analysis.

## **Future research**

Further studies should focus on examining the effects of neighbour density on seedling performance across a resource gradient. This will indicate if there is a threshold of nutrient availability, above which the competitive effects of neighbour plants are insignificant. In addition, the effects of competition along resource gradients may shed light on the classic Grime and Tilman debate, as to whether competition is prevalent under conditions of high and low productivity. Also in an attempt to resolve the Grime and Tilman debate, future studies should aim to differentiate between the importance and the intensity of competition (Grace 1995; Goldberg & Novoplansky 1997; Craine 2005). Here, we measured competitive effect (a measure of the importance of competition), and competitive response (a measure of the intensity of competition) (Carlyle, Fraser & Turkington 2010). I strongly recommend the measurement of both competitive effect and response when quantifying the competitive ability of a species, as do Goldberg & Landa (1991). Comparisons of both aspects of competitive ability among species are critical for connecting morphological and physiological traits to ability to succeed in a competitive environment (Goldberg & Fleetwood 1987). Competitive hierarchies and linkages to plant functional traits should also be a research focus. With increasing global climate change, more research is needed on the interactions between and responses of woody plants (Bond 2008), in order to predict biome changes in the future. Including other interaction terms in greenhouse-based studies of competition, such as fire or herbivory may also contribute to our understanding of savanna dynamics on a broader scale.

In terms of field studies of competition, I advocate the use of both experimental and inferential methods in investigations of vegetation structure and in further evaluations of the encroachment potential of woody savanna plants. This is especially valuable when the effects of competition are too subtle to detect by spatial patterns alone (Getzin et al. 2006). Further studies may incorporate neighbour removal experiments as well, which show the direct benefits of the removal of neighbourhood competition on plant performance (Kambatuku, Cramer & Ward 2011;

Schleicher, Wiegand & Ward 2011). I also recommend that future studies of field competition are conducted at multiple sites of humid, mesic and arid savannas, so that any marked differences in the spatial patterns can be detected.

## References

- Bond, W.J. (2008) What limits trees in C<sub>4</sub> grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*, **39**, 641-659.
- Carlyle, C.N., Fraser, L.H. & Turkington, R. (2010) Using three pairs of competitive indices to test for changes in plant competition under different resource and disturbance levels. *Journal of Vegetation Science*, **21**, 1025-1034.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343-366.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G. & Poorter, H. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.
- Cousens, R. (2000) Greenhouse studies of interactions between plants: the flaws are in interpretation rather than design. *Journal of Ecology*, **88**, 352-353.
- Craine, J.M. (2005) Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology*, **93**, 1041-1052.
- Getzin, S., Dean, C., He, F., A. Trofymow, J., Wiegand, K. & Wiegand, T. (2006) Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography*, **29**, 671-682.
- Goldberg, D.E. & Fleetwood, L. (1987) Competitive effect and response in four annual plants. *Journal of Ecology*, **75**, 1131-1143.

- Goldberg, D.E. & Landa, K. (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology*, **79**, 1013-1030.
- Goldberg, D.E. & Novoplansky, A. (1997) On the relative importance of competition in unproductive environments. *Journal of Ecology*, **85**, 409-418.
- Grace, J.B. (1995) On the measurement of plant competition intensity. *Ecology*, **76**, 305–308.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, Chichester, UK.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*, **88**, 213-229.
- Jeltsch, F., Weber, G.E. & Grimm, V. (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*, **150**, 161-171.
- Kambatuku, J., Cramer, M. & Ward, D. (2011) Intraspecific competition between shrubs in a semi-arid savanna. *Plant Ecology*, **212**, 701-713.
- Keddy, P., Nielsen, K., Weiher, E. & Lawson, R. (2002) Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science*, **13**, 5-16.
- Kraaij, T. & Ward, D. (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, **186**, 235-246.
- Meyer, K.M., Ward, D., Wiegand, K. & Moustakas, A. (2008) Multi-proxy evidence for competition between savanna woody species. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 63–72.
- Miller, T.E. & Werner, P.A. (1987) Competitive effects and responses between plant species in a first-year old-field community. *Ecology*, **68**, 1201-1210.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W.,

- Tews, J., Worden, J. & Zambatis, N. (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846-849.
- Sankaran, M., Ratnam, J. & Hanan, N.P. (2004) Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, **7**, 480-490.
- Schleicher, J., Wiegand, K. & Ward, D. (2011) Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. *Journal of Arid Environments*, **75**, 270-278.
- Scholes, R.J. & Archer, S.R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517-544.
- Skarpe, C. (1991) Spatial patterns and dynamics of woody vegetation in an arid savanna. *Journal of Vegetation Science*, **2**, 565-572.
- Suding, K.N., Goldberg, D.E. & Hartman, K.M. (2003) Relationships among species traits, separating levels of response and identifying linkages to abundance. *Ecology*, **84**, 1–16.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey, USA.
- Walter, H. (1939) Grasland, Savanne und Busch der arideren Teile Afrikas in ihrer ökologischen Bedingtheit. *Jahrbücher für Wissenschaftliche Botanik*, **87**, 750–860.
- Ward, D. (2005) Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science*, **22**, 101-105.
- Wiegand, K., Saltz, D., Ward, D. & Levin, S.A. (2008) The role of size inequality in self-thinning: A pattern-oriented simulation model for arid savannas. *Ecological Modelling*, **210**, 431-445.