The functional biogeography of African acacias (*Vachellia and Senegalia*) at adult and seedling life stages

by
Laura Milne
Submitted in fulfilment of the requirements for the degree
MSc Plant Science
In the Faculty of Natural & Agricultural Sciences
University of Pretoria
Pretoria
December 2022

Supervisor: Prof. Michelle Greve
Co-supervisor: Dr Kenneth Oberlander

UNIVERSITEIT VAN PRETORIA
UNIVERSITY OF PRETORIA
YUNIBESITHI YA PRETORIA

The financial assistance of the National Research Foundation (NRF) towards this research is hereby acknowledged. Opinions expressed and conclusions arrived at, are those of the author and are not necessarily to be attributed to the NRF.

DOI: 10.25403/UPresearchdata.21640706

Summary

Savannas constitute the largest biome on the African continent. Savanna systems are characterised by the coexistence of C4 grasses in the understorey and trees or shrubs in the overstorey. This balance is maintained by gradients of rainfall, fire and herbivory, which influence woody cover by limiting tree recruitment and persistence. Therefore, in order to persist in savannas, trees must possess adaptations to withstand these limiting factors. The aim of this thesis was to investigate the trait biogeography of African savanna trees of the Mimosoid clade, which is one of three taxa dominating the woody component of African savannas. More specifically, I assessed whether trait trade-offs exist, if fire, herbivory and precipitation drive species trait variation, and whether trait syndromes associated with fire, herbivory and precipitation exist, for a) southern African mimosoid seedlings and for b) African acacias (*Vachellia* and *Senegalia*). To measure seedling traits, twelve mimosoid species were grown in an experimental setup and several above- and belowground traits were recorded at an age of 60 days. To measure adult traits, a trait database was compiled using species descriptions of acacias from literature. Estimates of water stress, fire regime and browser biomass experienced across the distribution range of each species were extracted from macroecological maps. Linear models detected trade-offs between traits of adult *Senegalia* species only and revealed trait responses to aridity, fire and browser predictors for both seedlings and adults. Hierarchical clustering, t-tests and an NMDS ordination analysis were used to show drought severity was the only predictor that differed between the two trait clusters and formed a syndrome at the seedling stage. Adult syndromes were identified using hierarchical clustering, principal component analysis and canonical discriminant analysis; both *Vachellia* and *Senegalia* had four species clusters linked to different combinations of aridity, fire and browser gradients. The provenance of savanna species influenced the traits of woody species at both the seedling and adult stages. At the seedling stage, traits reflected strategies to secure a water supply and develop large resilient seedlings to avoid desiccation for species from arid areas. Certain adaptations seem to remain from seedling to adult stages, such as reduced leaf area in arid-adapted species or shorter architectures in species from highly browsed areas. In contrast, some strategies show the opposite trend in seedlings versus adults. Recovery strategies were prioritised in seedling species that originated from areas subjected to intense fire or browsing. In contrast, resistance strategies were prioritised in the adult stage and some strategies indicate a broad adaptation to more than one savanna driver. These findings have important ecological implications as they indicate how traits at both the seedling and the adult stage may offer resistance or tolerance to environmental pressures that would control woody densification and bush encroachment.

Table of Contents

Summary 1
Acknowledgements 3
Declaration of originality 4
Chapter One 5
General introduction 5
Chapter Two 12
Syndromes and symptoms: Traits of savanna seedlings linked to a gradient of aridity, fire and herbivory in southern African savannas 12
Introduction 12
Methods 16
Results 25
Discussion 31
Conclusion 34
Chapter three 35
Characterising acacia syndromes – how fire, herbivory and rainfall affect the functional traits of a flagship woody taxon in African savannas 35
Introduction 35
Methods 39
Results 45
Discussion 58
Conclusion 61
Chapter four 63
General conclusion 63
Chapter five 67
References 67
Chapter six 88
Appendix 88
Appendix Methods A. 88
Appendix Results A 100
Appendix Methods B 105
Appendix Results B 109

Acknowledgements

First and foremost, I would like to acknowledge my Father for helping me overcome many obstacles throughout the duration of this thesis and for making this possible. I also owe a debt of gratitude to my friends and family for providing endless support. I cannot express how much I valued your help through some very trying circumstances. This thesis would not have been completed without you.

I am truly grateful for the patience, understanding and guidance of my supervisor, Prof Michelle Greve; co-supervisor, Dr Kenneth Oberlander; and Dr Monique Botha. They went above and beyond the prescribed roles of supervision. Thank you for your contributions to the thesis and for the support provided during this time.

I would also like to thank the NRF and SASSCAL for funding the research experiment and providing a study bursary. Thank you for the grant-holder nomination Michelle and Prof. Sally Archibald.

Lastly, I would like to thank Buffelskloof Nature Reserve for their patience whilst finishing my thesis and for providing access to their herbarium library. Jennie Pretorius was an excellent editor and participant during brain-storming sessions.

UNIVERSITY OF PRETORIA

DECLARATION OF ORIGINALITY

Full names of student: Laura Lee Milne

Student number: 16078030

Declaration

1. I understand what plagiarism is and am aware of the University's policy in this regard.

2. I declare that this thesis is my own original work. Where other people's work has been used (either from a printed source, Internet or any other source), this has been properly acknowledged and referenced in accordance with departmental requirements.

3. I have not used work previously produced by another student or any other person to hand in as my own.

4. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.

SIGNATURE OF STUDENT:

Chapter 1

General introduction

What is a savanna at a global scale?

Savannas are widespread and contribute approximately 20% of the terrestrial biosphere globally (Solbrig 1991, Grace et al. 2006, Archibald et al. 2020). Originally, savannas were described as any habitat containing a herbaceous understorey with scattered woody species of variable height and density, where growth patterns were driven by alternating wet and dry seasons (Bourlière and Hadley 1983, Furley 2016). White (1983) based system classifications on the physiognomy of the vegetation, for example, 'wooded grassland' or 'bushland'. More recent descriptions specify that the understorey must contain C4 grasses and the overstorey has a discontinuous layer of woody species (Sankaran et al. 2004, Lehmann et al. 2011, Archibald et al. 2020). Maintaining the balance between these two growth forms is vital to sustaining savannas (Coetsee et al. 2010, Higgins et al. 2015). Grasses compete with woody plants for resources, provide flammable fuels and support greater herbivore density (Bond 2008) reducing juvenile growth rates and recruitment to the adult stage (Higgins et al. 2000).

Climatic drivers of global savanna distribution

Rainfall, fire and herbivory interact to maintain savannas and other grassy systems (Lehmann et al. 2011, Archibald and Hempson 2016, Hempson et al. 2020, Hamilton et al. 2022). Lehmann et al. (2011) identified water availability and rain seasonality as the main drivers of savanna distributions. Savannas show highly seasonal rainfall with wet summers and dry winters (Nix 1983), where the dry season can last for three to nine months (Solbrig et al. 1996). Rain seasonality and drought severity are important drivers of savanna stability (Strickland et al. 2016) because long dry periods diminish soil water (Bucci et al. 2005) and reduce nutrient availability for plant root systems (Barber 1962). Periodic dry seasons slow the rates of woody canopy closure (Sarmiento 1984) and cure fuel matter to facilitate the occurrence of frequent fires (Archibald et al. 2009, Bradstock 2010, Archibald et al. 2013). At high rainfall, grass growth is promoted and reduces the water accessible to trees resulting in the exertion of a higher competitive pressure on woody juveniles (February et al. 2013). During high rainfall years, increased grass biomass not only slows woody growth rates through competition (February et al. 2013), it also increases fire intensity which causes a decline in woody cover (Higgins et al. 2000).

Disturbance as drives of global savanna distribution

Disturbances, specifically fire and herbivory are also important drivers of savanna systems (Bond 2005). Fire occurrences have strong ties to savanna distributions (Lehmann et al. 2011). The effects of fire on vegetation depend on the fire size, intensity, season length, return interval and the type of combustion (Martin and Sapsis 1992, Archibald et al. 2013). Although fire and herbivory are both considered to be disturbances that shape the vertical structure of savannas (Higgins et al. 2007, Midgley et al. 2011, Levick et al. 2012), they differ in consumption patterns. Fire is a non-selective consumer of living or dead plant material, and low-quality forage burns easily (Bond and Keeley 2005). In contrast, herbivores have various dietary adaptations, body size and gut types that determine which plant matter will be consumed (Hempson et al. 2015, Wigley et al. 2020). These two disturbances also elicit different responses such as increased thorn production and thorn length after herbivory but reduced thorn investment after burning (Hean and Ward 2012).

The definition of African savannas

Savannas form the most widespread biome across Africa (Rutherford et al. 2006), occupying as much as 50% of the African continent's terrestrial biosphere (Scholes and Archer 1997). Huntley (1982) categorised savannas into arid savannas and moist (mesic). Arid savannas are classified as savannas that received <650mm of precipitation annually. In these systems, rainfall limitation constrains woody canopy cover (Sankaran et al. 2005). It has been suggested that arid savannas are associated with eutrophic soils, because low rainfall limits the leaching of soil nutrients, and that they support mostly fine-leaved savannas (Huntley 1982) that consist of fine-grained sediments and younger surfaces (Scholes and Scholes 1997). Limited water availability lowers productivity levels resulting in lower accumulation of grassy fuels for fires compared to mesic savannas (Archibald et al. 2009, Archibald et al. 2010, Lehmann et al. 2014). Dry savannas generally burn throughout the longer dry seasons but occur far less frequently (3 or more years apart) (Scholes 1997, Wigley et al. 2020). As a result, woody species in arid savannas that survive dry periods have a greater chance of escaping the fire trap (Sankaran 2019). Eutrophic soils, which are more fertile soils (Huntley 1982), produce greater forage quality which supports a higher herbivore abundance (Hempson et al. 2015, Archibald and Hempson 2016, Hempson et al. 2020). Increased grazer density also limits the accumulation of grassy fuels for fires (Archibald and Hempson 2016). Large herbivores, and water stress, keep the canopy structure open in arid savannas (Staver et al. 2009, Stevens et al. 2016).

Mesic savannas generally occur on nutrient-poor, leached (dystrophic) soils that arise from acid crystalline rocks or old erosion surfaces (Scholes and Scholes 1997, Lehmann et al. 2011). In mesic savannas, higher rainfall (>650mm per annum) supports high productivity levels and greater fuel accumulation for more frequent fires (annually or every two years) (Bond 2008, Staver et al. 2011a, Hempson et al. 2020). In Africa, it has been proposed that mesic savannas support so-called 'broad-leaved savannas'(Huntley 1982). Hoffmann et al. (2012) propose that savannas receiving high amounts of annual rainfall, with a long wet season and sufficient nutrient availability, will support the development of a closed woody canopy that will exclude the grass in the understorey and thereby eliminate fuels for surface fires. In addition, nutrient-poor soils result in the production of large quantities of low-quality forage which is consumed by ruminants (Illius and Gordon 1992) and large-bodied bulk feeders (Hempson et al. 2015). While it has long been presumed that the distribution of fine- and broad-leaved savannas is dependent on soil nutrient status, Wigley et al. (2018) did not find clear patterns of broad-leaved dominance on nutrient-poor soils and fine-leaved dominance on nutrient-rich soils.

Vegetation composition

African savannas are dominated by Mimosoideae, Combretaceae and Caesalpinioideae (Lehmann et al. 2014). Mimosoideae is a monophyletic group that diverged from within Caesalpinioideae (Elias 1981, Clarke et al. 2000, Bouchenak-Khelladi et al. 2010). Scholes et al. (2002) found that African acacias (*Vachellia* and *Senegalia*, belonging to the Mimosoideae subfamily) dominated the woody component of drier ('fine-leaved') savannas, whilst Combretaceae became more dominant at intermediate rain and Caesalpinioideae became dominant in moist ('broad-leaved') savannas, although acacias still occur in these systems (Timberlake 1980). Mimosoideae, the focus of this thesis, was revised after *Acacia sensu lato* (*Acacia s.l.*) was retypified using the Australian type *Acacia sensu stricto* (*Acacia s.s.*) based on molecular phylogenetic analysis (Luckow et al. 2003, Bouchenak-Khelladi et al. 2010). Five genera are now recognised within Mimosoideae, including *Acacia s.s* (formerly *Acacia* subgenus *Phyllodineae*), *Acaciella* (formerly *Acacia* subgenus *Aculeifeiferum* section *Filicinae*), *Mariosousa* (species belonging to the *Acacia coulteri* group, *Vachellia* (formerly *Acacia* subgenus *Acacia*) and *Senegalia* (*Acacia* subgenus *Aculeiferum* section *Aculeiferum*) (Murphy 2008, Thiele et al. 2011, Kyalangalilwa et al. 2013). The phylogenetic working group has since recircumscribed the Caesalpinioideae subfamily to include Mimosoideae as the Mimosoid clade (Group 2017). *Vachellia* and *Senegalia* are indigenous to Africa and contain approximately 69 and 73 species respectively (Lewis 2005).

Importance of acacias

African acacias (i.e. *Senegalia* and *Vachellia*) are one of the most widespread taxonomic groups in Africa (Dharani 2006, Bouchenak-Khelladi et al. 2010), and are important ecological indicators of various environmental conditions, including bush encroachment. Shifts in environmental regimes are causal agents of bush encroachment (O'Connor et al. 2014). The adaptive responses of woody species to different environmental regimes, and how traits drive these responses, will improve the understanding of the encroachment process. For example, in otherwise nutrient-poor savannas, the presence of *Vachellia tortilis* can suggest human or livestock disturbance may have occurred; *Vachellia erioloba* is indicative of deep sandy soils, and *Vachellia hebeclada* is an indicator of calcium-rich sands (Timberlake 1980). Acacias also provide ecosystem services. Some acacias retain green leaves during the dry season or produce new leaves towards the end of the dry season (Timberlake 1980). These leaves, along with fruit pods, provide fodder to support indigenous browsers or cattle in African communities (Timberlake 1980, Hassan and Styles 1990, Venter and Venter 1996). Acacias also provide a source of charcoal, firewood and construction materials (Hassan and Styles 1990). Therefore, African acacias and their distributions have important ecological and economic implications.

Linking traits to savannas

Savanna species are expected to show trait investment strategies to survive savanna drivers because biome transitions are determined by the different responses of grasses and woody species to environmental factors (Lehmann et al. 2011, Ratnam et al. 2011). Environmental conditions change throughout the life of a tree. Tree growth patterns, physiological shifts from juveniles to reproductive and mature stages, and plastic or predetermined responses are expressed accordingly. For example, the recruitment of seedlings to the adult stage in more mesic savannas is most likely to occur in drought years when grass competition is low and less grassy fuel accumulates (February et al. 2013). Seedling establishment is primarily limited by water availability whilst the transition from saplings to adults is constrained by frequent or intense fires (Higgins et al. 2000, O'Connor et al. 2014). Adult savanna trees rarely die as a result of drought or disturbances (Hoffmann et al. 2009, Zeppel et al. 2015); however, they can suffer tissue damage and lowered reproductive output (Lens et al. 2013, Hempson et al. 2019). Seedlings are therefore expected to show adaptations to maximise resource accumulation linked to recovery whilst adult traits describe various resistance syndromes.

The dominance of acacias in arid savannas may be attributed to lower specific leaf area and the presence of compound leaves which facilitate desiccation avoidance (Poorter and Markesteijn 2008). In addition, woody plants in mesic savannas can absorb nitrogen despite low soil concentrations (Song et al. 2020) because rain mineralises nitrogen thereby increasing nitrogen availability to plants (Scholes and Whittaker 1993). In contrast, nitrogen-fixing species (including acacias) are more abundant in arid systems (Pellegrini et al. 2015, Pellegrini et al. 2016), because plants are not dependent on rain for nitrogen mineralisation and because nitrogen-fixers tend to use water more efficiently (Song et al. 2015). Nitrogen-fixing may also contribute to greater belowground biomass (Varma et al. 2018); increased nodule investment improves plant nitrogen-fixation facilitating seedling growth (Mengel 1994, Voisin et al. 2003, Voisin et al. 2010). Nitrogen-fixing plants are thus increasingly abundant in arid areas (Pellegrini et al. 2016, Gei et al. 2018).

Another example is the investment of vegetation from mesic savannas in chemical defences against herbivores whereas the vegetation from arid savannas invest more in structural defences at the landscape scale (Scholes et al. 2002, Venter et al. 2003, Scholes and Walker 2004, Wigley et al. 2018). However, no evidence has been found to date to suggest species invest exclusively in chemical or structural defences (Moles et al. 2013, Wigley et al. 2018). Increased spinescence has been observed as an immediate but temporary response of trees to browsing (Within three years spines for the current growth season resembled the season's spine length after ten years of herbivore exposure) (Wigley et al. 2022).

Traits and survival strategies

Wigley et al. (2020) proposed a framework where species in disturbance-prone systems invest in four broad strategies for survival. These are to escape, resist, tolerate or promote the effects of the disturbance. Our research focuses on the first three and also applies this framework to both aridity- and disturbance-driven strategies.

1. Escape strategies

The first general strategy is to escape the effects of savanna drivers. For example, arid-adapted species invest in longer taproots to facilitate water absorption from deeper soil layers (Anderegg 2012, Choat et al. 2018, Holdo et al. 2018), thereby securing a stable water supply in unpredictable and water-limited environments (Rossatto et al. 2012, February et al. 2020) because plants with shallow rooting depths have higher drought-induced mortality rates (Johnson et al. 2018). Another example is an 'escape height'. Rapid height gain is prioritised to position the canopy above the consumptive zone created by fires resulting in a 'lanky' architecture (Dantas and Pausas 2013, Hempson et al. 2020).

2. Resistance strategies

The second strategy is to resist the effects of savanna drivers by reducing the damage sustained to exposed plant material (Wigley et al. 2020). For example, wood density indicates resource allocation to plant hydraulic systems (Bucci et al. 2004, Hao et al. 2008, Choat et al. 2018). Narrow xylem vessels, linked to high wood density, have low hydraulic conductance and transportation rates (Hacke et al. 2001, Wright et al. 2006, Poorter and Markesteijn 2008, Lens et al. 2013). This increases cavitation resistance (Hacke et al. 2001, Lens et al. 2013, Gleason et al. 2016), but results in a slower plant growth rate (Wright et al. 2010). Wood density also shows a positive correlation with the thickness of xylem vessel walls resulting in greater stem mechanical strength, linked to reduced stem breakage which may improve seedling establishment under high browser pressure (Pratt et al. 2007, Chave et al. 2009, Lagendijk et al. 2011). Resistance to embolism and mechanical damage are positively correlated (Baas et al. 2004); narrow xylem vessels may therefore reflect an exaptation to aridity or browser damage. Conversely, low wood density supports greater productivity to facilitate recovery after a disturbance (Bellingham and Sparrow 2000, Clarke et al. 2005, Clarke and Knox 2009, Lagendijk et al. 2011, Clarke et al. 2013). Stem diameter and bark thickness indicate investment in the insulation of internal stem tissues from external damage (Balfour and Midgley 2006, Brando et al. 2012, Pérez-Harguindeguy et al. 2013). Stem insulation is an adaptation to fire as it reduces heat transfer from fires that would otherwise cause loss of hydraulic conductivity and stem death (Midgley et al. 2011, Lawes et al. 2013, Schafer et al. 2015). However, allocation to bark production reduces resource investment to embolism resistance (Rueda et al. 2016, Karavani et al. 2018, Resco de Dios et al. 2018). Water-limitation is therefore expected to correlate with investment in robust hydraulic structures whereas insulation of stem tissues will be prioritised in response to fire (Hengst and Dawson 1994, Hoffmann and Solbrig 2003, Hoffmann et al. 2003, Balfour and Midgley 2006). However, inner bark may provide nutrient reserves in harsh conditions whereas outer bark is primarily associated with stem protection (Rosell et al. 2014, Rosell and Olson 2014). Strategies linked to greater inner bark storage may thereby facilitate desiccation avoidance in arid systems. Browsing is expected to exert little pressure on bark thickness but continual biomass removal results in lower xylem vessel density and thicker stems (Pittermann et al. 2014).

3. Recovery (tolerance) strategies

The third strategy is to replace the lost plant material. Resprouting is a good example; it is a key strategy for plant survival in savanna systems. Frequently burnt trees can develop a thick root that functions as a starch storage organ (Boonman et al. 2020). Starch reserves support new stem production after stem death (Higgins et al. 2000, Bond and Midgley 2001, Hoffmann and Solbrig 2003). Although browsing occurs towards the drier end of the mesic savanna rainfall spectrum, the main limiting effect is biomass consumption. Woody plants, therefore, invest in recovery strategies such as belowground biomass reserves (Archibald and Hempson 2016).

Trade-offs between traits and survival strategies

Adaptations within each of the three mentioned strategies often come at a cost to the plant. Trade-offs arise when the prioritised investment in one trait or survival strategy reduces the development of another trait or strategy (Brouwer 1963). For example, savanna woody species characteristically invest in higher root biomass, at a cost to shoot biomass (Diémé et al. 2019). In addition, larger xylem conduits, linked to lower wood density, increase water transportation for optimal photosynthetic rates (Anfodillo et al. 2013, Rosell et al. 2017, Olson et al. 2018). Therefore, a positive relationship between xylem conduit diameter and stem length was expected. In contrast, high wood density (linked to narrow xylem vessels) facilitates maintenance of hydraulic function under stress such as limited water availability (Hacke et al. 2001, Martínez-Cabrera et al. 2009, Lens et al. 2013), but this is also associated with reduced height gain, increasing the vulnerability to other pressures such as herbivory.

Aims and objectives

Traits are defined as any heritable characteristic (including morphological or physiological) which can be measured at the scale of an individual (Garnier et al. 2015). Plant functional traits reflect ecological strategies in response to environmental factors and contribute to ecosystem properties (Pérez-Harguindeguy et al. 2013). Community ecology and functional ecology aims to understand how functional traits determine species distributions, and the co-occurrence of species (Whittaker 1975, Westoby and Wright 2006). Understanding ecological patterns improve the prediction of species responses to changing environmental conditions (Corrêa Scalon et al. 2020). Therefore, this thesis sets out to investigate how the traits of savanna woody seedlings and adults vary along a gradient of aridity, fire and herbivory. In Chapter 2 I assessed how seedling traits are affected by provenance. Twelve Mimosoid species were grown in a greenhouse experiment and several above- and belowground traits were recorded at the age of 60 days. Variables representing aridity, fire and browsing were extracted across the species ranges for southern Africa. Linear models were used to investigate trait trade-offs, and to assess how the savanna drivers affect individual traits. Hierarchical clustering, t-tests and an NMDS analysis was used to identify trait syndromes. In Chapter 3 I investigated traits of adult *Vachellia* and *Senegalia* species across their native ranges in Africa. Linear models were used to explore the influence of savanna drivers on individual traits and to investigate trait trade-offs. Hierarchical clustering, principal component analysis and canonical discriminant analysis was used to describe syndromes from savanna systems. Seedling and adult stages were included to compare the survival strategies for establishment. As woody species mature, their investment strategies change as they overcome different pressures.

Chapter Two

Traits and trait syndromes of savanna seedlings linked to a gradient of aridity, fire and herbivory in southern African savannas

Introduction

African savannas can broadly be divided into mesic and arid savanna. At large geographic scales, these systems are differentiated by their mean annual precipitation (MAP) (Sankaran et al. 2005). In arid savannas (MAP < 650 mm), woody cover and species composition are at least partially climate-driven (Scholes and Archer 1997, Bond et al. 2003): limited water availability reduces tree recruitment, thereby regulating maximum woody cover (Higgins et al. 2000, Sankaran et al. 2004). In contrast, mesic savannas (MAP > 650 mm) (Sankaran et al. 2005) have suitable climates for both savanna and forest; in these systems, disturbances drive savanna-forest transition shifts (Staver et al. 2011b, Dantas et al. 2016). Fires are an important disturbance in the maintenance of open canopy structures, especially in mesic savannas (Bond 2008, Lehmann et al. 2011, Ratnam et al. 2011). In arid savannas, fire can reduce canopy density, but in mesic savannas, fires (often more frequent due to higher grass biomass) (Higgins et al. 2000, Beckage et al. 2009) are essential in maintaining an open vegetation canopy and thus drive the savanna-forest transition (Bond et al. 2003, Charles-Dominique et al. 2015b). Long dry seasons in mesic savannas increase the probability of fire occurrence (Spessa et al. 2005, Archibald et al. 2010). Savanna tree cover is also limited by browsing at local and continental scales (Prins and van der Jeugd 1993, Staver et al. 2009, Staver et al. 2011b). Herbivore biomass is greatest at intermediate levels of rainfall (Hempson et al. 2015). Therefore, the environmental drivers that affect savanna structure may fundamentally differ between arid and mesic savannas.

In savannas, seedling recruitment to the sapling stage is a major bottleneck in the establishment of woody species and is thus thought to be important in driving the structure of savannas (Bond and Midgley 2001, Gignoux et al. 2009, Williams et al. 2009). Aridity and disturbances (such as fire and herbivory) are major factors limiting woody seedling recruitment in African savannas (Midgley et al. 2010, Werner and Prior 2013). As a result, savanna trees must possess a range of traits that allow recruitment under the conditions that exist in savannas (Scholes and Archer 1997, Pausas et al. 2004, Bond and Keeley 2005). The suite of traits an organism possesses can be influenced by a number of factors. According to the functional equilibrium hypothesis, plants redirect resource allocation in response to the strongest limiting factor (Brouwer 1963). Consequently, increased investment to survive one stressor may reduce the development of functional traits linked to another stressor (Bucci et al. 2004, Resco de Dios et al. 2018). However, exaptation may also arise where preadaptation to one pressure provides an advantage to another pressure (Gould and Vrba 1982, Keeley et al. 2011). Whether adaptations of savanna trees to fire, herbivory and drought are similar or trade-off against one another remains to be determined (Archibald et al. 2018).

In savannas, periods of insufficient water availability constrain seedling establishment (Ward 2005, Joubert et al. 2008); extended periods of water deficit combined with high temperatures in savannas have been linked to woody vegetation mortality caused by the high evaporative demand (Fensham et al. 2009, Fensham et al. 2019, Sankaran 2019). Droughts are defined as periods where plant water availability levels during the growth season are significantly lower than the average annual conditions due to reduced rainfall (Sankaran 2019). Droughts are an existing phenomenon in many savannas, and they are predicted to increase in occurrences and severity, especially in Africa, under several climate change models (Dai 2013, Trenberth et al. 2014). Predicted increases in drought events and duration are expected to cause compositional shifts in savannas (Case et al. 2019, Sankaran 2019); because species differ in drought tolerance and recovery abilities (Breshears et al. 2009, Fensham et al. 2015). Seedling survival is strongly constrained by adaptations to drought as a prolonged stressor (Case 2019) such as the investment in deep roots to access groundwater (Markesteijn and Poorter 2009, Diémé et al. 2019, Boonman et al. 2020).

In contrast, both fire and herbivory limit seedling recruitment by causing damage to and the loss of aboveground materials (Higgins et al. 2007, Hoffmann et al. 2009). Fires typically occur as discrete annual events in mesic savannas, or biannual fires in highly productive savannas near the equator, resulting in a fire-induced recruitment bottleneck at the sapling stage (Archibald and Bond 2003, Hempson et al. 2020). In contrast, browsing may occur at any time, and in both wet and dry seasons (Hempson et al. 2020). Fire and herbivory limit the transition of seedlings to the adult stage, thereby affecting population structure more than population size (Midgley et al. 2010).

Water stress, fire and herbivory have different impacts on seedlings. Water deficit can result in hydraulic failure caused by the formation of gas emboli in xylem vessels (Kursar et al. 2009, Choat et al. 2012). Gas emboli reduce water transportation to photosynthetic plant organs required for gas exchange, resulting in desiccation and plant mortality (McDowell et al. 2008, Kursar et al. 2009). In comparison, fire either consumes the aboveground biomass of seedlings or the associated heat causes stem death (Bond and van Wilgen 1996, Balfour and Midgley 2006). More specifically, heat from surface fires damage cambium and xylem tissues within woody stems, causing a loss of hydraulic function (Trollope 1984, Bond and van Wilgen 1996, Balfour and Midgley 2006). Frequent fires and low water availability may therefore exert similar pressure on savanna seedlings resulting in stem death. In contrast, defoliation and twig browsing reduces aboveground biomass, similar to fire, but may not cause stem death (Wigley et al. 2018). Browsing may therefore select for traits to minimise biomass loss whereas aridity and fire may select for traits to avoid stem death or linked to regeneration.

Woody plants differ in their ability to persist or recover from an environmental filter (Fensham et al. 2015, Greenwood et al. 2017, Fairman et al. 2019); these pressures select for species with similar trait responses in areas experiencing similar environmental filters (Fukami et al. 2005, Rossatto and

Franco 2017). Different survival strategies are therefore characterised by suites of co-varying traits (Agrawal and Fishbein 2006). However, trade-offs between trait investment patterns also contribute to the formation of trait groups (Resco de Dios et al. 2018, Boonman et al. 2020). “Syndromes” refer to groups of plant traits that illustrate avoidance and tolerance strategies in response to certain environmental conditions (Sankaran 2019).

A suite of unique trait combinations, called complexes or trait syndromes, are expected to arise in response to the different environmental drivers. Arid-adapted species are expected to invest in strategies to facilitate desiccation avoidance. Species are more likely to invest in larger seeds to provide nutrients for the development of a bigger and more robust seedling in response to prolonged stress (Moles and Westoby 2004, dos Santos Costa et al. 2020). Reduced specific leaf area (SLA) and leaf-shoot ratios will facilitate desiccation avoidance by lowering the rates of leaf transpiration, stomatal conductance and leaf temperature linked to plant water loss (Poorter and Markesteijn 2008, Gotsch et al. 2010). Narrow xylem vessels show decreased embolism events (linked to desiccation) but this may reduce bark thickness (Resco de Dios et al. 2018); I expect arid-adapted species to prioritise investment in wood density (reflected by narrow xylem vessels) to provide embolism resistance. However, inner bark may provide nutrient stores to benefit species in water-limited systems (Rosell et al. 2014). Arid-adapted seedlings are expected to prioritise biomass allocation to rooting depth and the depth of root expansion resulting in higher seedling root-shoot ratios (Diémé et al. 2019, Boonman et al. 2020). Root nodules, which sustain nitrogen-fixing bacteria, support increased foliar nitrogen concentrations to facilitate efficient water use in arid systems (Adams et al. 2016, Pellegrini et al. 2016). However, nodule investment requires nutrient allocation to support the nitrogen-fixing bacteria (Voisin et al. 2010); in arid conditions, seedlings are expected to invest in fewer nodules, due to the high carbon cost.

Fire-adapted species are expected to reduce heat damage (small seeds, increased relative bark thickness and thicker stems) and possess adaptations to facilitate resprouting after stem death (increased SLA, high leaf-shoot ratios, thicker roots and numerous nodules). Small seeds are more resistant to fire-related heat (Liyanage and Ooi 2018) and species are able to produce a large number of small seeds (Henery and Westoby 2001). A greater proportion of outer bark and thick stems will better protect stems from heat damage (Balfour and Midgley 2006, Schafer et al. 2015). High SLA and increased leaf-shoot ratios will provide greater photosynthetic rates to support rapid biomass accumulation in response to disturbance (Poorter et al. 2009, Diémé et al. 2019). To resprout in fire-limited systems, species are expected to invest in a high root-shoot ratio, due to greater root thickness, with a lower rooting depth and increased lateral roots close to the soil surface (Archibald and Hempson 2016, Boonman et al. 2020).

Intense herbivory will select traits that reduce seedling biomass loss (reduced SLA, lower leaf-shoot ratios and narrow xylem vessels) and facilitate recovery after frequent biomass removal (thick roots and numerous nodules). Reduced SLA and leaf-shoot ratios minimise leaf palatability and reduce biomass removal (Poorter et al. 2009) whilst dense stems reduce breakage (Chave et al. 2009). Thick roots may reflect belowground storage to facilitate resprouting after defoliation (Archibald and Hempson 2016). Increased nodule count may reflect strategies to facilitate rapid recovery after disturbance (Voisin et al. 2010).

Fires are more frequent in mesic savannas than in arid savannas (Higgins et al. 2000) and browsing is more intense in savannas with intermediate rainfall (Hempson et al. 2015). As a result, I expect unique physiognomies for arid-adapted, fire-adapted and browser-adapted savanna woody species due to different drivers of trait selection

This study aims to investigate how traits and trait syndromes vary along environmental gradients of aridity, fire and browsers.

The main objectives of this study are: to investigate potential trait interactions and trait investment trade-offs due to different survival strategies, and to identify unique trait complexes linked to aridity, fire or herbivory.

Methods

Species selection

Large swathes of African savannas are dominated in the tree layer by members of the Mimosoid clade, within the Fabaceae (Huntley 1982). Twelve species belonging to the Mimosoid clade *sensu* (Group 2017) were selected to investigate traits of legume seeds and seedlings driving species recruitment (Table 1). Species that are indigenous to southern Africa and that occur across different environmental gradients were selected.

Table 1: List of savanna woody species belonging to the Fabaceae family, Mimosoid clade, used in this experiment. The method of seed scarification selected for each species is shown. # Locality records= final number of final locality records from which the environmental data were extracted

Species	**Scarification**	**#Locality records**
Albizia forbesii Benth.	Mechanical	16
Dichrostachys cinerea (L.) Wight & Arn.	Mechanical	46
Senegalia galpinii (Burtt Davy) Seigler & Ebinger	Mechanical	22
Senegalia senegal var. rostrata (Brenan) Kyal. & Boatwr.	Boiled	28
Vachellia erioloba (E.Mey.) Seigler & Ebinger	Mechanical	40
Vachellia exuvialis (I.Verd.) Kyal. & Boatwr.	Mechanical	27
Vachellia karroo (Hayne) Banfi & Galasso	Mechanical	62
Vachellia nilotica (L.) P.J.H.Hurter & Mabb.	Mechanical	45
Vachellia rehmanniana (Schinz) Kyal. & Boatwr.	Mechanical	15
Vachellia robusta (Burch.) Kyal. & Boatwr.	Mechanical	45
Vachellia sieberiana (DC.) Kyal. & Boatwr.	Boiled	44
Vachellia swazica (Burtt Davy) Kyal. & Boatwr.	Mechanical	30

Experimental set-up

Seeds were sourced from the Silverhill Seed Company. The efficacy of different scarification techniques on the species germination was investigated using 60 seeds per species (Appendix Methods A1). Seeds were scarified using the most effective technique (Table 1 and Appendix Table A1). Two scarified seeds of the same species were planted in 3.5-litre soil bags filled with a 1:1:1 ratio of river sand, compost and topsoil to produce ten replicates per species. Soil bags were placed in one of four greenhouses situated on Innovation Africa @ UP of the University of Pretoria. Species were assigned to soil bags using a randomisation approach. Greenhouses were covered with 40% white shade cloth netting, with an average photosynthetically active radiation of 1296 µmols/m^{2}s (Appendix Table A2). Seedlings received 0.333 litres of water every Monday, Wednesday and Friday. The date of germination was recorded every second day.

Species traits

Several seed and seedling traits were measured (Table 2). Average seed mass was calculated from ten seeds per species prior to planting. Several traits representing seedling size (stem length, stem diameter and aboveground dry mass) were recorded on up to ten individuals per species at sixty days post-germination to characterise seedling growth patterns during the establishment phase (Table 2). The stem length-diameter ratio was derived to indicate prioritised height relative to stem diameter (Gignoux et al. 2016). However, stem length, stem diameter, and stem length-diameter ratio were positively correlated (Appendix Table A4); therefore, the stem length-diameter ratio was removed from subsequent analyses.

Leaf traits were measured for each species at the end of the growing season (early April 2021). One leaf was sampled from the stem midpoint of three seedlings per species. The flattened leaf was scanned (Figure 1), and the leaf area was calculated from calibrated images in ImageJ (Schneider et al. 2012). The green area of the leaf was calculated using the automated threshold routine. The same leaves were oven-dried over a minimum of three days at 40˚Celsius and their leaf mass was measured. Leaf mass and area measured were used to calculate specific leaf area (Table 2).

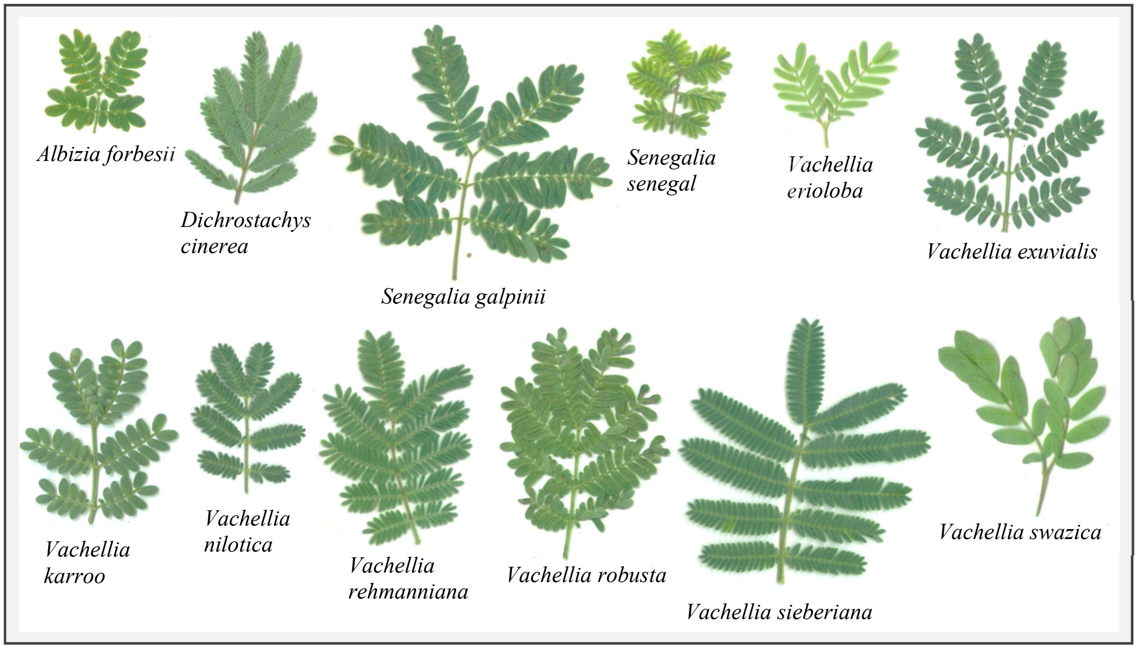


Figure 1: A representative leaf scan of each species to shows the interspecific variation in leaf characteristics at the final harvest.

Up to five seedlings per species were harvested 60 days after germination to conduct stem cross-sections. Basal stem cross-sections were performed on fresh material and stained with toluidine blue dye and photographed using a Moticam 5.0 MP camera and a Motic light microscope. Inner bark thickness, total bark thickness and stem diameter were recorded for each specimen (Figure 2, Table 2). Five xylem conduit diameters were measured per seedling to derive the average xylem conduit diameter per species. Outer bark thickness was derived using the difference between the total bark thickness and the inner bark thickness. Outer bark thickness was highly correlated with inner bark thickness (Appendix Table A4) and was thus not used in data analyses. Relative bark thickness was calculated by dividing total bark thickness by stem diameter (Table 2).

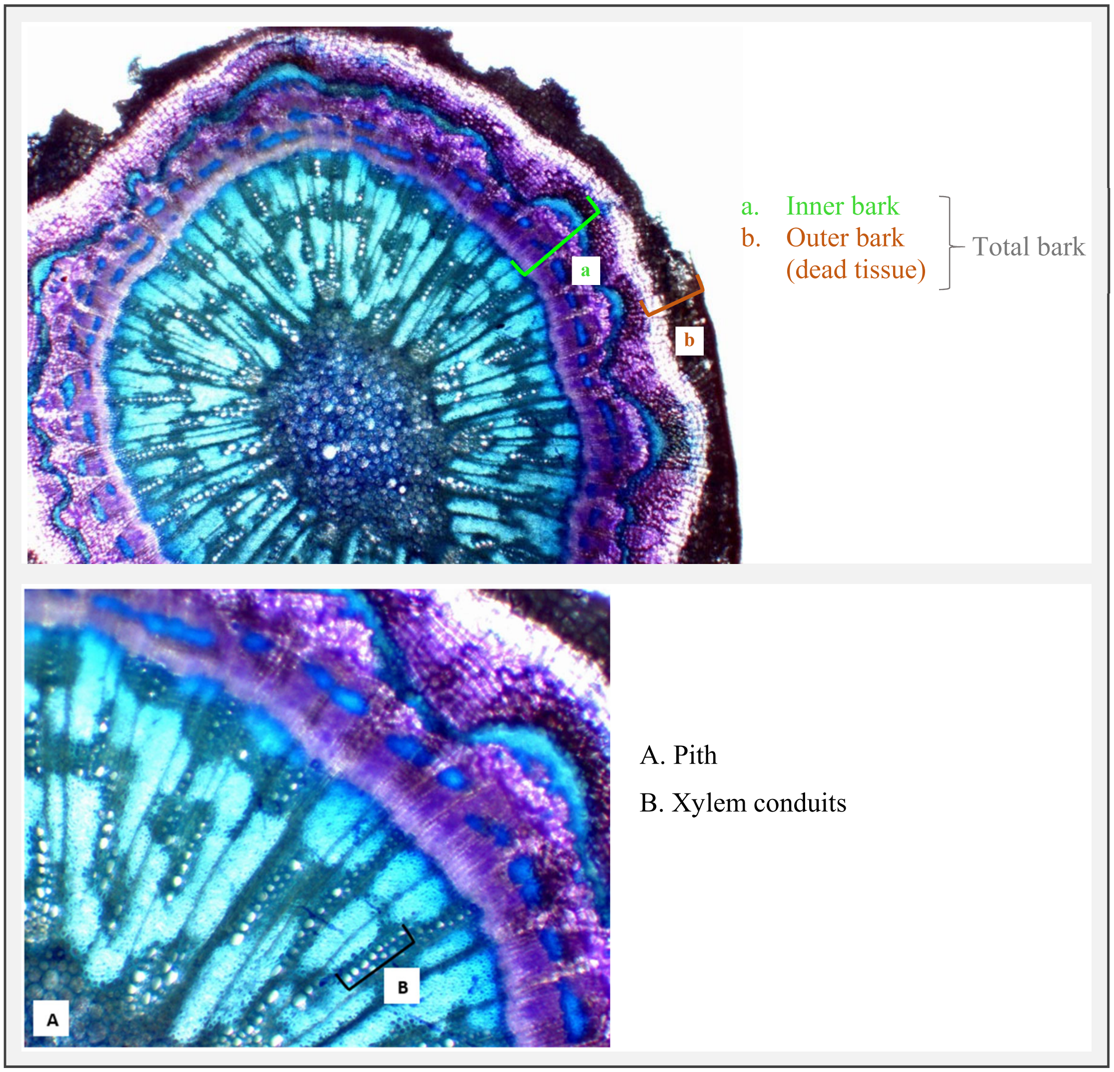


Figure 2: A microscopic image of the cross-section conducted on the basal stem region of a Vachellia erioloba seedling, captured using a microscope lens magnification setting of 4 x 0.1 (above) and 10 x 0.25 (below). The maximum diameter of five random xylem conduits were recorded and averaged per individual.

To measure belowground traits, the roots of the 60-day-old harvested seedlings were carefully exhumed by carefully rinsing the seedling roots in a bucket. The depth of the stem-root transition, the depth of the fifth lateral root, the taproot length and taproot diameter were measured for each seedling, and the root length-diameter ratio was derived. To describe nodulation, root nodules were counted. Additionally, they were separated and dried at 50 °Celsius for a minimum of 72 hours and their dry mass was recorded (Table 2).

For each of the 60-day-old harvested seedlings, seedling biomass was separated into aboveground and belowground biomass, placed in brown paper bags and oven-dried for at least 72 hours at a constant temperature of 50 °Celsius. The total seedling leaf mass, the total aboveground dry mass and the total belowground dry mass (including nodules) per seedling were weighed. All dry masses were recorded using an analytical balance (accurate to 0.01 mg). Shoot mass, seedling leaf-shoot ratio, specific leaf area and seedling aboveground-belowground biomass ratio were derived (Table 2).

Table 2: Description of seed and seedling traits used to investigate survival strategies of woody savanna species during the establishment phase, the environmental filters expected to influence each trait (💧 aridity, 🔥fire and 🦌 herbivory), and the methods used to derive the trait values. Blue environment icons indicate an expected positive relationship between the trait and the environmental filter, whereas orange indicates an expected negative relationship. References: citations of the literature where the trait was originally described and literature that formed the basis for new traits.

Trait	**Definition**	**Environment**	**Method**	**References**
Seed size	A surrogate of seed nutrient reserves.	💧 🔥	The oven-dried seed mass.	Moles (2018)
Specific leaf area (SLA)	The one-sided area of a leaf divided by the leaf mass.	💧 🔥	The area of a fresh leaf (including the rachis) divided by the leaf dry mass.	Garnier et al. (2001), Pérez-Harguindeguy et al. (2013)
Stem length (L)	A measure of plant allocation to vertical growth.	🔥	The distance along the stem from the soil surface to the apical bud.	Gignoux et al. (2016)
Stem diameter (D)	A measure of stem thickness.	🔥	The stem diameter at one cm above the soil surface.	Balfour and Midgley (2006)
Height of lowest bud	An indication of potential resprouting height.	🔥 🦌	The distance along the stem from the soil surface to the base or the lowest bud (cotyledon or leaf; no branches were observed as the lowest bud during this experiment).	
Xylem conduit diameter	Base cross-sectional conduit lumen diameter that provides a measure of embolism resistance.	💧 🦌	Using a basal stem cross-section (stained), the diameter of 5 vessels was measured using image analysis software. The five values were averaged to derive the mean conduit diameter.	Klimešová et al. (2019)
Total bark thickness (TBT)	A measure of the maximum distance from the stem surface to the vascular cambium.	*Used to derive (IBT_P) and (RBT)*	The distance from the stem surface to the vascular cambium. Obtained from the stained basal stem cross-section.	Rosell et al. (2014), Rosell (2016), Morris and Jansen (2017)
Inner bark (IBT_P)	The proportion of total bark thickness represented by the inner bark.	💧	Using the basal stem cross-section (stained), the thickness of the living bark cells as indicated by the stain (inner bark thickness) was measured. The measured inner bark thickness was divided by the total bark thickness. $IBT_P = \frac{Inner\ bark\ thickness}{Total\ bark\ thickness}$	Rosell (2016)
Relative bark thickness (RBT)	A species-specific trait linked to plant life histories and biogeography is represented by the total bark thickness (TBT) ratio to the bole diameter (BD).	🔥	The bole diameter was calculated as the sum of the stem diameter and the total bark thickness. The ratio of the total bark thickness to the bole diameter was derived. 1. $BD = stem\ diameter - 2(TBT)$ 2. $RBT = \frac{TBT}{BD}$	Midgley and Lawes (2016), Pellegrini et al. (2017), Wigley et al. (2020)

Trait	**Definition**	**Environment**	**Method**	**References**
Seedling leaf-shoot ratio (SLS)	A measure of seedling investment in rapid production versus the occupation of vertical space	💧 🔥 🦌	The ratio of the oven-dried mass of the seedling leaf matter and the seedling shoot mass.	Wigley et al. (2020)
Depth of the fifth lateral root (D5)	A description of how woody species explore vertical space	💧 🔥	Adaptation of Charles-Dominique's height of the fifth fork concept to describe the depth of the fifth lateral root; measure the distance along the taproot from the soil surface to the fifth lateral root.	Wigley et al. (2020)
Root length (RL)	A measure of the depth of the main taproot from the soil surface	💧 🔥	The extent of the gently straightened main root axis.	Harrison and LaForgia (2019)
Root diameter (RD)	A measure of the primary root thickness	💧 🔥 🦌	Measure the diameter of the primary root at 1 cm below the soil surface using callipers.	Pérez-Harguindeguy et al. (2013)
Root length-diameter ratio (RT)	A measure of the primary root taper with length as an indication of plant allocation strategies to belowground reserves (greater diameter) or increased rooting depth (greater root length)	💧 🔥	An adaptation of the stem length-diameter ratio in Gignoux et al. (2016), to describe root tapering; the relative root taper was calculated using the root length and root diameter measurements. $RT = \frac{RL}{RD}$	Gignoux et al. (2016)
Aboveground mass	A measure of the aboveground biomass accumulation	🔥 🦌	The oven-dried aboveground seedling biomass.	
Belowground mass	A measure of the belowground biomass	💧	The oven-dried belowground seedling biomass.	
Total mass	A measure of the whole plant biomass	💧 🔥	The total plant biomass (leaves, stems, roots and nodules).	Diémé et al. (2019)
Seedling root-shoot ratio (*SRS*)	A ratio of the aboveground seedling dry mass to the belowground dry mass as an estimate of seedling investment in belowground reserves	💧 🔥	The ratio of the oven-dried belowground and aboveground seedling biomass. $SRS = \frac{Belowground\ dry\ mass}{Aboveground\ dry\ mass}$	Gignoux et al. (2016), Wigley et al. (2020)
Nodule count	A measure of the total number of nodules observed on the seedling root	💧 🔥 🦌	The number of root nodules present on a seedling.	Voisin et al. (2010)
Total nodule mass	A measure of the total nodule biomass accumulation.	💧 🔥 🦌	The combined oven-dried mass of the nodules collected from the roots of a given seedling	Voisin et al. (2003)

Environmental predictors

To assess the effects of water availability, fire and herbivory on the traits of savanna woody seedlings, various environmental variables were collated from large-scale datasets to create multiple spatial layers. Several climatic variables were chosen to represent water stress. Rainfall is an important predictor of savanna structure and production (Sankaran et al. 2005). At finer scales, rainfall may influence seedling investment strategies such as increased rooting depths at low rainfall (Holdo et al. 2018); thus mean annual precipitation (MAP) was obtained from the WorldClim database at a 0.5-degree resolution (Fick and Hijmans 2017). Intermittent rainfall facilitates tree-grass coexistence in arid savanna systems (D'Onofrio et al. 2015), and regular wet and dry periods increase fire probability (Archibald et al. 2013). A rainfall seasonality index was acquired from WorldClim at a 0.5-degree resolution to describe periodic water availability within a year (Fick and Hijmans 2017). Low values suggest a more even rainfall distribution whereas greater values indicate rainfall is constrained to a single month (Markham 1970), reducing the growing season for savanna vegetation (Scholes and Archer 1997). Extended periods of water deficit increase vegetation mortality (Greenwood et al. 2017); severe droughts increase the risk of hydraulic failure leading to desiccation-induced stem death (McDowell et al. 2008, Hartmann et al. 2018). Drought proneness and severity was represented by the standardized precipitation evapotranspiration index (SPEI) (Begueria et al. 2014), obtained at 36-month intervals and 0.5-degree resolution. The SPEI is calculated using the monthly differences between precipitation and potential evapotranspiration (PET) estimates, based on the FAO-56 Penman-Monteith PET estimation method (Allen et al. 2011).

Two variables representing the fire regime were obtained from Archibald et al. (2013). First, fire intensity is defined as a measure of the radiative energy released by a flame per unit length of the fire front; fire radiative power (FRP) values capture the rate of radiant energy released by active fire points (megawatts per pixel, Kaufman et al. (1996)), providing a spatially and temporally continuous measure of fire intensity (Smith and Wooster 2005). This accounts for the effects of fire on tree size classes and top-kill avoidance strategies (Archibald et al. 2013). Second, the fire return interval represents the period available for plant growth between successive fires; short fire return intervals reflect frequent fires and have been linked to the resprouting of woody species (Archibald et al. 2013). A fire return time index (fire return interval) was obtained from the calculated coefficient of variation of the annual area burned (Archibald et al. 2013).

Mammalian browsers have been linked to the trait variation, including spinescence and architecture, of savanna trees (Archibald and Bond 2003, Staver et al. 2009, Greve et al. 2012, Staver et al. 2012, Wigley et al. 2015). Browser biomass estimates from Hempson et al. (2015) were used as a proxy for the consumptive pressure exerted on woody vegetation (Archibald and Hempson 2016).

Linking species traits and environmental factors

Locality records for each of the mimosoid species were obtained from Greve et al. (2012) and, for *Albizia forbesii* and *Dichrostachys cinerea,* from the Global Biodiversity Facility (GBIF, see Appendix Table A3 in Appendix Methods A for the database references per species). Duplicate records were removed and locality records were georeferenced using a spatial points data frame of the locality records and removing records that did not match the country provided in the description. Because seeds were sourced from South African populations, locality records from only South Africa and Swaziland were extracted. To remove sampling bias from the locality records, only one record per degree cell was randomly selected using a grid for stratified sampling provided by the '*dismo*' package (Hijmans et al. 2021) (Table 1). For each locality record, the mean annual precipitation, rainfall seasonality index, SPEI, fire intensity, fire return interval and browser biomass were extracted; the environmental data was then averaged per species. Mean annual precipitation was transformed using '$\log(max(x+1))$' (Kassambara 2020) to correct for negative skew.

Highly correlated predictor variables were identified using a Pearson's correlation analysis (Appendix Table A4). If two variables were highly correlated ($r > 0.65$), only one was retained. Fire return interval was thus excluded from subsequent analyses due to a high correlation with fire intensity (fire radiative power, FRP).

Analyses

To account for phylogenetic non-independence, the phylogenetic tree from Bouchenak-Khelladi et al. (2010), containing most of the study species, was extracted using the '*ape*' package (Paradis and Schliep 2019). *Albizia kalkora* (Roxb.) Prain. and *Dichrostachys richardiana* Baill. were used to represent *Albizia forbesii* and *Dichrostachys cinerea*¸ which were not on the extracted tree (Appendix, Figure A2). The phylogenetic tree was subsetted to the species used in this study. For each linear regression model performed for trait-trait relationships and trait-environment relationships, best subset selection was conducted based on the lowest Bayesian information criterion (BIC) scores using the '*leaps*' package (Lumley 2017). Benjamini-Hochberg corrections were performed on the regression model outputs to adjust variable p-values after accounting for multiple comparisons (Benjamini and Hochberg 1995) using the '*stats*' package (R Core Team 2021).

Trait-trait relationships

Based on observations made during the seed germination experiment (Appendix Methods A) species, such as *Vachellia erioloba*, had large seeds and produced larger seedlings for the same germination period as small-seeded species, such as *Vachellia nilotica*. To investigate the effect of seed size on seedling biomass accumulation patterns, univariate phylogenetic least-squares regression (PGLS) models were performed (Wigley et al. 2016) using the '*caper*' package. Seedling biomass accumulation patterns were represented by the stem length, stem diameter, aboveground biomass, belowground biomass and total biomass estimates. In some models, PGLS lambda (λ) values were statistically indistinguishable from zero, indicating an absence of phylogenetic signal in the model. In such cases, ordinary least squares (OLS) regression models were run (Appendix Table A5). To meet linear model assumptions, influential outliers with high residual leverage were removed based on Cook's distance above 0.5, 1 (Abdelhamed 2020).

OLS models were run to investigate potential trade-offs and constraints in resource allocation to different traits. The following trade-offs were tested based on previous literature: the relationship between leaf area and seedling size (represented by total plant mass) (Pérez-Harguindeguy et al. 2013, Diémé et al. 2019); between cavitation resistance (represented by narrower xylem conduit diameter) and stem growth (represented by stem length) (Pérez-Harguindeguy et al. 2013, Olson et al. 2018); between aboveground (aboveground mass and stem length) versus belowground biomass accumulation (belowground mass) (Pérez-Harguindeguy et al. 2013, Boonman et al. 2020); and between nodule count and nodule mass (Telford et al. 2021). Seed mass was included in the models if seed size had a significant influence on a trait reflecting seedling biomass accumulation patterns, based on the analyses in the previous section.

Trait-Environment relationships

To evaluate whether environmental variables drive variation in individual traits; PGLS models were performed to test the effect of the environmental predictors (mean annual precipitation, rainfall seasonality, SPEI, fire radiative power and browser biomass index) on each of the traits. Variables were transformed to meet model assumptions (Appendix tables A8 and A9); variables with strong, negative skew were transformed using the equation $\frac{1}{[\log(max(x+1))+1]}$ (Kassambara 2020). Best subset modelling was used to select the most parsimonious model based on the lowest Bayesian Information Criterion (BIC) values.

Additionally, to evaluate how species trait variation is explained by the combined effects of all the environmental predictors, a constrained ordination was performed using redundancy analysis (RDA) from the '*vegan*' package (Oksanen et al. 2019). Aboveground mass, belowground mass and total mass were excluded because the seedling root-shoot ratio was used to represent biomass accumulation patterns.

Trait syndromes

To identify trait syndromes and evaluate which environmental drivers relate to the different trait complexes, '*pvclust*' (Suzuki et al. 2019) was used to perform a hierarchical cluster analysis with centred Pearson distance and average linkage. Trait clusters were identified based on species trait similarities. Welch two-sample t-tests, from the '*stats*' package (R Core Team 2021), were performed to detect differences in the average trait values between the clusters (Appendix table A10). An NMDS was performed to visualise species trait dissimilarities using a Euclidean distance matrix (Goslee and Urban 2007, Lucas 2019). To assess whether the clusters differ by environmental factors, t-tests were performed comparing the mean of each environmental variable for the clusters (Appendix table A11).

Analyses were performed in R version 4.0.5 (R Core Team 2021).

Results

The effects of seed size on seedling biomass accumulation patterns

Seed size showed a significant positive relationship with several measures of seedling size (Table 3), namely stem length, stem diameter and root diameter. Total plant mass, above- and belowground mass did not show a significant relationship with seed size (Appendix table A5).

Table 3: Results of phylogenetic least-squared (PGLS) ǂ and ordinary least-squared (OLS) regression models depict relationships between seed size and various traits linked to seedling size at the age of 60 days. Model estimates and p-values are shown. All trait variables were log-transformed, scaled, and centred. PGLS models are indicated (ǂ), and p-values that remained significant after performing Benjamini-Hochberg corrections are shown (*). Non-significant results are shown in Appendix table A5.

	Fixed effects:	Estimate	Std. error	t-value	p-value	Multiple R^2
log(Stem length) ×	log(Seed mass)	1.092	0.377	2.897	0.020*	0.512
log(Stem diameter) ǂ	log(Seed mass)	0.672	0.218	3.091	0.011*	0.489
Root length ×	log(Seed mass)	1.022	0.417	2.452	0.040	0.536
Root diameter	log(Seed mass)	0.899	0.264	3.398	0.007*	0.429

× *D. cinerea and V. erioloba were removed as influential outliers. PGLS model lambda branch estimate (λ) = 0.575*

Trait-trait relationships

Surprisingly, seedlings did not show evolutionary trade-offs at the species level or from an evolutionary perspective. Instead, positive relationships were revealed between above- and belowground biomass accumulation, stem length and stem diameter, xylem conduit diameter and stem length (associated with rapid growth rates) and between nodule mass and nodule count (Table 4). Additionally, seed size correlated positively with several biomass traits as mentioned above.

Table 4: Results of the significant best subset OLS regression models depict potential trade-offs and constraints in trait resource allocation. P-values highlighted by an asterisk (*) remained significant after performing the Benjamini-Hochberg correction. All trait variables were log-transformed, scaled, and centred. Model R^2 and p-values are shown in Appendix Table A6. Non-significant model results are shown in Appendix Table A7.

	Fixed effects:	Estimate	Std. error	t-value	p-value
Belowground mass	log(Stem length)	-0.391	0.487	-0.803	0.442
	Aboveground mass	1.015	0.307	3.302	0.009*
Stem length	Stem diameter	0.786	0.251	3.137	0.012*
	Seed mass	0.580	0.251	0.232	0.822
Nodule mass	Nodule count	0.741	0.212	3.487	0.006*
Xylem conduit diameter	log(Stem length)	1.614	0.291	5.557	<0.001*
	log(Seed mass)	0.169	0.186	0.911	0.386

Trait-Environment Relationships

Low mean annual precipitation was linked to a greater depth of root expansion (depth of the fifth lateral root) and reduced leaf production relative to shoot investment (leaf-shoot ratio; Table 5). Highly seasonal rainfall was an important driver of prioritised belowground investment relative to aboveground biomass accumulation (higher root-shoot ratio) and showed a negative effect on nodule count. Increased drought proneness and severity exerted a negative effect on relative bark thickness, but showed a positive relationship with taller, thicker stems. Contrary to the hypothesis, xylem conduit diameter increased with drought severity. This may be attributed to the larger seed size which supported rapid growth rates.

Intense fires selected for smaller seeds, prioritised leaf production relative to shoot investment (leaf-shoot ratio) and smaller leaf area relative to leaf mass (SLA; Table 5).

High browser pressure appeared to exert a negative effect on seedling biomass accumulation (above- and belowground mass and total mass, Table 5). Specific leaf area showed an unexpected increase with higher browser pressure. Nodule mass showed a negative response to greater browser pressure.

Table 5: Results of ordinary least-squares regression models (OLS) depicting relationships between a trait and selected environmental variables based on the best subset model with the lowest Bayesian Information Criterion (BIC) values. Variables that were transformed using $\frac{1}{[log(max(x+1)-x)+1]}$ are indicated using ‘Kassambara’. P -values highlighted by an asterisk (*), remained significant after performing the Benjamini-Hochberg correction. Model R^2 and p-values are shown in Appendix Table A8. Non-significant models are shown in Appendix Table A9.

	Fixed effects:	**Estimate**	**Std. error**	**t-value**	**p-value**
Specific leaf area	(Precipitation) $^{\text{Kassambara}}$	-3.610	1.472	-2.452	0.040
	Fire intensity	-0.799	0.227	-3.527	0.008*
	(Browser)$^{\text{Kassambara}}$	3.396	1.133	2.998	0.017*
log(Stem length)	Drought	0.647	0.214	3.025	0.014*
	Fire intensity	-0.384	0.214	-1.795	0.106
log(Xylem conduit diameter)	log(SPEI)	1.320	0.442	2.989	0.015*
	log(Fire intensity)	-0.528	0.494	-1.070	0.313
Relative bark thickness	(Precipitation) $^{\text{Kassambara}}$	-3.582	1.546	-2.317	0.046
	Drought	-0.876	0.245	-3.582	0.006*
log(Depth of the fifth lateral root)	(Precipitation) $^{\text{Kassambara}}$	-5.222	1.530	-3.414	0.008*
	log(Drought)	-0.793	0.472	-1.682	0.127
log(Aboveground mass)	log(Drought)	-0.399	0.562	-0.710	0.496
	log(Browser)	-0.742	0.263	-2.815	0.020*
log(Belowground mass)	log(Rain seasonality)	-0.763	0.545	-1.400	0.195
	log(Browser)	-0.749	0.262	-2.860	0.019*
log(Total mass)	log(Rain seasonality)	0.435	0.294	1.480	0.173
	Browser	-0.755	0.189	-3.986	0.003*
log(Seedling root-shoot ratio) × [1]	Rain seasonality	0.760	0.128	5.942	0.001*
	Drought	-3.05	0.126	-2.429	0.046
log(Seedling leaf-shoot ratio) × [2]	(Precipitation) $^{\text{Kassambara}}$	4.654	1.163	4.004	0.004*
	log(Fire intensity)	2.122	0.398	5.326	0.001*
log(Nodule count) × [3]	Rain seasonality	-0.639	0.219	-2.923	0.022*
	log(Fire intensity)	-1.539	0.489	-3.148	0.016*
Total nodule mass	Drought	-0.121	0.168	-0.719	0.493
	Browser	-0.571	0.174	-3.283	0.011*
log(Seed mass)	Rain seasonality	-0.198	0.186	-1.060	0.320
	log (Fire intensity)	-1.612	0.412	-3.909	0.004*

× [1] *V. karroo* and *V. rehmanniana* removed as influential outliers; × [2] *V. rehmanniana* removed as an influential outlier; × [3] *A. forbesii* and *V. sieberiana* removed as influential outliers

.

The permutation test for the RDA showed a significant model (p = 0.047). The results of the RDA support the findings from the least-squared regression analyses. Based on the first RDA axis (Figure 3a), drought severity (SPEI) showed a positive relationship with xylem conduit diameter, seed mass and seedling size (stem length, stem diameter and root length); browser pressure had a negative relationship with nodule mass and total biomass, and fire intensity had a negative relationship with seed size but a positive effect on seedling leaf production relative to shoot investment. The second RDA axis shows a negative relationship between fire intensity and specific leaf area (SLA) and increased SLA with high browser pressure (Figure 3b). The third RDA axis (Figure 3b) shows an increase in the depth of the fifth lateral root, reduced leaf production (leaf-shoot ratio) and less nodule investment at low rainfall; and seasonal rainfall showed a positive relationship with prioritised root mass accumulation (root-shoot ratio), and a negative effect on nodule mass.

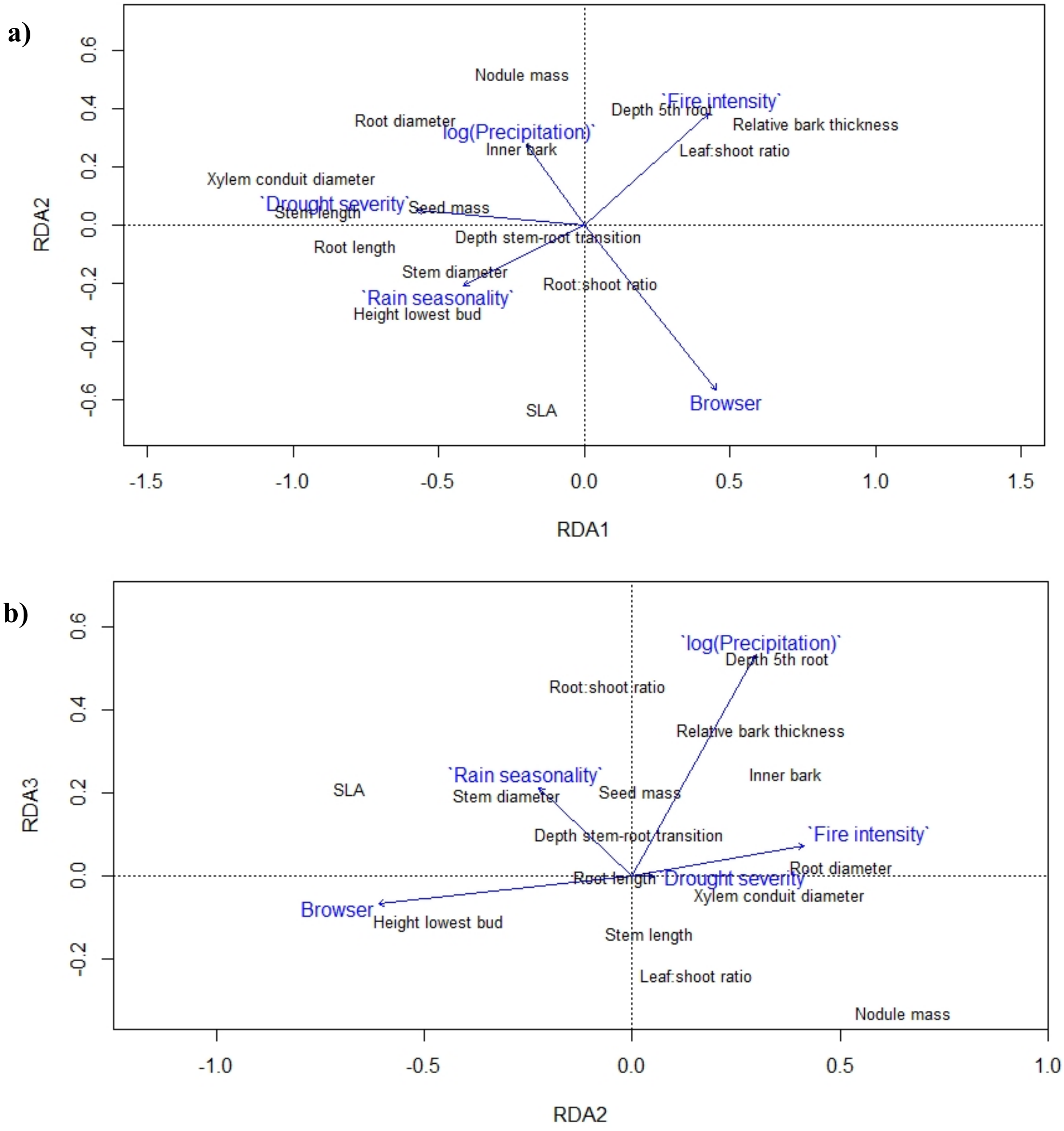


Figure 3: *RDA plots showing the amount of trait variation explained by the environmental variables (56.78%, p = 0.047). The first three RDA axes explain 50.81%, 21.80% and 13.89% of the constrained eigenvalues respectively (cumulative proportion = 86.50%).* ***A)*** *RDA plot using the first and second axes and* ***b)*** *RDA plot using the second and third axes*

How environmental drivers affect trait complexes

The hierarchical cluster analysis revealed two significantly different species groups, based on the approximately unbiased p-values from multiscale bootstrap sampling (Figure 4a). Species from cluster A showed reduced investment in seedling size, indicated by shorter and thinner stems, narrower xylem vessels linked to slower growth rates, thinner roots, and less aboveground biomass (Figure 4b, Appendix Table A10). In contrast, species from cluster B prioritised robust seedling development represented by the taller and thicker stems, increased xylem vessel diameter linked to rapid growth rates, thicker roots and increased aboveground biomass.

Species from cluster A showed a lower mean SPEI value, associated with lower drought proneness and severity (Figure 4c), whereas species from cluster B had a higher mean SPEI value indicating increased drought occurrence and severity (Appendix Table A11). Drought severity was the only environmental predictor that differed significantly between the two clusters (Appendix Table A10).

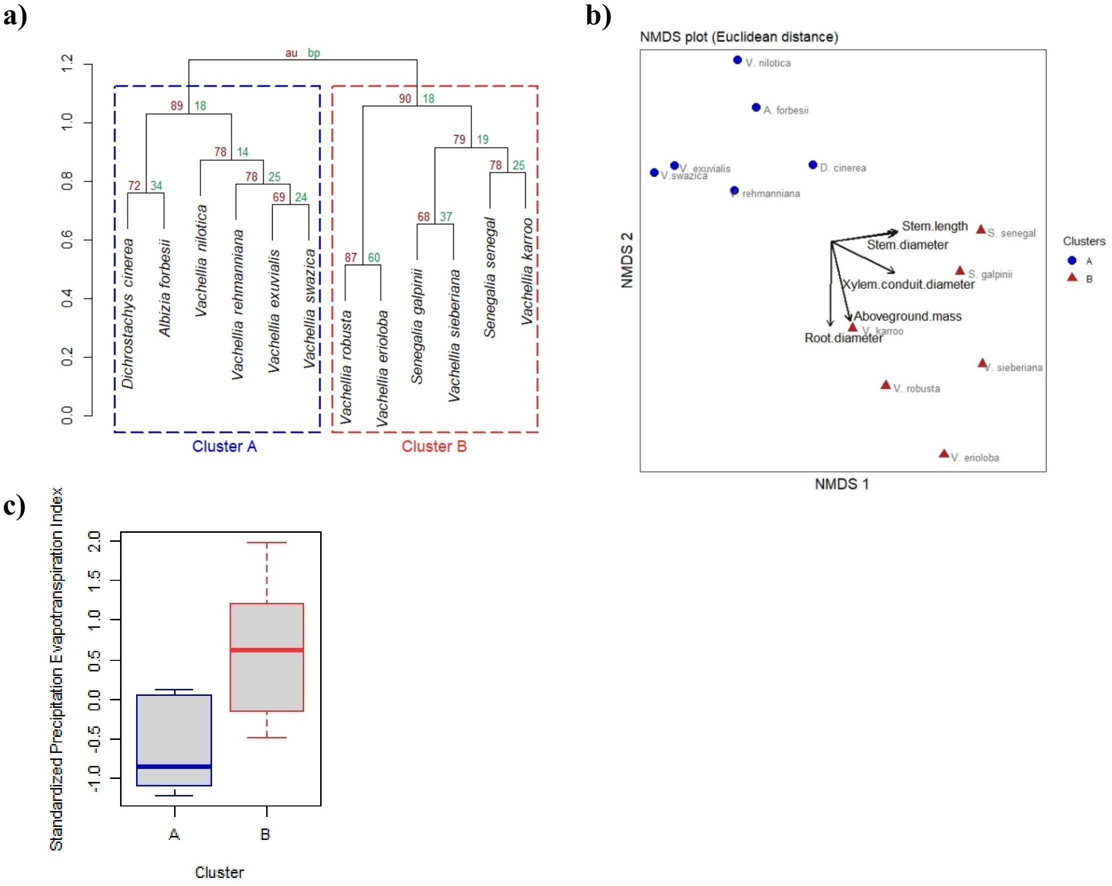


Figure 4: a) *A cluster dendrogram showing species clustered according to the similarity in trait values. brown = approximately unbiased p-values from multiscale bootstrap resampling, green = bootstrap probability.* ***b)*** *An NMDS ordination plot illustrating the different trait investment strategies for species in Cluster A and Cluster B, based on the Euclidean distance matrix of the traits that differed*

significantly between the species clusters (Appendix Table A10). The minimum stress for the given dimensionality = 0.051 and $R^2 = 0.972$. ***c)*** *Comparison of each environmental factor averaged for species in Cluster A and Cluster B. SPEI was the only environmental factor that differed significantly between the two clusters.*

Discussion

In this chapter, I assessed whether seedlings showed trait trade-offs and how provenance affected the traits of mimosoid seedlings. No trait trade-offs were observed for the traits selected in this study; instead seed size determined a number of trait characters. Variations in individual traits corresponded to gradients of water stress, fire intensity and browsing. Two trait clusters were identified and drought severity was revealed as the only predictor of these clusters.

Trait trade-offs

Plant investment strategies were expected to show trade-offs because increased investment in one trait may impair the development of another trait (Brouwer 1963). Surprisingly, the seedlings in this study did not show any significant trade-offs in any of the tested plant resource allocation strategies. Seed size appears to be a primary determinant of seedling growth patterns and thus also of several size-related traits (Jurado and Westoby 1992); large seeds supported the development of taller and thicker stems, as well as larger root diameters (Table 3). As a result, stem length increased with stem diameter, which contradicted the expectation that stem length trades off against stem diameter (Archibald and Bond 2003, Dantas and Pausas 2013). The expected trade-off between above- and below-ground biomass accumulation was also not seen; instead, they were positively associated. Additionally, taller stems had wider xylem vessels (larger xylem conduit diameters). This supports the findings of Wright et al. (2010), that the correlation between reduced growth and increased wood density (narrower xylem diameters) observed in adult trees is seen at the seedling stage. Also, there was no evidence to suggest a trade-off between strategies to minimise water loss, such as reduced specific leaf area (SLA), and seedling biomass accumulation, which implies seed reserves drive biomass accumulation at the early seedling stage. This is in contrast to the adult stage where higher photosynthetic rates, associated with higher SLA, result in faster growth rates (Diémé et al. 2019). Root nodule abundance and mass also did not trade off; increased nodulation enhances nitrogen availability for plant growth (Telford et al. 2021).

The absence of the trait trade-offs in seedlings that are usually seen in adult trees suggests that trade-offs primarily occur at the seed production stage of the parent plant: the trade-off between producing more smaller seeds *vs* fewer large seeds is well-known (Jakobsson and Eriksson 2000). The amount of energy invested in the seed by the parent plant thus seems to be the primary determinant of many seedling traits, and the trait trade-offs seen in adult trees are likely to only appear in individuals older than the ones measured here.

Trait-environment relationships

Aridity

Reduced leaf production (represented by decreased leaf-shoot ratios) in species from more arid regions reflected desiccation-avoidance strategies in water-limited environments. Arid-adapted species are expected to show trait investment strategies to overcome limited water availability as the main constraint on seedling establishment (Anderegg et al. 2016, Choat et al. 2018, Sankaran 2019). Fewer and smaller leaves are advantageous in water-deficit environments due to the reduction of tissues prone to water loss (Wright et al. 2001, Wright and Westoby 2002, Poorter et al. 2009), leading to plant desiccation (Gotsch et al. 2010, Choat et al. 2018).

Narrower xylem vessels are less prone to embolism linked to hydraulic failure in water-limited environments (Hacke et al. 2001, Lens et al. 2013, Gleason et al. 2016), but here, xylem conduit diameter increased with drought severity. Larger xylem vessels may reflect the rapid stem growth rates I found for seedling species that originated from areas of high drought proneness and severity. Larger seedlings tend to have wider xylem vessels (Olson et al. 2018).

Low rainfall and increased drought risk were important predictors of seedling allocation to rooting depth. This may facilitate seedling procurement of a stable water supply in water-limited systems (Rossatto et al. 2012, February et al. 2020). Shallow rooting depths have higher drought-induced mortality rates (Johnson et al. 2018). The depth of the fifth lateral root increased with decreasing rainfall. We propose that the trait 'depth of the fifth lateral root', used here for the first time, may represent the depth of seedling root expansion. This trait may facilitate field observations where the entire root system is difficult to exhume. Further investigation of this trait is recommended before accepting it as an appropriate indicator in root development strategies.

Nodule size was expected to increase for species from areas with limited rainfall because nodulating plants use water more efficiently (Adams et al. 2016) but the cost of nodule maintenance may be too high at this stage, resulting in the reduced nodule size with aridity, because seedlings prioritise biomass accumulation (Nishida and Suzaki 2018). Also, nodule investment increases with age and production is triggered by water stress (Pellegrini et al. 2016, Telford et al. 2021). Here, seedlings were grown in greenhouses that received regular irrigation, thus nodule investment may not have been prioritised.

Fire intensity

Intense fires were expected to drive seedling trait investment strategies because the associated heat may damage plant tissues (Midgley et al. 2011, Archibald et al. 2013). Small seeds correlated with greater fire intensity. Small seeds provide an adaptation to intense fires due to their greater tolerance of high temperatures (Liyanage and Ooi 2018). Some acacia species recruit from soil-stored seedbanks in response to severe fires (Palmer et al. 2018).

Intense fires select for prioritised investment in recovery strategies rather than rapid height gain represented by larger leaf-shoot ratios in adult trees (Wigley et al. 2020). However, decreased specific leaf area (SLA) found here seemed contradictory because increased SLA is associated with greater photosynthetic rates to support rapid recovery (Wright et al. 2001, Wright and Westoby 2001, Westoby et al. 2002, Poorter et al. 2009). However, leaves with reduced SLA may be less flammable providing an adaptation to intense fires (Pausas et al. 2017). Additionally, areas prone to frequent fires tend to be more abundant in nodulating species in savanna systems (Högberg 1986, da Silva and Batalha 2008), but frequent fires constrain fire intensity (Archibald et al. 2013). Intense fires may therefore select contrasting adaptations to frequent fires, resulting in unique plant physiognomies for the former.

Herbivory

Woody plants alter growth strategies to reduce browsing events (Dantas and Pausas 2013, Archibald and Hempson 2016, Archibald et al. 2019). Decreased specific leaf area is associated with tougher leaves which deter browsers (Poorter et al. 2009, Pérez-Harguindeguy et al. 2013). We thus expected species from highly browsed areas to have reduced SLA. Instead, the results showed that SLA increased with high browser biomass. Larger leaves facilitate rapid recovery after biomass loss and are less expensive to produce (Wright et al. 2001, Wright and Westoby 2001, Westoby et al. 2002, Poorter et al. 2009). Instead of investing in an escape height, seedlings of species from highly browsed areas were short. Prioritised height gain reduces species' ability to survive disturbance (Kühner and Kleyer 2008) because single stems, associated with rapid height gain, are less protected against browsers than multi-stemmed shrubs (Staver et al. 2012). Nodulation facilitates recovery in disturbed environments because plants can meet high nitrogen requirements and resprout rapidly (Cramer et al. 2010, Batterman et al. 2013, Vitousek et al. 2013, Sheffer et al. 2015); however, the cost of nodule maintenance may be too high at this age resulting in the reduced nodule mass observed for species from areas with high browser biomass.

Trait syndromes

Groups of traits may represent seedling survival strategies in response to a main limiting factor to form syndromes (Brouwer 1963, Sankaran 2019, Boonman et al. 2020). Two syndromes were detected in this study and drought severity was revealed as the driver. These results support the findings of Markesteijn and Poorter (2009) by showing common trait investment strategies of species groups adapted to drought tolerance. It also suggests water stress is an important filter for the establishment of savanna species. In this study, species adapted to severe or frequent droughts had taller and thicker stems, larger xylem vessels, greater aboveground biomass and thicker roots compared to species from less drought-prone areas. These traits depicted strategies to develop larger seedlings which increases the survival probability in arid systems (Moles and Westoby 2006). Taller plants develop deeper and thicker root systems to reach belowground water reserves and soil nutrients (Comas et al. 2013, Li and Bao 2015, Moles 2018). Thicker roots facilitate soil penetration (Goss 1977) and are more persistent in arid areas (James et al. 2011, Merino-Martín et al. 2017); root diameter also regulates root length (Fitter 1996). Multivariate analyses revealed that the variation in seed size may be associated with drought severity; larger seeds provide more nutrient reserves to support seedling development and survival in harsh environments (Leishman et al. 2000, Moles and Westoby 2004, Moles 2018, dos Santos Costa et al. 2020). Therefore, the surprising result of taller stems with wider xylem vessels is likely attributed to the large seed size which supports rapid growth rates. It is also possible that temperature may influence xylem vessel diameter (Olson et al 2021), although temperature was not included in this study.

Conclusion

My results indicate that mimosoid species are not only adapted to climatic conditions but also to disturbances such as fire intensity and browser pressure, and that these adaptations are seen in seedlings as young as 60 days (Hoffmann et al. 2012, Lehmann et al. 2014). It is important to note that these adaptations are at an evolutionary scale and should be interpreted with caution because the seedlings were not subjected to aridity, fire or herbivory. Thus, these traits link to the provenance of the species, rather than the seedling responses. Trait syndromes could only be separated along a drought severity gradient; traits linked to intense fires and increased browser pressure overlapped and did not separate species into clusters. This contradicts the expectation that savanna seedlings possess preadaptations to survive disturbance. Water availability may therefore present the first environmental filter that savanna seedlings must overcome. As plants mature, seedlings are likely to shift their investment strategies as the importance of fire and herbivory increase as drivers of adaptations (Chapter 3) (Hinckley et al. 2011, Hoffmann et al. 2012, Charles-Dominique et al. 2015a, Charles-Dominique et al. 2016).

Future research could be aimed at going beyond a correlative approach to infer the role of adaptations to withstand stressors (as used here), to assessing the direct impact of these stressors on seedling survival, and the role of traits in seedling fitness in the face of stressors, in an experimental setting (e.g. Boonman et al. (2020), Botha et al. (2020)). Additionally, opportunities for integrating experimental and field observations (e.g. Stevens et al. (2014)) could provide more clarity on the complexities of adaptations to a range of stressors that are unequally distributed in the landscape. My study provides a starting point for subsequent research to better understand savanna seedling development patterns.

Chapter three

Characterising acacia syndromes – how fire, herbivory and rainfall affect the functional traits of a flagship woody taxon in African savannas

Introduction

Environmental factors drive vegetation distribution and species occurrences (Hoffmann et al. 2012). In African savannas, the rainfall regime (including mean annual precipitation, rainfall seasonality and drought) is one of the most important determinants of woody cover and savanna distribution (Greve et al. 2011, Staver et al. 2011c, Devine et al. 2017). In low rainfall areas, limited water availability constrains woody cover (Sankaran et al. 2005, Lehmann et al. 2011) and filters species composition (Bond et al. 2003). In contrast, disturbances such as fire and herbivory are responsible for maintaining open vegetation cover at higher rainfall (Sankaran et al. 2005, Sankaran et al. 2008, Hoffmann et al. 2012), and preventing shifts in species composition from savanna to forest-like vegetation (Roques et al. 2001, Van Langevelde et al. 2003, Bond et al. 2005, Staver et al. 2009).

At low rainfall, seasonal rain events facilitate tree persistence in savannas by increasing soil moisture availability at greater soil depths (Kulmatiski and Beard 2013, D'Onofrio et al. 2015, Berry and Kulmatiski 2017), thereby reducing the competitive pressure of grasses on trees (February et al. 2013). Conversely, severe drought can cause tree mortality and thus limit tree cover (Case et al. 2019, Case et al. 2020). Therefore, species from arid systems must possess critical adaptations to tolerate frequent and prolonged periods of limited water availability (Pellegrini et al. 2016). In contrast, vegetation in disturbance-driven systems require adaptations to persist frequent fires or herbivory (Belsky 1992, Bond and Keeley 2005, Staver et al. 2009). Fire and herbivory are both primary consumers of savanna trees (Hempson et al. 2020), creating a ‘consumptive zone’ below the canopy of most mature trees (Zirka et al. 2014, Hempson et al. 2020). Fire is considered to be the dominant vegetation consumer in higher rainfall savannas, whereas browsers (elephants excluded) are the primary biomass consumers at intermediate rainfall (Hempson et al. 2015, Archibald and Hempson 2016). As a result, woody species show an overlap in traits to recover after frequent biomass removal (Pausas et al. 2016), or to escape fire and browser traps by investing in rapid height gain where the canopy is no longer within reach of surface fires or browsers (Dantas and Pausas 2013, Kirker and Scogings 2019). However, fires and browsers differ in the mechanism and amount of biomass consumption, resulting in some antagonistic plant adaptations to either fire or herbivory (Staver and Levin 2012, Archibald et al. 2013, Hempson et al. 2015). For example, acacia seedlings show increased thorn production after simulated herbivory, but reduced thorn production and size after burning (Hean and Ward 2012). Another example is the different architectures. Although woody species can sometimes adopt a shorter architecture with greater bark production at a smaller stem diameter to resist fire (Gignoux et al. 1997, Pausas 2015), they mostly grow tall and lanky to escape fires in Afrotropical savannas (Dantas and Pausas 2013). A lanky architecture requires rapid shoot extension, increasing the vulnerability to browsing (Bond et al. 2001). In contrast, a highly branched, 'cage-like' architecture deters browsing, but at the cost of investment in plant height (Staver et al. 2012).

Functional traits of dominant species contribute heavily to ecosystem properties and processes (Tang and Bartlein 2008, Castro-Díez et al. 2011). Environmental filters assemble specific community traits and ecological responses linked to species success in each set of conditions (Bond et al. 2001, Maracahipes et al. 2018). For example, leaf size has different advantages and disadvantages under herbivory, fire and aridity. Reduced leaf area minimises water loss caused by transpiration (Munné-Bosch and Alegre 2004, Otieno et al. 2005), though at a cost to the photosynthetic capacity and overall plant growth rates (Jones 1992, Wakeling et al. 2011). Larger leaves facilitate rapid recovery in response to disturbance by supporting higher photosynthetic rates (Ackerly et al. 2002, Westoby and Wright 2006, Poorter et al. 2009, Diémé et al. 2019). However, smaller leaves may reduce the foliage consumed by browsers per bite (Charles-Dominique et al. 2015a).

Diversity in physical bark characteristics has been linked to environmental pressures acting at the species and family levels (Rosell and Olson 2014, Morris and Jansen 2017). Rough bark may facilitate water capture in areas with seasonal rainfall (Pérez-Harguindeguy et al. 2013), but reduces the water storage capacity of the inner bark (Rosell et al. 2014). Water storage provides a buffer against highly seasonal water availability and droughts (Borchert 1994; Scholz et al. 2007). Thick outer bark is often associated with the protection of woody stems against fire damage (Schafer et al. 2015, Rosell 2016); the scales of thick bark produce rough-textured or fissured bark which create air-pockets to reduce heat penetration through the stem (Romero 2014). In addition, rough bark shows lower flammability which implies less biomass is consumed and at a lower burning rate (Fréjaville et al. 2013). Browsers may also influence bark by consuming bark tissues and bark exudates (Romero 2014), or by inflicting structural damage on the tree (Guy 1989, Gill 1995). Thick bark and bark projections may provide a defence against browsers (Jager et al. 2015, Rosell 2019). Therefore, bark morphology may represent different strategies to survive aridity, fire or browser pressure.

Plant size, including height, is an important trait at the core of the plant life cycle (Grime et al. 1997, Westoby 1998). Species growth rates, reflected by size (Pérez-Harguindeguy et al. 2013), are limited by water availability and drought (Trugman et al. 2018). Taller trees show high drought-induced mortality rates (Case et al. 2019, Stovall et al. 2019) due to greater water requirements and increased vulnerability to hydraulic stress (Zhang et al. 2009, Bennett et al. 2015). However, repeated exposure to intense fires selects woody species with 'pole-like' (i.e. tall and little-branched) architectures and reduces the abundance of cage-like species (Bond et al. 2001, Archibald and Bond 2003, Archibald et al. 2019); taller, single-stemmed trees maximise the investment in a single trunk instead of maintaining multiple stems (Mlambo and Mapaure 2006). In contrast, shorter 'shrubby' trees reflect an investment in structural defences to deter browsers (Archibald and Bond 2003, Mlambo and Mapaure 2006, Staver et al. 2012). Additionally, the canopy shape and the location of the canopy relative to the plant height reflects the different environmental drivers. For example, trees in arid areas develop broad canopies with greater lateral branching (Archibald and Bond 2003, Gaillard et al. 2018) which will be reflected by a wider, umbrella-like canopy shape. Increased canopy height may be prioritised over canopy spread in frequently disturbed systems because fires and browsers create a consumptive zone below the canopy height (Zirka et al. 2014, Hempson et al. 2020). However, highly branched shrubs reduce the browser biting range within the structure (Charles-Dominique et al. 2017). This strategy will be reflected by a rounder canopy shape (reduced canopy width relative to canopy length). Plant architecture may therefore reflect the different driving factors.

Spinescence broadly reflects investment in structural defence against herbivory (Pérez-Harguindeguy et al. 2013, Wigley et al. 2015); increased spinescence deters browsers and reduces foliage consumption (Rooke et al. 2004, Fornara and du Toit 2008, Barton 2015, Charles-Dominique et al. 2017). However, spinescence comes at a cost to the plant; therefore, investment in other adaptations is presumably diminished in plants which invest heavily in spinescence (Wigley et al. 2015, Hempson et al. 2019).

Reproductive structures are also expected to reflect environmental drivers. Limited resource availability drives variation in acacia pod characteristics (Ayadi et al. 2012). Investment in woody pod structures provides greater seed protection against damage, and are more nutritious, compared to thin or 'papery' pods, resulting in a higher cost for production (Gwynne 1969, Lamont et al. 1991, Groom and Lamont 1997). In addition, pod glands are associated with scent production to attract herbivores for seed dispersal via pod consumption (Coe and Coe 1987), but may prove too costly to produce in nutrient-limited environments.

Woody species invest in different survival strategies to survive the environmental drivers of savanna systems (Charles-Dominique et al. 2015b, Wigley et al. 2015, February et al. 2020). However, species traits are expected to reflect the most limiting factor (Brouwer 1963) and so increased investment in one adaptation reduces the ability to invest in another trait resulting in a trade-off in resource allocation (Nardini and Luglio 2014, Gleason et al. 2016, Corrêa Scalon et al. 2020). Survival strategies are therefore characterised by a group of co-occurring traits and trait trade-offs in response to a particular set of environmental conditions (Staver et al. 2012, Sankaran 2019, Boonman et al. 2020).

At macroecological scales, species' functional responses to varying environmental variables have been linked to species ranges and biome distribution (Hoffmann et al. 2012, Dantas et al. 2013, Charles-Dominique et al. 2015b). African acacias (genus *Vachellia* and *Senegalia*) are one of the characteristic taxa associated with savannas Acacias, are widespread and contribute extensively to the woody component in many African savannas (Ross 1972, Timberlake 1980, Dharani 2006). In general, acacias dominate more arid savannas (Dharani 2006), although some species also occupy moister zones (Bouchenak-Khelladi et al. 2010). Several African acacia species are classified as woody encroachers (O'Connor et al. 2014). Some *Vachellia* and *Senegalia* species are therefore considered environmental indicators; shifts in their abundance or species turnover reflect a change in environmental condition or ecological degradation (Bond et al. 2001, Dharani 2006, Staver et al. 2012).

The aim of this work is to characterise unique functional trait combinations in response to the most prevalent climatic and disturbance-based drivers of acacia species distributions across African savannas. The objectives are to a) investigate how environmental factors influence the traits, b) investigate trade-offs between traits and c) identify trait syndromes or groups of traits that reflect strategies to survive savanna drivers in adult acacias across the African continent. We expect functional traits of African acacias to reflect the strongest limiting factor, based on the functional equilibrium hypothesis, whereby plants prioritise resources allocation to overcome the main environmental constraint (Brouwer 1963, Boonman et al. 2020), and that adaptation to a main limiting factor will cause trade-offs between different trait investment strategies (Gleason et al. 2016, Corrêa Scalon et al. 2020). For example, I anticipate a positive correlation between leaf size and the maximum plant height because larger leaves are able to support rapid growth while smaller leaves have a lower productivity rate. Plant development also shows a trade-off between growth and defence investment (Dayrell et al. 2018); therefore, adults are expected to show a negative relationship between maximum height and leaf protection. Rough or corky bark protects the stem from fire-related heat damage (Fréjaville et al. 2013); I expect at a cost to plant growth and thus plant height (Gignoux et al. 1997, Hoffmann et al. 2009, Keeley et al. 2011, Lawes et al. 2013). Species adaptations and trade-offs are expected to drive the formation of groups of traits linked to a survival strategy (syndrome). Therefore, syndromes linked to aridity are expected to include smaller leaves, reduced height and smoother bark. In contrast, fire syndromes will either have larger leaves and taller individuals or shorter stems with rougher bark. Similarly, browser syndromes should reflect avoidance (increased height and canopy height) or resistance (reduced height, rounded canopy, increased spine-leaf ratio).

Methods

Acacia trait database

Trait descriptions of each African *Senegalia* and *Vachellia* species (See Appendix Table B1 for the full list of species) were extracted from floras and field guides of trees native to African savannas (Oliver 1871, Harvey 1894, Glover and Brenan 1944, Brenan 1970, Bognounou 1972, Ross 1972, 1979, Timberlake 1980, Davidson and Jeppe 1981, Coates Palgrave 1983, Hassan and Styles 1990, Thulin 1993, Barnes et al. 1997, Smit 1999, Dharani 2006, Lötter 2018) and, for architectural traits, supplemented images (Renoult 2008, Birnbaum et al. 2014, Fictl et al. 2014, Musch et al. 2014, Schmidt et al. 2014, Erb 2021); were incorporated to quantify trait values (Table 1). The traits covered a range of possible adaptations to the pressures experienced in savannas (see Table 1 for descriptions of the importance of the traits). *Senegalia ankokib*, *Senegalia oliveri*, *Senegalia somalensis*, *Senegalia zizyphispina* and *Vachellia farnesiana* were missing estimates for most traits and were thus excluded from the analyses. Species with less than four traits missing had estimates imputed for the missing values using the 'imputePCA()' function from the *missMDA* package (Josse and Husson 2016).

Species leaf area estimates were derived by multiplying the calculated leaflet area, the number of leaflets per pinna and the number of pinnae per leaf (Figure 1, Table 1, Castro-Díez et al. (2011)).

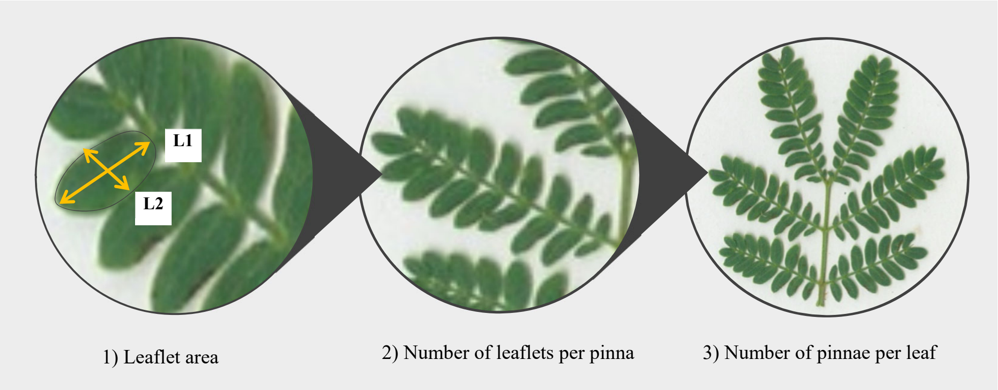


Figure 1: *Diagram of the process used to calculate the leaf area. 1) Leaflet area was calculated using the leaflet length (L1) and leaflet width (L2). 2) The approximate pinna area was then calculated by multiplying the leaflet area by the number of leaflets per pinna. 3) The approximate pinna area was multiplied by the number of pinnae per leaf to obtain an estimate for the leaf area. See Table 1 for more details.*

Bark texture was categorised and ranked as smooth, thin and flaky, variable (smooth to rough) or rough, fissured (characteristic of thicker bark layers) (Smit 1999) and corky (Dantas and Pausas 2013) (Table 1).

Tree architecture characterises different growth strategies linked to varying environmental factors (Archibald and Bond 2003, Charles-Dominique et al. 2017, Charles-Dominique et al. 2018). The maximum height of the described species was used to indicate the vertical size of a species, and to derive the various measures of the canopy. Images of the species were used to measure the height of the canopy, the canopy length and the canopy diameter, all relative to the height of the pictured tree. These ratios were then multiplied by the maximum tree height per species (Table 1, Pérez-Harguindeguy et al. (2013)) to approximate the canopy height, canopy length, canopy diameter and canopy width-length ratio.

African acacias possess either prickles or spines: prickles are an extension of the bark layer that arise from hardened epidermal growth (Timberlake 1980), and occur in *Senegalia* (Smit 1999); spinescent stipules are modified leaflet-like outgrowths formed at the petiolar base and are characteristic of *Vachellia* (Timberlake 1980, Smit 1999). Spines are costly to produce as photosynthetic material is sacrificed (Coverdale 2020). Spine length (Table 1), indicates species' investment to reduce browser bite-size (Cooper and Owen-Smith 1986, Zinn et al. 2007, Wigley et al. 2015), but acacias also reduce leaf size in response to high browser pressure (Rohner and Ward 1997, Schmitt and Shrader 2020). A ratio of the spine length to leaf length was therefore used to assess the relative leaf protection (Table 1). Prickles in *Senegalia* are short; thus the spine-leaf ratio is probably fairly meaningless in this group, as the prickles probably function primarily to protect stems from herbivory rather than to protect leaves (Midgley et al. 2001). Therefore, the spine-leaf ratio was used to quantify leaf protection for only *Vachellia* species in this study.

Pod characteristics were used to capture resource allocation to reproductive structures in acacias (Table 1). Pod texture represented the pod hardiness and investment in seed protection (Khan et al. 2013). More woody and thickened pods have greater resistance to mechanical damage (Groom and Lamont 1997). Pod hardiness was categorised using species descriptions ranging from low pod hardiness (papery pods) to high pod hardiness (woody and thickened pods) (Table 1). Additionally, the presence of pod glands was recorded; where no pod gland presence was mentioned in species descriptions, it was assumed that pod glands were absent.

Table 1: Description of trait values derived from a compilation of African acacia species descriptions, the predicted environmental filters of each trait (💧 aridity, 🔥fire and 🦌herbivory) and the methods used to calculate species trait values. Blue environment icons indicate an expected positive relationship between the trait and the environmental filter, whereas orange indicates an expected negative relationship. References: citations of the literature where the trait was originally described, examples of the ecological applications and literature that formed the basis for new traits.

Trait	Definition	Environment	Methods	References
Leaf area (*LA*)	A measure of leaf size, defined as the one-sided or projected area of a leaf, used to reflect the plant's ecological strategy under environmental stress and photosynthetic capacity.	💧 🔥 🦌	Average leaflet area ($la_{1,}$) was calculated using the leaflet length (*L1*) and width (*L2*) using the formula for the area of an ellipse. Leaf area was derived by multiplying the leaflet area by the average leaflets per pinna (n_l) multiplied by the pinnae per leaf (n_p) (Figure 1). 1. $la_1 = \frac{\pi}{4} \times L1 \times L2$ 2. $LA = la_1 \times n_l \times n_p$	Pérez-Harguindeguy et al. (2013), Otieno et al. (2005), Castro-Díez et al. (2011)
Bark texture	Description of bark texture on the trunk ranging from little bark investment to greater bark investment: rough and deeply fissured bark or thick and corky bark.	💧 🦌 🔥	Bark texture was assigned to the following categories: Smooth-smoothish bark or longitudinally striated = 1, Variable (smooth or rough) = 2, Flaking (papery and scaly) = 3, Rough and fissured (coarsely, deeply or longitudinally furrowed) or corky = 4. Treated as ordinal variable.	Smit (1999), Morris and Jansen (2017)
Maximum height (H_{max})	A measure of plant investment to height gain.	💧 🔥 🦌 🔥	The maximum plant height ($H_{max,}$) as reported by field guides.	Wakeling et al. (2011)
Canopy height (*CH*)	Estimate of the canopy position, relative to the plant size, represented by the approximate height of the canopy bottom.	🔥	Using the species images in field guides, the height of the canopy bottom was calculated ($H_{b,}$) relative to the plant height ($H_{t,}$) and multiplied by the maximum plant height (H_{max}). $CH = \frac{H_b}{H_t} \times H_{max}$	Dantas and Pausas (2013), Kirker and Scogings (2019), Higgins (2020)
Canopy diameter (*CD*)	Canopy diameter estimate relative to plant height.	Used to calculate the canopy shape	Using the species images obtained from field guides and supplemented sources listed in the text, the canopy diameter (C_d) was measured relative to the plant height (H_t). This ratio was multiplied by the maximum plant height (H_{max}) of a species, to obtain an approximate canopy diameter of a species. $CD = \frac{C_d}{H_t} \times H_{max}$	Higgins (2020)

Trait	**Definition**	**Environment**	**Methods**	**References**
Canopy shape (*CS*)	Estimation of canopy shape derived from the canopy length and canopy diameter. A value > 1 represents a wider and flatter shape, and a value < 1 represents a rounder shape.	💧/🌵 🦌	The distance between the highest canopy and the lowest canopy point was recorded ($H_t - H_b$), relative to the height of the tree in an image. This ratio was multiplied by the maximum plant height of a species (H_{max}) to obtain the approximate canopy length (C_L). The crown shape is described as the ratio of canopy diameter (*CD*) to canopy length ($C_{L,}$). 1. $C_L = (H_t - H_b) \times H_{max}$ 2. $CS = CD\colon C_L$	Higgins (2020)
Spine-leaf ratio	An indication of how protected a leaf is by the spine closest to it.	🦌	The ratio of the spine length (L_{SS}) to the length of the leaf rachis (L_r). $LP = L_{SS}\colon L_r$	Pérez-Harguindeguy et al. (2013)
Texture (Pod investment)	A measure of resource allocation to fruiting structure development; linked to seed protection, dispersal strategies and environmental constraints.	💧/🌵 🦌	Pod hardiness was assigned to the following categories: papery, thinly textured, brittle (*Low = 1*); thinly woody, slightly constricted, glutinous, coriaceous (*Medium = 2*); woody, thickened walls, thick, hardened, tough (*High = 3*). Treated as ordinal variable.	Pérez-Harguindeguy et al. (2013), Tybirk (1993), Timberlake (1980), Ayadi et al. (2012)
Glands	The presence of glands may be an adaptation to attract herbivores to aid fruit dispersal.	🦌	Pod glands were assigned to the following categories: Absent = 0, scarce/scattered = 0.5 and dense = 1. Treated as an ordinal variable.	Coe and Coe (1987)

Environmental indices

Spatial maps of aridity, fire and herbivory were obtained for Africa. Aridity was represented by two bioclimatic variables sourced from WorldClim at 0.5-degree resolution (Fick and Hijmans 2017): mean annual precipitation (MAP, in mm) and rainfall seasonality (coefficient of variation); and by the standardized precipitation and evapotranspiration index (SPEI) which conveys the drought proneness and severity of an area (Begueria et al. 2014). Fire intensity (Fire radiative power, in megawatts per pixels) provides a measure of the rate of energy released by fire, where more intense fires are 'hotter' and are more likely to cause tree top-kill because it correlates with flame length (Archibald et al. 2013). Fire intervals (Fire return intervals, in years) provide an estimate of the period between successive fire events that allow plant growth or recovery from disturbance (Giglio et al. 2010, Archibald et al. 2013). Data for both were obtained from Archibald et al. (2013); the fire return interval and fire intensity were calculated for a fourteen-year (1997-2010) dataset. Herbivore pressure was calculated as the sum of the browser biomass estimates and half of the mixed feeder biomass estimates from Hempson et al. (2015). Elephants were removed from the biomass estimates because it was assumed that the adaptations of trees to elephant consumption would be different to those of other mammalian herbivores considered here. Elephants cause excessive non-specific damage to woody plants, which is often unrelated to plant consumption, such as tree snapping and bark stripping (Midgley et al. 2005). Other herbivores are more selective feeders.

Linking species traits and environmental factors

Locality records for native African acacia (i.e. *Vachellia* and *Senegalia*) species were obtained for the African continent from Greve et al. (2012). To investigate how species traits are influenced by environmental factors, raster values of the environmental data per species locality record were extracted using the '*raster*' (Hijmans 2022), '*rgdal*' (Bivand et al. 2022), '*sp*' (Pebesma and Bivand 2005, Bivand et al. 2013) and *maxent'* (Phillips 2017) packages in R. To remove sampling bias from the locality records, only one record per degree cell was randomly selected using grid sampling from the '*dismo*' package (Hijmans et al. 2021).

Analyses

Analyses were performed in RStudio version 1.2.1335 (R Core Team 2021). All analyses were conducted separately for *Vachellia* and for *Senegalia* species to account for their separate phylogenetic placement (Bouchenak-Khelladi et al. 2010), and to account for phylogenetic non-independence between these two genera. Species-level phylogenetic non-independence was not further considered because the most complete phylogenetic tree of African acacias is missing the majority of species of this group (Bouchenak-Khelladi et al. 2010).

Skewed variables were transformed and all variables were scaled and centred before the analyses were performed to meet model assumptions. Pearson's correlation analysis was conducted to identify highly correlated predictor variables (Appendix Table B2), using the '*stats*' package (R Core Team 2021).

Trait-environment relationships

To investigate how the expression of a single trait is influenced by different environmental filters, an ordinary least squares (OLS) regression model was fitted for each continuous trait (i.e. excluding bark texture, pod investment and pod glands) in response to the best subset of environmental predictors (mean annual precipitation, rain seasonality, drought severity, fire interval, fire intensity and browser pressure). The best subset model was used to select the most parsimonious model using the '*leaps*' package (Lumley 2017). Predictor and response variables were transformed to meet model assumptions (Table 2 and Appendix tables B3 and B4). To investigate the effects of environmental variables on ordinal trait variables, regression analyses were performed using cumulative link models from the '*ordinal*' package (Christensen 2019) and '*RVAideMemoire*' (Hervé 2022); the best subset models with a Hessian condition below e^{+04} were accepted (Christensen 2018). Predictor variables were transformed if there was sufficient evidence of non-proportional odds. Benjamini-Hochberg corrections were performed on the OLS regression model outputs and the cumulative link model results to correct for the comparisons of multiple analyses (Benjamini and Hochberg 1995) using the '*stats*' package (R Core Team 2021).

A constrained ordination was performed for *Vachellia* and *Senegalia* using redundancy analyses, from the '*vegan*' package (Oksanen et al. 2019) and '*car*' (Fox et al. 2019), to assess how much trait variation is explained by the combined environmental variation. The ordinal variables were treated as numeric values (Robitzsch 2020).

Trade-offs among traits

An OLS regression model was used to assess whether a reduced leaf area and greater leaf protection (spine-leaf ratio) showed a trade-off with plant height (Wakeling et al. 2011) and (Dayrell et al. 2018). A cumulative link model was used to investigate the expected trade-off between bark roughness and plant height (Lawes et al. 2013), using bark texture as an ordinal response variable.

Clustering/syndromes

Species with similar trait investment strategies were identified using hierarchical cluster analysis, from the '*pvclust*' package (Suzuki et al. 2019), with centred Pearson distance and average linkage. A principle component analysis was performed to visualise the species clusters based on traits, using the '*stats*' package (R Core Team 2021), '*ggbiplot*' (Vu 2011) and '*ggplot2*' (Wickham 2016). To investigate how environmental variables drive species cluster formation, a generalized canonical discriminant analysis was performed using the '*candisc*' package (Friendly and Fox 2021). Ordinal variables were treated as numeric data.

Results

Trait-environment relationships

The results of the regression analyses for *Vachellia* species suggested that leaf area, maximum plant height, canopy height, and the spine-leaf ratio was lower for more mesic (i.e. higher precipitation) species (Table 2). The constrained ordination analysis (Figure 2a) supported these findings. The canopy width-length ratio increased (i.e. the crown became more umbrella-like and less rounded) as rainfall increased (Table 2), but this relationship was not clearly indicated in the RDA analysis. Instead, higher rainfall seasonality appeared to select for umbrella-shaped rather than round canopies (Table 2 and Figure 2b). Highly seasonal rain and severe droughts also showed a weak positive relationship with the spine-leaf ratio and a negative relationship with rougher bark texture (Figure 2a) and leaf area (Figure 2b). Increased fire return intervals (infrequent fires) had a weak relationship with increased spine-leaf ratios, a strong relationship with smoother (less rough) bark texture (Figure 2a) and decreased leaf area (Table 2, Figure 2b). The crown was also more umbrella-shaped as the fire return interval increased (Table 2 and Figure 2b). Infrequent fires showed a positive relationship with maximum tree height and canopy height (Table 2) but this relationship was not clear in the RDA. More intense fires were associated with taller plants with greater canopy height (Table 2 and Figure 2b). For every one unit increase in fire intensity, the odds of having dense pod glands multiplied 3.653 times for *Vachellia* species (Table 3) and this positive relationship corresponded with the results of the RDA analysis (Figures 2a and 2b). Intense fires also showed a weak relationship with rougher bark texture and a more rounded canopy shape (decreased canopy width-length ratios; Figures 2a and 2b). High browser pressure selected for higher spine-leaf ratios (Table 2), although this association was weak in the RDA plots (Figures 2a and 2b). Browsers also showed a weak, negative relationship with tree height, canopy height and pod investment (Figures 2a and 2b).

In *Senegalia* seasonal rainfall and greater drought severity showed a negative relationship with leaf area and the maximum plant height (Table 2). Both genera had decreased leaf area and height in response to measures of aridity, although the specific variables differed (precipitation for *Vachellia*, versus rain seasonality and drought severity for *Senegalia*). The RDA analysis suggests drought severity has a stronger, negative relationship with leaf area (Figures 3a and 3b) but not with height, whereas high rainfall seasonality has a negative relationship with height and a weak relationship with decreased leaf area (Figure 3a). Severe drought also had lower canopy heights (Figure 3a). Highly seasonal rainfall showed decreased pod investment whereas tree height and pod investment increased with precipitation (Figures 3a and 3b). Precipitation also showed a weak, negative relationship with increased canopy width-length ratios. Unlike *Vachellia, Senegalia* did not show fire return interval and fire intensity as significant predictors of leaf area or height in the OLS regression analyses. The RDA of *Senegalia* shows a negative relationship between leaf area and longer fire return intervals (Figure 3a) and intense fires showed a negative relationship with tree height (Figure 3b). Long fire return intervals (infrequent fires) also had a weak relationship with reduced canopy height (Figure 3a) and smoother bark (decreased bark texture, Figure 3b). Similar to *Vachellia*, each unit increase in fire intensity showed a greater likelihood of having dense pod glands (increases 29.099 times) in *Senegalia* species (Table 3, Figures 3a and 3b). Intense fires also showed a positive relationship with rough bark (increased bark texture) and a weak relationship with more umbrella-shaped canopies (Figures 3a and 3b). Browsers also had a weak relationship with more umbrella-shaped canopies, rough bark and dense pod glands (Figure 3a). Browsers also showed a negative relationship with pod texture (less woody, more coriaceous or thinly-textured pods; Figures 3a and 3b).

Table 2: Results of ordinary least-squares regression models (OLS) for *Vachellia* and *Senegalia* species depicted significant relationships between a trait and selected environmental variables based on the best subset model with the lowest Bayesian Information Criterion (BIC) values. P -values highlighted by an asterisk (*), remained significant after performing the Benjamini-Hochberg correction. R^2 and model p-values of the below models, as well as non-significant models, are shown in Appendix Tables B3 and B4. Fire interval = fire return interval.

Vachellia	**Coefficients:**	**Estimate**	**Std. error**	**t-value**	**p-value**
Leaf area	Precipitation	0.450	0.155	2.913	0.006*
	sqrt(Rain seasonality)	0.669	0.462	1.449	0.154
	Fire interval	-0.310	0.145	-2.137	0.038*
Height	sqrt(Precipitation)	1.468	0.437	3.363	0.002*
	log(Fire interval)	1.095	0.420	2.605	0.012*
	sqrt(Fire intensity)	0.956	0.389	2.456	0.018*
Canopy height	sqrt(Precipitation)	1.522	0.447	3.402	0.001*
	log(Fire interval)	0.926	0.423	2.192	0.034*
	Fire intensity	0.168	0.144	1.163	0.251
sqrt(Canopy width-length ratio)	Precipitation	0.163	0.058	2.823	0.007*
	Rain seasonality	0.158	0.050	3.158	0.003*
	Fire interval	0.150	0.054	2.780	0.008*
sqrt(Spine-leaf ratio)	sqrt(Precipitation)	-0.331	0.119	-2.790	0.008*
	Browser	0.104	0.045	2.297	0.026*
Senegalia	**Coefficients:**	**Estimate**	**Std. error**	**t-value**	**p-value**
log(Leaf area)	Rain seasonality	-0.368	0.108	-3.395	0.002*
	Drought severity	-0.236	0.108	-2.179	0.035*
log(Height)	Rain seasonality	-0.195	0.062	-3.149	0.003*
	Drought severity	-0.133	0.062	-2.143	0.038*

Table 3: Results of cumulative link models for *Vachellia* and *Senegalia* species depicting significant relationships between an ordinal trait and selected environmental variables based on the best subset model with the lowest Bayesian Information Criterion (BIC) values. P-values highlighted by an asterisk (*), remained significant after performing the Benjamini-Hochberg correction. Log-likelihood, model Hessian values, and non-significant models, are shown in Appendix Tables B5 and B6.

Vachellia	**Coefficients:**	**Estimate**	**Std. error**	**2.5% CI**	**97.5% CI**	**Odds ratio**	**χ^2**	**p-value**
Pod glands	Precipitation	-0.556	0.477	-1.578	0.330	0.573	1.466	0.226
	Fire intensity	1.296	0.418	0.539	2.111	3.653	12.129	<0.001*
	Browser	-0.138	0.397	-0.934	0.651	0.871	0.120	0.728
Senegalia	**Coefficients:**	**Estimate**	**Std. error**	**2.5% CI**	**97.5% CI**	**Odds ratio**	**χ^2**	**p-value**
Pod glands	Rain seasonality	-0.553	0.502	-1.623	0.413	0.575	1.262	0.261
	log(Fire intensity)	3.371	1.304	1.181	6.6360	29.099	11.475	<0.001*

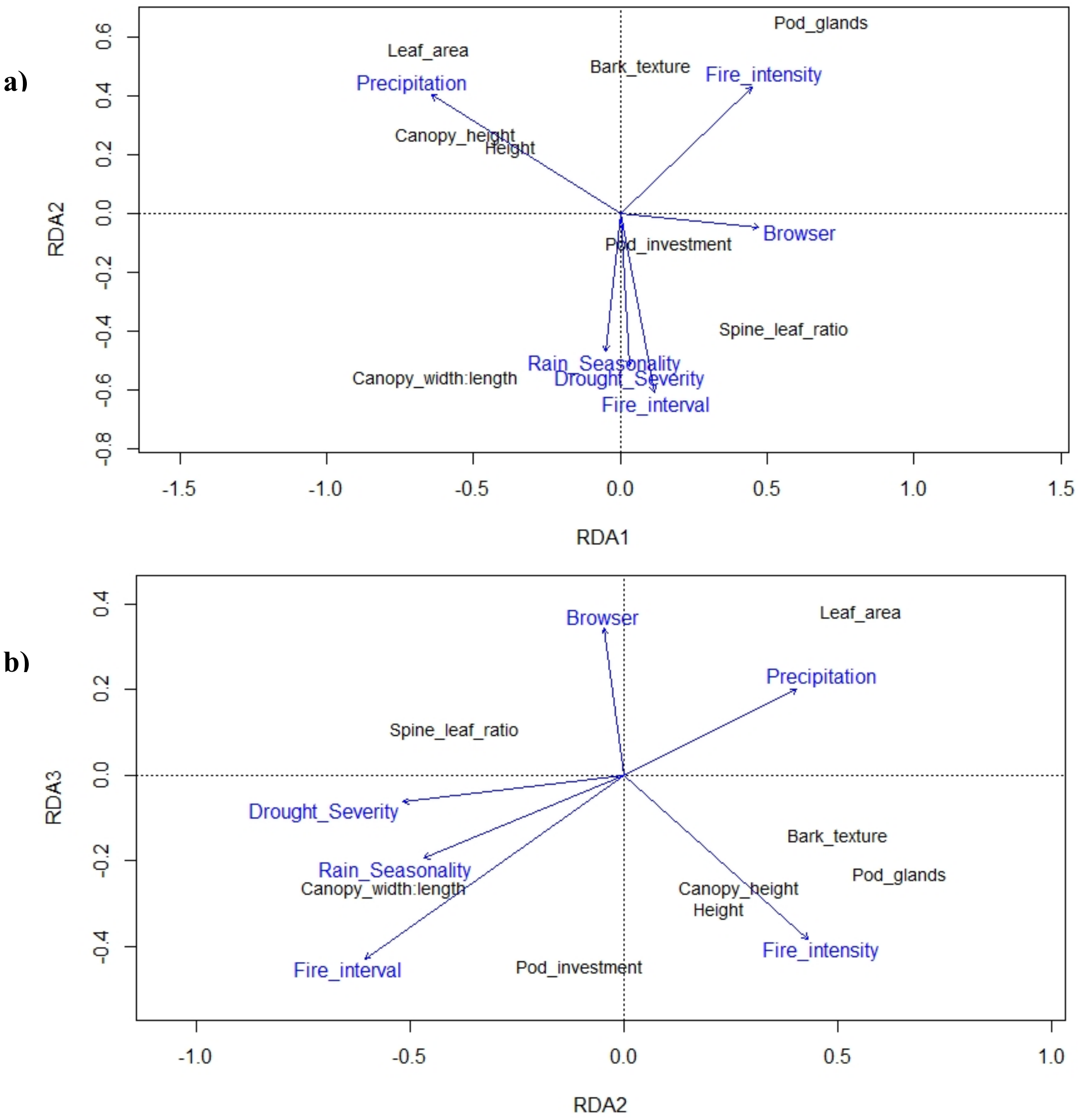


Figure 2: *RDA plots showed the amount of trait variation in* Vachellia *species explained by the environmental variables (25.52%, p = 0.001). The first three RDA axes explain 42.33%, 31.96% and 13.53% of the constrained eigenvalues respectively (cumulative proportion = 87.81%).* ***a)*** *RDA plot of the first and second RDA axes.* ***b)*** *RDA plot of the second and third RDA axes. Fire interval = fire return interval.*

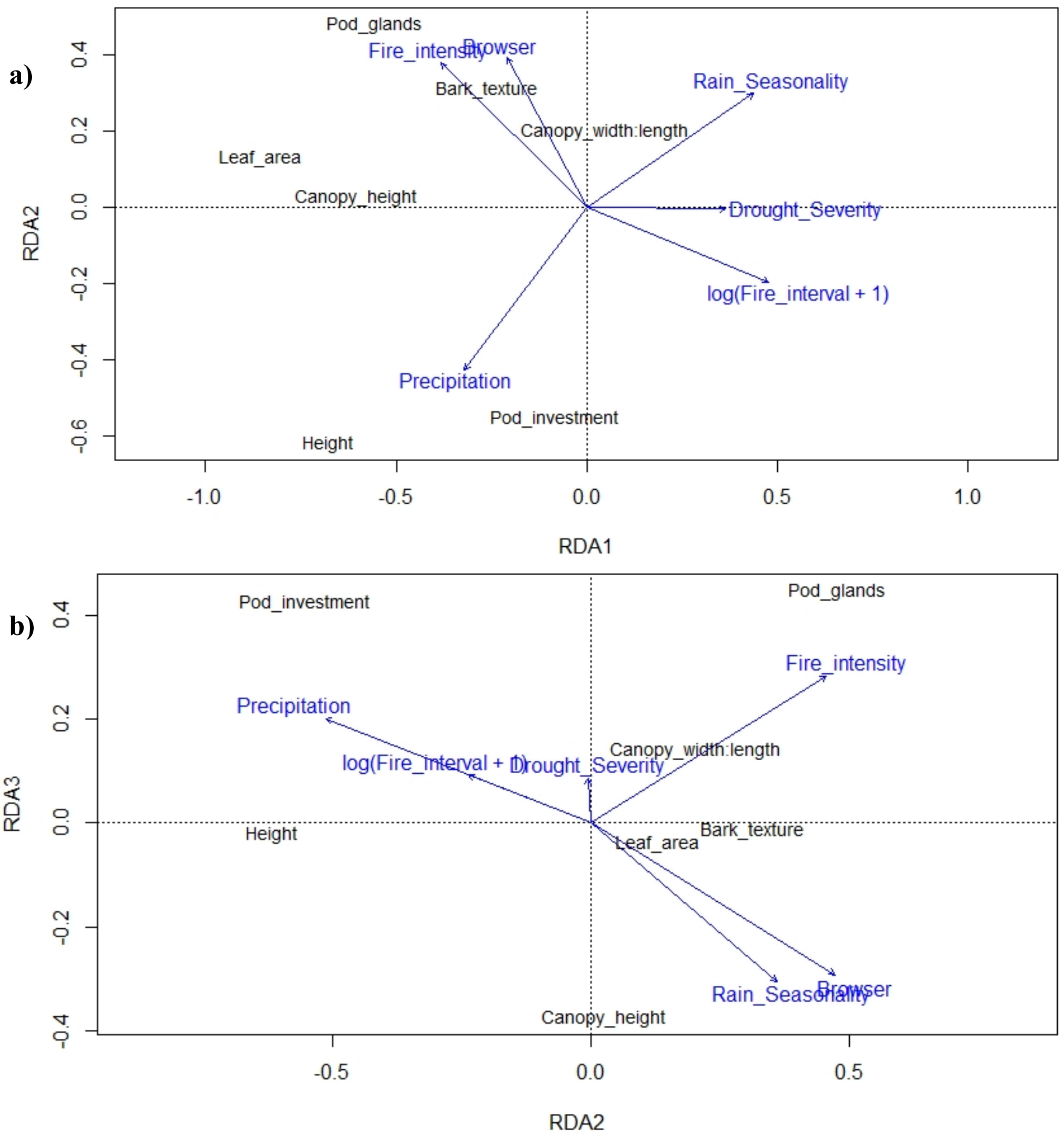


Figure 3: *RDA plots showed the amount of trait variation in Senegalia species explained by the environmental variables (23.52%, p = 0.008). The first three RDA axes explained 48.22%, 26.56% and 13.49% of the constrained eigenvalues respectively (cumulative proportion = 88.28%).* ***a)*** *RDA plot of the first and second RDA axes.* ***b)*** *RDA plot of the second and third RDA axes. Fire interval = fire return interval*

Trade-offs

Vachellia species did not show any significant trade-offs, based on the linear regression model and cumulative link model (Appendix Table B7 and B8). *Senegalia* species revealed that larger leaf areas correspond with increased height gain (R^2=0.152 and p=0.01, refer to Appendix Table B7). Contrary to predictions, each unit increase in plant height increased the probability of having rougher bark by 2.178 (Appendix Table B8).

Clustering/Syndromes

The hierarchical cluster analysis revealed four significantly different species clusters for *Vachellia* (clusters A-D), based on the approximately unbiased p-values from multiscale bootstrap sampling (Figure 4a). Based on the principal component biplot (Figure 4b), species from cluster A showed greater canopy height, increased canopy width-length ratio (more umbrella-shaped) and greater plant height. Species with these traits occurred in areas with short fire return intervals (frequent fires), higher mean annual precipitation, low browser biomass, low rain seasonality and lower drought severity (Figure 4c). Species from cluster A and cluster B showed more similar trait investment strategies than with clusters C and D (Figure 4a). Unlike species from cluster A, species from cluster B had larger leaf areas, greater pod investment (woodier pods), rougher bark texture and lower spine-leaf ratios (Figure 4b). Both trait clusters (clusters A and B) were associated with species that shared similar environmental conditions (Figure 4c), where frequent fires seemed to be the main environmental constraint. Species from cluster A and species from cluster C seemed to invest in opposing syndromes (Figures 4a and b). Species from cluster C showed lower canopy height, rounder canopies and reduced plant height (Figure 4b). These species originated from areas with greater drought severity, increased rainfall seasonality and longer fire return intervals (Figure 4c). Species in cluster D showed higher pod gland density, smaller leaves, lower pod investment (papery or thinly-textured pods) and lower bark texture (smoother bark, Figure 4b). Species in cluster D occurred in a distinct set of environmental conditions with higher browser biomass, greater fire intensity and lower mean annual precipitation (Figure 4c).

a)

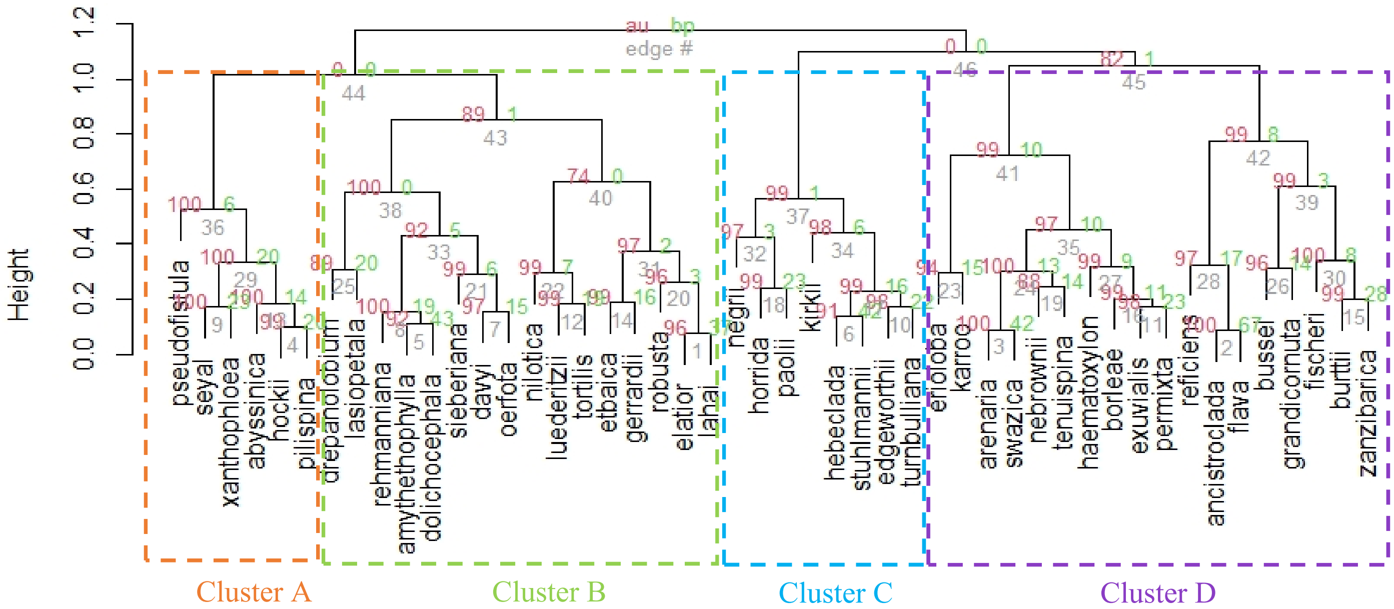


Figure 4 a) *A cluster dendrogram revealed four* Vachellia *species clusters as indicated by the different colours (cluster A = orange, B = green, C = blue and D = purple). Dendrogram branch values: au (brown) = Approximately unbiased p-values from multiscale bootstrap resampling, bp (green) = Bootstrap probability.*

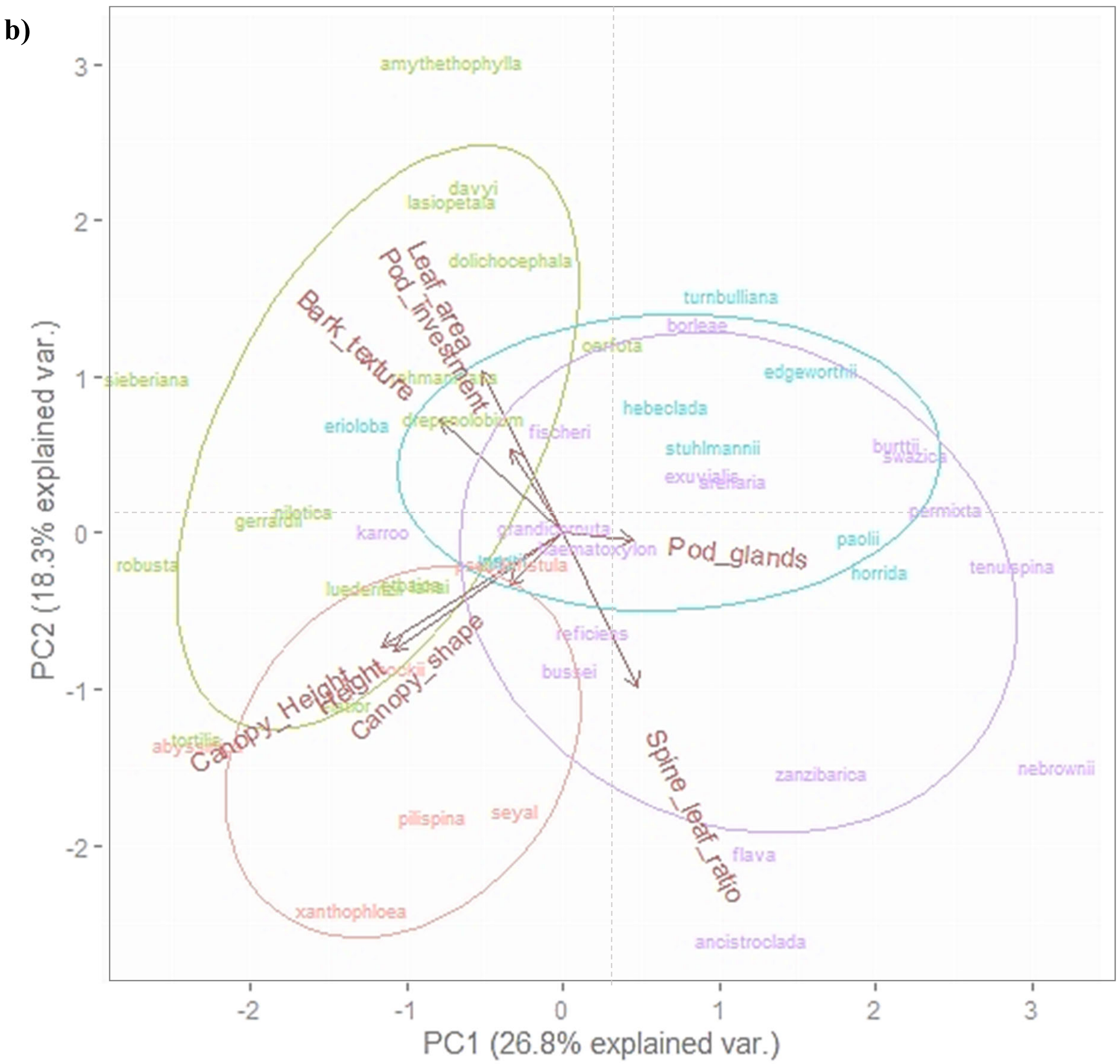


Figure 4b) *A principal component analysis (PCA) biplot showed* Vachellia *species clustered according to the similarity in trait values. Clusters were identified using the same colour scheme as figure 4a (i.e. cluster A = orange, B = green, C = blue and D = purple). The biplot ellipses represent the 95% confidence intervals of the species cluster responses.*

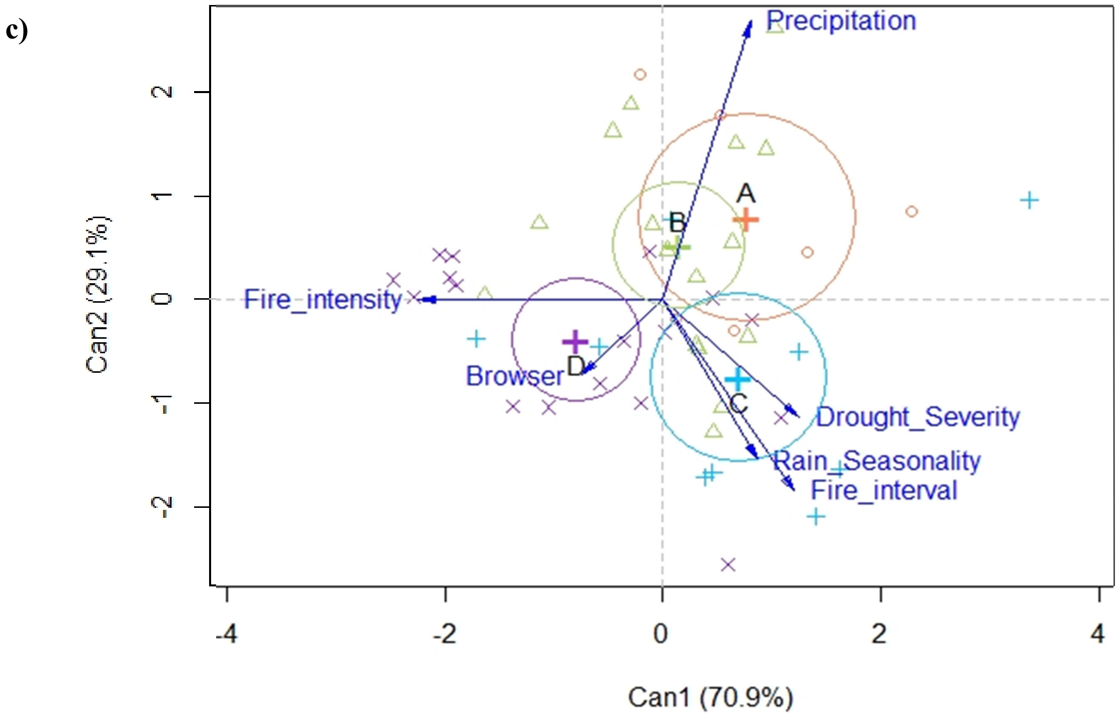


***Figure** 4c) Canonical discriminant analysis (CDA) plot displayed* Vachellia *species clusters in response to the various environmental drivers (cluster A = orange, B = green, C = blue and D = purple). The CDA plot ellipses represent the 95% confidence intervals of the species cluster responses. Fire interval = fire return interval.*

The hierarchical cluster analysis of the *Senegalia* species also showed four significant group clusters based on the approximately unbiased p-values from the bootstrap probabilities (Figure 5a). Species from cluster A seemed to have distinct traits (Figure 5a). The principal component analysis biplot indicated species from cluster A had denser pod glands, high canopy width-length ratios (more umbrella-shaped canopies), lower pod investment (more papery pods) and decreased plant height (Figure 5b). Species with these traits originated from regions with higher rainfall seasonality, greater fire intensity, higher browser biomass, lower mean annual precipitation, and reduced drought severity (Figure 5c). Cluster B showed increased pod investment (woodier pods), sparse to absent pod glands and lower canopy width-length ratios (rounder canopies, Figure 5b). These species occurred in distinct environmental conditions with no overlap in the 95% confidence intervals (Figure 5c); cluster B had increased drought severity, lower browser biomass and reduced fire intensity (Figure 5c). Species in cluster C had denser pod glands, increased canopy width-length ratios (more umbrella-shaped canopies), rougher bark texture, higher canopies and lower pod investment (thinly textured or more papery pods, Figure 5b). Species with these traits originated from regions with higher browser biomass, increased fire intensity and reduced mean annual precipitation (Figure 5c). Similar to cluster C, cluster D had rougher bark and increased canopy height, however, species from cluster D also had greater height, higher woody pod investment, larger leaves and less dense or absent pod glands (Figure 5b).

Cluster D species originated from regions with higher rainfall seasonality and shorter fire return intervals (Figure 5c).

There was some similarity in trait syndromes between the two genera. *Vachellia* and *Senegalia* both showed similar syndromes linked to frequent fire (Figures 4c and 5c). Traits included taller canopies, increased plant height, high pod investment, rough bark and larger leaves (Figures 4b and 5b). Severe droughts selected for rounder canopies in *Vachellia* and *Senegalia*, although *Senegalia* also showed increased pod investment with little to no glands whilst *Vachellia* had reduced height and lower canopies (Figures 4c and 5c). Both genera showed low pod investment and high pod gland density in regions with high browser biomass, high fire intensity and low precipitation (Figures 5b and 5c). However, there were also differences in trait syndromes at these conditions with *Vachellia*, but not *Senegalia*, displaying smaller leaves and smoother bark and *Senegalia*, but not *Vachellia*, had increased height and taller umbrella-shaped canopies.

a)

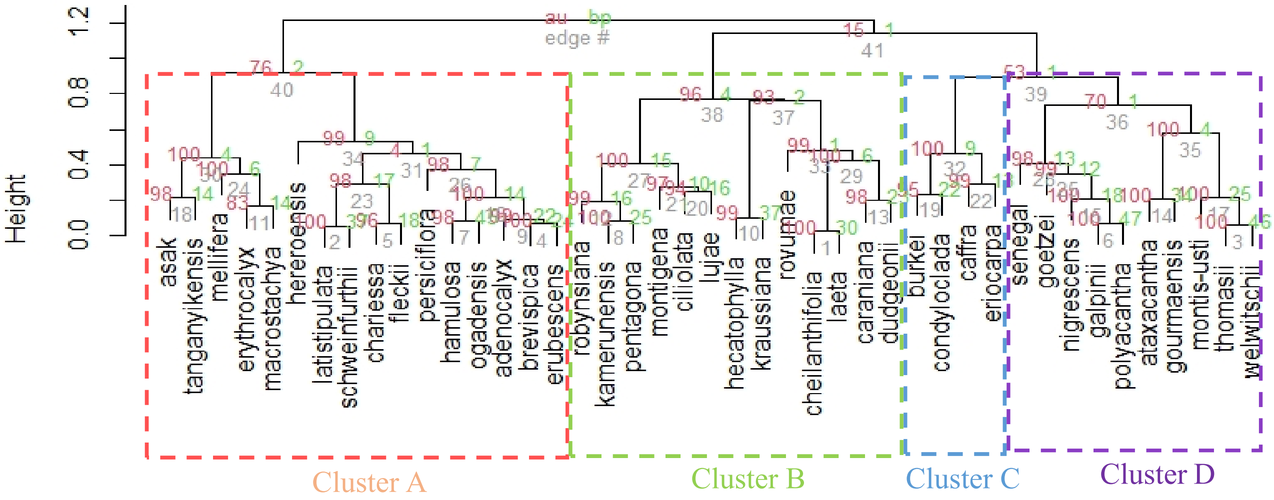


Figure 5a) *A cluster dendrogram revealed four* Senegalia *species clusters as indicated by the different colours (cluster A = orange, B = green, C = blue and D = purple). Dendrogram branch values: au (brown) = Approximately unbiased p-values from multiscale bootstrap resampling, bp (green) = Bootstrap probability.*

b)

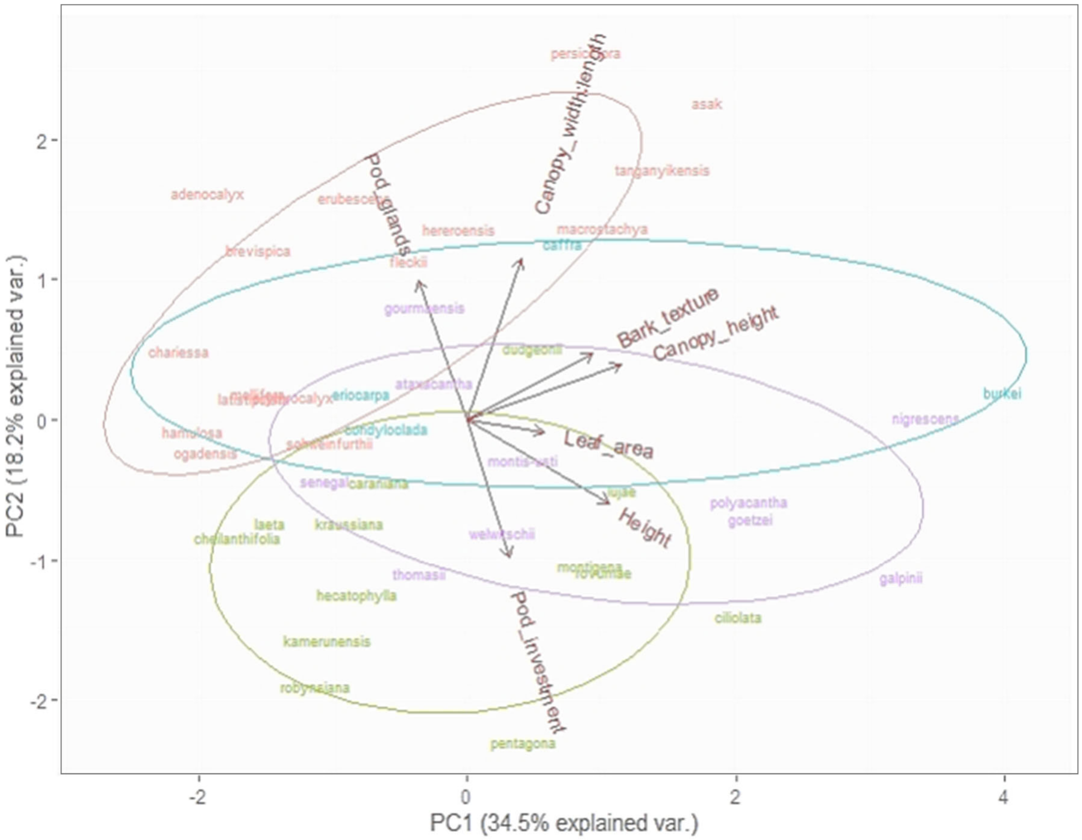


Figure 5b) *A principal component analysis (PCA) biplot showed species clustered according to the similarity in trait values. Clusters were identified using the same colour scheme as figure 5a (i.e. cluster A = orange, B = green, C = blue and D = purple). The biplot ellipses represent the 95% confidence intervals of the species cluster responses.*

c)

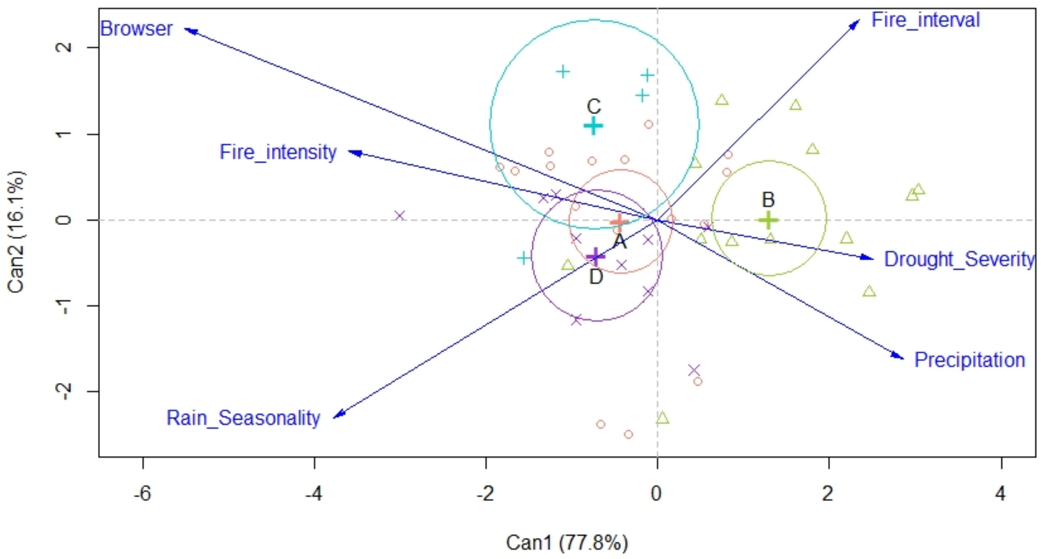


***Figure* 5c)** *Canonical discriminant analysis (CDA) plot displayed* Senegalia *species clusters in response to the various environmental drivers (cluster A = orange, B = green, C = blue and D = purple). The CDA plot ellipses represent the 95% confidence intervals of the species cluster responses. Fire interval = fire return interval.*

Discussion

Here I have investigated how savanna drivers influence adult acacia traits and trait syndromes. We found that traits of *Vachellia* and *Senegalia* species varied along gradients of aridity, fire and browsing. Only limited evidence was found to indicate trade-offs between traits. Four different syndromes were identified for each genus with unique combinations of traits, with specific syndromes being associated with different environmental conditions.

Trait responses to savanna drivers

Because savannas occur across wide rainfall gradients (Lehmann et al. 2011, February et al. 2020, Ratnam et al. 2020) and because water is a major limiting factor for tree establishment in more arid savannas (Sankaran et al. 2008) I expected that aridity would be an important driver of acacia traits. Species from arid areas displayed smaller leaves, decreased height, umbrella-shaped canopies, lower canopies, smoother bark and thinly textured or papery pods. Reduced leaf size minimises water loss (Otieno et al. 2005) and provides an advantage where water availability is limited. Shorter trees have lower water requirements than tall trees, resulting in reduced vulnerability to hydraulic stress (Zhang et al. 2009, Bennett et al. 2015). Shorter trees also had lower canopies. Lower canopies can also lead to the exclusion of other plants by competition (Blaser et al. 2013). In general, species from arid environments have a more umbrella-shaped canopy (Gaillard et al. 2018) which corresponded with my results. Wider, umbrella-shaped canopies lower soil temperatures beneath the canopy which reduces evapotranspiration (Belsky et al. 1993). Lower, umbrella-shaped canopies in *Vachellia* species at higher rainfall can out-shade, and thus reduce competition with grasses and other plant species, particularly for nitrogen which has low concentrations in highly leached mesic savannas, (Scholes and Scholes 1997, Bond et al. 2008, February and Higgins 2010, February et al. 2013). *Vachellia* species also invested in smoother bark which reflects a higher water storage capacity of the inner bark (Rosell et al. 2014). This provides a buffer for woody species adapted to highly periodic rainfall (Scholz et al. 2007). *Senegalia* species invested in thinly textured or papery pods in arid systems; these may be cheaper to produce (Lamont et al. 1991, Ayadi et al. 2012).

Fire

Fire is a non-selective consumer of aboveground biomass (Archibald and Hempson 2016). Fire frequency and intensity often show an antagonistic relationship where shorter fire return intervals are associated with reduced fire intensity and *vice versa* (Archibald et al. 2013). In flammable systems, woody species were therefore expected to show traits to survive either frequent or intense fires. *Vachellia* and *Senegalia* species from areas with frequent fires invested in larger leaves and species from areas exposed to frequent or intense fires had rough bark and dense pod glands. Larger leaves have greater photosynthetic capacity; this may facilitate rapid recovery after the loss of aboveground biomass (Ackerly et al. 2002, Poorter et al. 2009). Fast recovery may be especially important in areas that experience frequent fires for plants to escape the fire trap (Staver et al. 2012). In areas with hotter fires, rough bark can provide resistance to fires. Rough bark creates air pockets that reduce heat penetration (Romero 2014) and result in slower burning (Fréjaville et al. 2013). The advantage of pod gland secretion in fire-prone environments was not clear. Coe and Coe (1987) theorised that pod gland secretions deter insects or seed predators; however, how this relates to fire regime is uncertain.

The two genera possess different architecture strategies in areas with frequent *vs* hot fires. *Vachellia* species from systems with intense fires were taller, had greater canopy height and rounded canopies. Longer fire return intervals allow species to grow above the flame height despite greater fire intensity; this may result in taller individuals with higher canopies (Levick et al. 2019). Unlike *Vachellia, Senegalia* species tended to be short trees or shrubs with umbrella-shaped canopies where fire intensity is high. Shorter trees must persist within the flame zone by prioritising bark accumulation rates to obtain thick, corky bark (Dantas and Pausas 2013, Pausas 2015, Hempson et al. 2020).

Browsing

I expected acacias to possess structural defences to reduce browser access to foliage (Archibald and Bond 2003, Wigley et al. 2015) and slow browser feeding rates (Charles-Dominique et al. 2020). In areas with high browser biomass, *Vachellia* species displayed greater spine-leaf ratios, reduced height and low canopies. Both genera had thinly textured or coriaceous pods. *Senegalia* species showed umbrella-shaped canopies, rough bark and dense pod glands. Increased spine length relative to leaf size in highly browsed environments indicates that *Vachellia* prioritise leaf protection (Pérez-Harguindeguy et al. 2013, Wigley et al. 2015). Longer spines slow down the rate of browsing and are an important browser deterrent in *Vachellia* species (Wigley et al. 2022). Shorter trees with low canopies are more exposed to herbivory than taller trees. However, height trades off against a cagey architecture (Hempson et al. 2020), which in turn provides structural defence against herbivory (Archibald and Bond 2003, Staver et al. 2012). Therefore, the low height of *Vachellia* in areas with high browsing may reflect the investment of trees in caginess at a cost to tree height. (Ayadi et al. 2012). Indehiscent or woody pods have a hardy structure to protect seeds against damage and are more nutritious than thinly textured pods (Gwynne 1969, Lamont et al. 1991, Groom and Lamont 1997). Indehiscent pods were expected to be an adaptation to herbivore-assisted seed dispersal via pod consumption (Coe and Coe 1987, Miller 1994) but are costly to produce (Gwynne 1969). Species from highly browsed systems invested less in hardy pods but perhaps in a greater quantity to spread the risk of seed damage during consumption (Paul-Victor and Turnbull 2009). Umbrella-shaped canopies reflect increased lateral branching (Ding et al. 2021) which reduces browser access to foliage at the top of the canopy. Rough bark with projections observed in *Senegalia* may reduce the consumption of bark by browsers, protecting the stem cambium (Romero 2014, Jager et al. 2015, Rosell 2019). Dense pod glands in *Senegalia* could deter browsers to prevent the consumption of immature pods before the pods dehisce (Miller 1994).

Adult acacias mainly showed resistance strategies in response to environmental pressures. The effects of aridity could be mitigated by reducing the embolism events (smaller leaves and shorter trees) and by decreasing the loss of soil evapotranspiration (umbrella-shaped canopies). In fire-prone systems, rough bark texture may minimise fire-related heat damage, particularly for *Senegalia* species that persist within the flame zone. Lastly, species from highly browsed areas showed structural defences to minimise foliage loss, such as high spine-leaf ratios, low or umbrella-shaped canopies and rough bark.

Trade-offs

The selected traits did not show any trade-offs for *Vachellia* species. *Senegalia* species showed that smaller leaves constrain plant height gain, possibly indicating a trade-off in strategies linked to desiccation avoidance or plant growth (Otieno et al. 2005, Pérez-Harguindeguy et al. 2013). Prioritised investment in stem insulation against fire damage creates a trade-off with plant growth (Lawes et al. 2013). Contrary to expectation, *Senegalia* species showed rougher bark for taller individuals.

Clustering/Syndromes

Both *Vachellia* and *Senegalia* species revealed syndromes linked to certain environmental conditions. In both genera, four unique trait clusters were identified that were mostly associated with combinations of different predictors. However, the combination of traits that defined the syndromes differed between the two genera. For example, in *Vachelli*a, one syndrome possessed tall trees with a high canopy height and an umbrella-shaped crown. In contrast, in *Senegalia* these three architectural traits were not strongly associated with one another in a single syndrome.

Our results also suggest that for some environmental conditions, species can display different trait syndromes. For example, in *Vachellia* species from areas which especially experience high precipitation and frequent fires, species were grouped into two distinct clusters based on traits: one displayed taller trees with higher umbrella-shaped canopies and the other displayed larger leaves with reduced spine development, rough bark and woody pods.

Furthermore, species showed evidence of adaptations where one strategy was used in different environments. For example, both *Vachellia* and *Senegalia* species displayed shrub-like architecture in areas that experienced both aridity and browsing. The functional advantage differs in arid vs highly browsed environments. Shrubs are less susceptible to water stress than trees, indicating an adaptation to aridity. However, shrubs, which are mostly cage-like in architecture, also reduce browser access to the foliage at the centre of the tree. A desiccation avoidance strategy thus also serves as a strategy to resist browsing.

Caveats

The number of functional traits that can be gleaned from field guide descriptions is limited, and the traits that were available do not necessarily reflect the most important adaptive responses to the pressures experienced by savanna trees. For example, bark thickness is an important adaptation to fire (Schafer et al. 2015, Rosell 2016), but was not available. This necessitated the use of morphological traits as proxies for physiological trait investment strategies (i.e. bark texture as a proxy for bark thickness). Furthermore, field guides provide a general description of species characteristics, but only maximum values were used in analyses. It is well-known that widespread acacias show variation in traits based on their provenance (Archibald and Bond 2003, Wigley et al. 2019, Tsvuura and Ward 2022), which could suggest local adaptation to varying conditions experienced by these species across their range. Such interspecific variation was not considered in the analyses here. Finally, phylogenetically informed analyses strengthen detected trait-environment and trait-trait relationships (Martins and Hansen 1997, Wigley et al. 2016). However, a complete phylogenetic tree was unavailable for African acacias. The most updated tree (Bouchenak-Khelladi et al. 2010) omits a large percentage of African acacia species. Therefore, non-phylogenetically informed analyses were used, but separately for the two genera to reduce the effects of phylogenetic non-independence on results. Also, Wigley et al. (2016) showed for African savanna trees that non-phylogenetically informed analyses produce similar results to phylogenetically informed methods despite the anticipated constraint of species phylogeny on trait variation.

Conclusion

Here I show that morphological traits of African acacias could be linked to their biogeography; more specifically the most important drivers of savanna structure (Lehmann et al. 2011, Ratnam et al. 2011). Little evidence of trait trade-offs was evident for adult trees; though this could be a result of the limited trait data that were available from the literature from which to assess trade-offs. Trait clusters reflected the survival strategies in response to aridity, fire and herbivory. This suggests that trait syndromes reflect the most limiting factors (Brouwer 1963, Sankaran 2019, Boonman et al. 2020). Understanding species responses to environmental constraints enables a better understanding of how species may respond to changing environmental conditions (Corrêa Scalon et al. 2020). Indeed, in Africa, fire regimes are changing, large herbivores have been lost from large expanses, and climates are changing (Hempson et al. 2015, Sankaran 2019, Hamilton et al. 2022). Therefore, an increasing demand exists for research characterising trait syndromes and trait functions of savanna woody species linked to climate (including precipitation and drought), and the survival of disturbances (fire and browsing) (Osborne et al. 2018). Climate change and predicted increases in drought intensity, economic development and cropland expansion linked to fire suppression and a transition from migratory native herbivores towards sedentary grazing livestock, and loss of herbivore biomass interact and result in savanna degradation and bush encroachment (Stevens et al. 2016, Andela et al. 2017, Osborne et al. 2018, Sankaran 2019). Our study includes two of the broad categories linked to encroachment (climate and disturbances) and provides a starting point for further research into the mechanics of savanna ecosystems.

Chapter four

General conclusion

Savannas constitute the largest biome on the African continent (Rutherford et al. 2006). The coexistence of both the grass and tree layer is required to maintain savanna structure (Coetsee et al. 2010, Higgins et al. 2015). Savanna biome transitions are regulated by the responses of grass and woody species to aridity, fire and herbivory (Lehmann et al. 2011, Ratnam et al. 2011). Species' adaptations to their environment are indicated by the functional traits they possess (Stevens et al. 2016, Corrêa Scalon et al. 2020). Therefore, I used a range of data sources (seedling traits recorded from a greenhouse experiment, species locality records, spatial datasets, literature sources, field guides and photographs) to identify traits and syndromes of savanna woody species at both the seedling and the adult stage that respond to gradients of aridity, fire and browser pressure.

The trait biogeography of seedling and adult mimosoids

Savanna woody species experience a demographic bottleneck caused by the limited recruitment of seedlings to the sapling phase (Bond and Midgley 2001, Gignoux et al. 2009). Therefore, Chapter 1 assessed how providence affects seedling traits in 12 mimosoid species. Although several relationships between the various aridity, fire and browser predictors and woody traits were detected in the univariate linear models, drought severity was the only predictor that differed between the two trait clusters and formed a drought syndrome. The results from this study, therefore, provide further evidence that insufficient water availability and high evaporative demand may form the first environmental constraint savanna seedlings need to overcome. Arid adaptations included deeper and thicker roots that are more likely to penetrate the soil (Goss 1977) and grow deeper to reach belowground water and nutrient reserves (Moles 2018, Boonman et al. 2020). The depth of the fifth lateral root was described as a new trait in this work, inspired by the height of the fifth fork (Charles-Dominique et al. 2015b). The height of the fifth lateral fork represents the exploration of vertical space by woody species based on the height of canopy expansion in response to environmental drivers where decreased height indicates rapid canopy expansion and increased height indicates prioritised height gain (Charles-Dominique et al. 2015b, Wigley et al. 2020). Similarly, we expect the depth of the fifth lateral root to represent the exploration of soil depths by woody seedlings, before the lateral expansion of taproot systems in response to water availability. This trait may facilitate the description of root architecture for woody species in the field where the entire root system cannot be exhumed.

Chapter 2 investigated traits of adult *Vachellia* and *Senegalia* species linked to the average environmental conditions across their native ranges in Africa. A trait database was compiled for most of the native African acacias and syndromes were identified for aridity, fire and browsers. Both genera shared some traits but differed in syndromes and survival strategies. A shrub-like architecture was identified as an exaptation that increases fitness in arid and heavily browsed systems. Low precipitation, intense fires and browsing selected for a unique trait cluster in each genus. Low precipitation was the strongest driver of the aforementioned trait cluster in *Vachellia* and was reflected by prioritised investment in smooth bark, linked to inner bark storage, instead of rough bark for insulation against fire or structural defence against browsing. Furthermore, *Senegalia* species generally persisted at reduced heights within the fire and browser consumption zone, except at low precipitation, intense fires and high browser density where an increased escape height was prioritised. Trait complexes may thus reflect a main limiting factor, or the combined factors select for an alternate survival strategy of other trait complexes that experience similar pressures. Alternatively, different trait clusters identified for regions that experience similar conditions may represent differences in microclimatic conditions experienced by such clusters that are not captured by the macroecological variables used in this work.

A major strength of this work is that trait complexes of both seedling and adult life stages were assessed. Although it was not possible to use identical sets of traits to assess trait relations and syndromes of seedlings and adults, some important trends nevertheless do appear. Certain adaptations seem to remain from seedling to adult stages, such as reduced leaf area in arid-adapted species or shorter architectures in species from highly browsed areas. In contrast, some strategies show the opposite trend in seedlings versus adults. For example, seedlings for species from arid systems were tall, but adult trees were short. The comparison of the broad survival strategies recorded for seedling *vs* adult trees suggests that woody species alter trait investment and survival strategies as they mature (Hinckley et al. 2011). At the seedling stage, traits linked to recovery seemed particularly important. This was especially the case in systems that are prone to fire and herbivory. In these systems, seedlings prioritised traits that facilitate recovery, such as maximising photosynthetic efficiency in disturbance-prone systems. Resistance traits, such as relative bark thickness, showed relatively little differentiation along the disturbance gradients. In contrast to seedlings, resistance seemed to be the dominant strategy to overcome limiting factors by adults. For example, in arid or highly browsed systems species tended to possess a shrub-like architecture. Shrubs are less susceptible to water stress than trees (Götmark et al. 2016, Gaillard et al. 2018) and minimise the consumption of foliage by browsers (Archibald and Bond 2003, Staver et al. 2012). The only trait evidence of a recovery strategy was larger leaves that support resprouting after fire.

Management implications

The survival strategies used by woody species may influence management decisions for the control of encroachment. Management policies aimed at conserving ecosystem services either slow recruitment rates or actively reduce woody cover (Osborne et al. 2018). For example, protocols should consider that seedlings show little investment in resistance strategies. Woody seedlings are thus more vulnerable to disturbances, such as fire and browsing than adults. My findings support the view that established trees are more difficult to eradicate because they possess traits to resist disturbances and would most likely require mechanical intervention for each individual (such as ring-barking). Management strategies should thus be implemented at the seedling stage because fire and browsing can be applied at a landscape-level which requires less effort than the mechanical or chemical removal of seedlings. It is important to note that the mimosoid seedlings studied showed traits to tolerate disturbance, such as belowground reserves, to facilitate seedling recovery after the loss of aboveground biomass by resprouting (Bellingham and Sparrow 2000). However, alteration of the fire regime, such as reducing the recovery time between fires (shorter fire return intervals) or increasing the fire intensity, may kill fire-tolerant seedlings (Archibald et al. 2013, Scholtz et al. 2022).

Opportunities for future research

In order to identify syndromes, the most relevant environmental variables were selected to best represent aridity, fire and herbivory as the main constraints to the survival of woody species in savannas. Syndromes consist of multiple traits that reflect survival strategies in response to the most limiting factor (Brouwer 1963, Sankaran 2019). To isolate the main limiting factor, environmental variables were selected to minimise the interaction between the environmental predictors. Several climatic variables are available to represent water availability. The standardised precipitation evapotranspiration index (SPEI) was selected because it used the average rainfall received whilst accounting for the water lost via evaporation. Further investigation using alternate water availability indices, such as soil water content, would be useful to support the findings of this study. Similarly, two variables were selected to describe the fire regime but five characteristics have been identified to fully describe savanna fire regimes (Archibald et al. 2013). Fire size, for example, might influence canopy height or plant height and warrants further investigation. Browser height would also provide additional information on whether species preferentially invest in escape or resistance strategies. A different set of environmental predictors (to represent aridity, fire and herbivory) may produce additional insights into the formation of syndromes in woody species.

In addition, the selected environmental predictors were extracted across the range of a species and then averaged by species. Also, traits were averaged per species. Therefore, this work does not explore trait adaptations across species ranges. Several African acacias and mimosoids have large geographic ranges (Ross 1979) and can vary in their traits across their distributions, indicating local adaptation (Archibald and Bond 2003, Wigley et al. 2019). Therefore, future research could assess intraspecific trait variation of species, or a subset of species, with a widespread distribution that extends across environmental gradients, to assess whether the patterns assessed at the species-level also hold within species (such as Archibald and Bond (2003), Diatta et al. (2022), Tsvuura and Ward (2022))

Conclusion

Across Africa, shifts from a more grassy, open system to a wooded system with a closed canopy have been observed, with changing rainfall and disturbance patterns being considered major drivers of these trends (Stevens et al. 2016, Hamilton et al. 2022). Vegetation changes can only be predicted or detected if researchers understand: 1) how woody species respond to a biotic or abiotic factor across varying intensities, 2) how the predictors interact to increase or decrease their effects on the vegetation, and 3) which are the main limiting factors for trees across different environmental gradients. These research questions may seem complex but integrating different disciplines (such as experimental observations, literature and spatial distributions) allowed me to disentangle the effects of multiple drivers on both seedling and adult species traits for species with a range of provenances. This study provides a starting point to address the knowledge gap of seedling and adult responses of woody species to disturbances and aridity gradients across African savannas. These functional traits will facilitate the anticipation of floristic responses to changing environments and increasing threats to biodiversity.

Chapter five

References

Abari, A. K., M. H. Nasr, M. Hodjati, D. Bayat, and M. Radmehr. 2012. Maximizing seed germination in two *Acacia* species. *Journal of Forestry Research.* **23**:241-244. doi:10.1007/s11676-012-0248-210.1007/s11676-012-0248-2

Abdelhamed, A. 2020. Residuals and diagnostics for linear regression. RPubs. RStudio. https://rpubs.com/Amrabdelhamed611/669768,

Ackerly, D., C. Knight, S. Weiss, K. Barton, and K. Starmer. 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia.* **130**:449-457. doi:10.1007/s00442010080510.1007/s004420100805

Adams, M. A., T. L. Turnbull, J. I. Sprent, and N. Buchmann. 2016. Legumes are different: Leaf nitrogen, photosynthesis, and water use efficiency. *Proceedings of the National Academy of Sciences.* **113**:4098-4103. doi:doi:10.1073/pnas.1523936113doi:10.1073/pnas.1523936113

Agrawal, A. A., and M. Fishbein. 2006. Plant defense syndromes. *Ecology.* **87**:S132-S149. doi:10.1890/0012-9658(2006)87[132:PDS]2.0.CO;210.1890/0012-9658(2006)87[132:PDS]2.0.CO;2

Allen, K. J., J. Ogden, B. M. Buckley, E. R. Cok, and P. J. Barker. 2011. The potential to reconstruct broadscale climate indices associated with southeast Australian droughts from *Arthrotaxis* species, Tasmania. *Climate Dynamics.* **37**:1799-1821.

Andela, N., D. C. Morton, L. Giglio, Y. Chen, G. R. van der Werf, P. S. Kasibhatla, R. S. DeFries, G. J. Collatz, S. Hantson, S. Kloster, D. Bachelet, M. Forrest, G. Lasslop, F. Li, S. Mangeon, J. R. Melton, C. Yue, and J. T. Randerson. 2017. A human-driven decline in global burned area. *Science.* **356**:1356-1362. doi:doi:10.1126/science.aal4108doi:10.1126/science.aal4108

Anderegg, W. R. L. 2012. Complex aspen forest carbon and root dynamics during drought: a letter. *Climatic Change.* **111**:983-991. doi:10.1007/s10584-012-0421-910.1007/s10584-012-0421-9

Anderegg, W. R. L., T. Klein, M. K. Bartlett, L. Sack, A. F. A. Pellegrini, and e. al. 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences.* **113**:5024-5029. doi:https://doi.org/10.1073/pnas.1525678113https://doi.org/10.1073/pnas.1525678113

Anfodillo, T., G. Petit, and A. Crivellaro. 2013. Axial conduit widening in woody species: A still neglected anatomical pattern. *IAWA journal / International Association of Wood Anatomists.* **34**:352-364. doi:10.1163/22941932-0000003010.1163/22941932-00000030

Archibald, S., and W. J. Bond. 2003. Growing tall vs growing wide: tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos.* **102**:3-14. doi:https://doi.org/10.1034/j.1600-0706.2003.12181.xhttps://doi.org/10.1034/j.1600-0706.2003.12181.x

Archibald, S., W. J. Bond, W. Hoffmann, C. E. R. Lehmann, C. Staver, and N. Stevens. 2020. Distribution and determinants of savannas.In: P. F. Scogings and M. Sankaran, editors.eds *Savanna Woody Plants and Large Herbivores*. Wiley, Hoboken, NJ. Pages 1-24

Archibald, S., and G. P. Hempson. 2016. Competing consumers: contrasting the patterns and impacts of fire and mammal herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences.* **371**:1-14. doi:10.1098/rstb.2015.030910.1098/rstb.2015.0309

Archibald, S., G. P. Hempson, and C. Lehmann. 2019. A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytologist.* **224**:1490-1503. doi:https://doi.org/10.1111/nph.15986https://doi.org/10.1111/nph.15986

Archibald, S., C. E. R. Lehmann, C. M. Belcher, W. J. Bond, R. A. Bradstock, A. L. Daniau, K. G. Dexter, E. J. Forrestel, M. Greve, T. He, S. I. Higgins, W. A. Hoffmann, B. B. Lamont, D. J. McGlinn, G. R. Moncrieff, C. P. Osborne, J. G. Pausas, O. Price, B. S. Ripley, B. M. Rogers, D. W. Schwilk, M. F. Simon, M. R. Turetsky, G. R. Van der Werf, and A. E. Zanne. 2018. Biological and geophysical feedbacks with fire in the Earth system. *Environmental Research Letters.* **13**:033003. doi:10.1088/1748-9326/aa9ead10.1088/1748-9326/aa9ead

Archibald, S., C. E. R. Lehmann, J. L. Gómez-Dans, and R. A. Bradstock. 2013. Defining pyromes and global syndromes of fire regimes. *Proceedings of the National Academy of Sciences.* **110**:6442-6447. doi:doi:10.1073/pnas.1211466110doi:10.1073/pnas.1211466110

Archibald, S., D. P. Roy, B. W. Van Wilgen, and R. J. Scholes. 2009. What limits fire? An examination of the drivers of burnt areas in southern Africa. *Global Change Biology.* **15**:613-630. doi:https://doi.org/10.1111/j.1365-2486.2008.01754.xhttps://doi.org/10.1111/j.1365-2486.2008.01754.x

Archibald, S., R. J. Scholes, D. P. Roy, G. Roberts, and L. Boschetti. 2010. Southern African fire regimes as revealed by remote sensing. *International Journal of Wildland Fire.* **19**:861-878. doi:10.1071/WF1000810.1071/WF10008

Ayadi, F., F. Msanda, F. Baniaameur, and E. M. Abdelhamid. 2012. Morphological and shape pods variability of *Acacia tortilis* ssp. *raddiana* (Savi) Brenan in south of Morocco. *International Journal of Plant Breeding and Genetics.* **6**:151-167. doi:10.3923/ijpbg.2012.151.16710.3923/ijpbg.2012.151.167

Azani, N., M. Babineau, C. D. Bailey, H. Banks, A. R. Barbosa, R. B. Pinto, J. S. Boatwright, L. M. Borges, G. K. Brown, A. Bruneau, E. Candido, D. Cardoso, K.-F. Chung, R. P. Clark, A. d. S. Conceição, M. Crisp, P. Cubas, A. Delgado-Salinas, K. G. Dexter, J. J. Doyle, J. Duminil, A. N. Egan, M. de la Estrella, M. J. Falcão, D. A. Filatov, A. P. Fortuna-Perez, R. H. Fortunato, E. Gagnon, P. Gasson, J. G. Rando, A. M. G. de Azevedo Tozzi, B. Gunn, D. Harris, E. Haston, J. A. Hawkins, P. S. Herendeen, C. E. Hughes, J. R. V. Iganci, F. Javadi, S. A. Kanu, S. Kazempour-Osaloo, G. C. Kite, B. B. Klitgaard, F. J. Kochanovski, E. J. M. Koenen, L. Kovar, M. Lavin, M. le Roux, G. P. Lewis, H. C. de Lima, M. C. López-Roberts, B. Mackinder, V. H. Maia, V. Malécot, V. F. Mansano, B. Marazzi, S. Mattapha, J. T. Miller, C. Mitsuyuki, T. Moura, D. J. Murphy, M. Nageswara-Rao, B. Nevado, D. Neves, D. I. Ojeda, R. T. Pennington, D. E. Prado, G. Prenner, L. P. de Queiroz, G. Ramos, F. L. R. Filardi, P. G. Ribeiro, M. de Lourdes Rico-Arce, M. J. Sanderson, J. Santos-Silva, W. M. B. São-Mateus, M. J. S. Silva, M. F. Simon, C. Sinou, C. Snak, É. R. de Souza, J. Sprent, K. P. Steele, J. E. Steier, R. Steeves, C. H. Stirton, S. Tagane, B. M. Torke, H. Toyama, D. T. da Cruz, M. Vatanparast, J. J. Wieringa, M. Wink, M. F. Wojciechowski, T. Yahara, T. Yi, and E. Zimmerman. 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The Legume Phylogeny Working Group (LPWG). *TAXON.* **66**:44-77. doi:https://doi.org/10.12705/661.3https://doi.org/10.12705/661.3

Baas, P., F. W. Ewers, S. D. Davis, and E. A. Wheeler. 2004. Evolution of xylem physiology.In: A. R. Hemsley and I. Poole, editors.eds *The Evolution of Plant Physiology*. Elsevier Academic Press, London, San Diego. Pages 273-295

Balfour, D. A., and J. J. Midgley. 2006. Fire induced stem death in an African acacia is not caused by canopy scorching. *Austral Ecology.* **31**:892-896. doi:https://doi.org/10.1111/j.1442-9993.2006.01656.xhttps://doi.org/10.1111/j.1442-9993.2006.01656.x

Barber, S. A. 1962. A diffusion and mass-flow concept of soil nutrient availability. *Soil Science.* **93**:39-49.

Barnes, R. D., C. W. Fagg, and S. J. Milton. 1997. *Acacia erioloba Monograph and annotated bibliography*. Oxford Forestry Institute, Oxford Forestry Institute, South Parks Road, Oxford OX1 3RB.

Barton, K. 2015. Tougher and thornier: general patterns in the induction of physical defence traits. *Functional Ecology.* **30**:181-187.

Batterman, S. A., L. O. Hedin, M. van Breugel, J. Ransijn, D. J. Craven, and J. S. Hall. 2013. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature.* **502**:224-227.

Beckage, B., W. Platt, and L. Gross. 2009. Vegetation, fire, and feedbacks: A disturbance-mediated model of savannas. *The American Naturalist.* **174**:805-818. doi:10.1086/64845810.1086/648458

Begueria, S., S. Vincente-Serrano, F. Reig, and B. Latorre. 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. Pages 3001-3023 *in* S. Begueria and S. Vincente-Serrano, editors. International Journal of Climatology. CSIC. http://sac.csic.es/spei, Bellingham, P. J., and A. D. Sparrow. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos.* **89**:409-416. doi:10.1034/j.1600-0706.2000.890224.x10.1034/j.1600-0706.2000.890224.x

Belsky, A. J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science.* **3**:187-200. doi:https://doi.org/10.2307/3235679https://doi.org/10.2307/3235679

Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology.* **30**:143-155. doi:10.2307/240427810.2307/2404278

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B.* **57**:289-300. doi:10.1111/j.2517-6161.1995.tb02031.x10.1111/j.2517-6161.1995.tb02031.x

Bennett, A. C., N. G. McDowell, C. D. Allen, and K. J. Anderson-Teixeira. 2015. Larger trees suffer most during drought in forests worldwide. *Nature Plants.* **1**:1-5. doi:https://doi.org/10.1038/nplants.2015.139https://doi.org/10.1038/nplants.2015.139

Berry, R. S., and A. Kulmatiski. 2017. A savanna response to precipitation intensity. *PLOS ONE.* **12**:e0175402. doi:10.1371/journal.pone.017540210.1371/journal.pone.0175402

Bewley, J. D., K. Bradford, H. W. M. Hilhorst, and H. Nonogaki. 2013. Measurement of germination. *Seeds: Physiology of Development. Germination and Dormancy*. Springer, New York, USA. Pages 136-140

Birnbaum, P., S. Dressler, M. Schmidt, and G. Zizka. 2014. *Acacia ehrenbergia* Hayne. . African Plants - A Photo Guide, Forschungsinstitut Senckenberg, Germany. www.africanplants.senckenberg.de, Location: Mali, Gossi, Gourma Rharous

Bivand, R., T. Keitt, and B. Rowlingson. 2022. rgdal: Bindings for the 'geospatial' data abstraction library. https://CRAN.R-project.org/package=rgdal, R package version 1.5-29

Bivand, R. S., E. Pebesma, and V. Gomez-Rubio. 2013. *Applied spatial data analysis with R*. Second edition edition. Springer, New York.

Blaser, W. J., J. Sitters, S. P. Hart, P. J. Edwards, and H. Olde Venterink. 2013. Facilitative or competitive effects of woody plants on understorey vegetation depend on N-fixation, canopy shape and rainfall. *Journal of Ecology.* **101**:1598-1603. doi:https://doi.org/10.1111/1365-2745.12142https://doi.org/10.1111/1365-2745.12142

Bognounou, O. 1972. *Acacia dudgeonii* Craib ex Holl. [family Leguminosae-Mimosoideae]. Herbarium Specimens. Institut de l'Environnement et de Recherche Agricola, Herbier National du Burkina, JSTOR Global Plants.

Bond, W. J. 2005. Large parts of the world are brown or black: A different view on the 'Green World' hypothesis. *Journal of Vegetation Science.* **16**:261-266. doi:https://doi.org/10.1111/j.1654-1103.2005.tb02364.xhttps://doi.org/10.1111/j.1654-1103.2005.tb02364.x

Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics.* **39**:641-659. doi:10.1146/annurev.ecolsys.39.110707.17341110.1146/annurev.ecolsys.39.110707.173411

Bond, W. J., and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution.* **20**:387-394. doi:https://doi.org/10.1016/j.tree.2005.04.025https://doi.org/10.1016/j.tree.2005.04.025

Bond, W. J., G. F. Midgley, and F. I. Woodward. 2003. What controls South African vegetation - climate or fire? *South African Journal of Botany.* **69**:79-91. doi:https://doi.org/10.1016/S0254-6299(15)30362-8https://doi.org/10.1016/S0254-6299(15)30362-8

Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution.* **16**:45-51. doi:https://doi.org/10.1016/S0169-5347(00)02033-4https://doi.org/10.1016/S0169-5347(00)02033-4

Bond, W. J., K. Smythe, and D. A. Balfour. 2001. *Acacia* species turnover in space and time in an African savanna. *Journal of Biogeography.* **28**:117-128.

Bond, W. J., K. L. Smythe, and D. A. Balfour. 2008. Acacia species turnover in space and time in an African savanna. *Journal of Biogeography.* **28**:117-128.

Bond, W. J., and B. W. van Wilgen. 1996. *Fire and plants*. Chapman and Hall, London.

Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist.* **165**:525-538. doi:https://doi.org/10.1111/j.1469-8137.2004.01252.xhttps://doi.org/10.1111/j.1469-8137.2004.01252.x

Boonman, C. C. F., F. van Langevelde, I. Oliveras, J. Couédon, N. Luijken, D. Martini, and E. M. Veenendaal. 2020. On the importance of root traits in seedlings of tropical tree species. *New Phytologist.* **227**:156-167. doi:https://doi.org/10.1111/nph.16370https://doi.org/10.1111/nph.16370

Botha, M., S. Archibald, and M. Greve. 2020. What drives grassland-forest boundaries? Assessing fire and frost effects on tree seedling survival and architecture. *Ecology and Evolution.* **10**:10719-10734. doi:https://doi.org/10.1002/ece3.6730https://doi.org/10.1002/ece3.6730

Bouchenak-Khelladi, Y., O. Maurin, J. Hurter, and M. van der Bank. 2010. The evolutionary history and biogeography of Mimosoideae (Leguminosae): An emphasis on African acacias. *Molecular Phylogenetics and Evolution.* **57**:495-508.

Bourlière, F., and M. Hadley. 1983. Present-day savannas: an overview.In: F. Bourlière, editor. *Tropical savannas*. Elsevier, Amsterdam.

Bradstock, R. A. 2010. A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography.* **19**:145-158. doi:https://doi.org/10.1111/j.1466-8238.2009.00512.xhttps://doi.org/10.1111/j.1466-8238.2009.00512.x

Brando, P. M., D. C. Nepstad, J. K. Balch, B. Bolker, M. C. Christman, M. Coe, and F. E. Putz. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology.* **18**:630-641. doi:https://doi.org/10.1111/j.1365-2486.2011.02533.xhttps://doi.org/10.1111/j.1365-2486.2011.02533.x

Brenan, J. P. M. 1970. *Acacia chariessa Milne-Redh. [family Leguminosae]*. Royal Botani Gardens, Kew (K), JSTOR Global Plants.

Breshears, D. D., O. B. Myers, C. W. Meyer, F. J. Barnes, C. B. Zou, and e. al. 2009. Tree die-off in response to global change-type drought: Mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment.* **7**:185-189.

Brouwer, R. 1963. Some aspects of the equilibrium between overground and underground plant parts. *Jaarboek van het Instituut voor Biologisch en Scheikundig onderzoek aan Landbouwgewassen.* **1963**:31-39.

Bucci, S., G. Goldstein, F. Meinzer, A. Franco, P. Campanello, and F. Scholz. 2005. Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plants in Neotropical savanna trees. *Trees.* **19**:296-304. doi:10.1007/s00468-004-0391-210.1007/s00468-004-0391-2

Bucci, S., G. Goldstein, F. Meinzer, F. Scholz, A. Franco, and M. Bustamante. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: From leaf to whole plant. *Tree physiology.* **24**:891-899. doi:10.1093/treephys/24.8.89110.1093/treephys/24.8.891

Case, M., B. Wigley, C. Coetsee, and A. Staver. 2020. Could drought constrain woody encroachers in savannas? *African Journal of Range & Forage Science.* **37**:19-29. doi:10.2989/10220119.2019.169736310.2989/10220119.2019.1697363

Case, M. F., C. Wigley-Coetsee, N. Nzima, P. F. Scogings, and A. C. Staver. 2019. Severe drought limits trees in a semi-arid savanna. *Ecology.* **100**:e02842. doi:https://doi.org/10.1002/ecy.2842https://doi.org/10.1002/ecy.2842

Castro-Díez, P., T. Langendoen, L. Poorter, and A. Saldaña-López. 2011. Predicting *Acacia* invasive success in South Africa on the basis of functional traits, native climatic niche and human use. *Biodiversity and Conservation.* **20**:2729-2743. doi:10.1007/s10531-011-0101-510.1007/s10531-011-0101-5

Charles-Dominique, T., J.-F. Barczi, and S. Chamaillé-Jammes. 2020. Woody plant architecture and effects on browsing herbivores in savannas.In: P. F. Scogings and M. Sankaran, editors.eds *Savanna Woody Plants and Large Herbivores*. John Wiley & Sons Ltd., Hoboken, NJ. Pages 469-488 10.1002/9781119081111.ch14

Charles-Dominique, T., J. F. Barczi, E. Le Roux, and S. Chamaillé-Jammes. 2017. The architectural design of trees protects them against large herbivores. *Functional Ecology.* **31**:1710-1717.

Charles-Dominique, T., T. J. Davies, G. P. Hempson, B. S. Bezeng, B. H. Daru, R. M. Kabongo, O. Maurin, A. M. Muasya, M. van der Bank, and W. J. Bond. 2016. Spiny plants, mammal browsers, and the origin of African savannas. *Proceedings of the National Academy of Sciences.* **113**:E5572-E5579. doi:doi:10.1073/pnas.1607493113doi:10.1073/pnas.1607493113

Charles-Dominique, T., G. Midgley, and W. Bond. 2015a. An index for assessing effectiveness of plant structural defences against mammal browsing. *Plant Ecology.* **216** doi:10.1007/s11258-015-0522-410.1007/s11258-015-0522-4

Charles-Dominique, T., G. Midgley, K. Tomlinson, and W. Bond. 2018. Steal the light: shade vs fire adapted vegetation in forest-savanna mosaics. *New Phytologist.* **218**:1419-1429. doi:10.1111/nph.1511710.1111/nph.15117

Charles-Dominique, T., A. C. Staver, G. F. Midgley, and W. J. Bond. 2015b. Functional differentiation of biomes in an African savanna/forest mosaic. *South African Journal of Botany.* **101**:82-90. doi:https://doi.org/10.1016/j.sajb.2015.05.005https://doi.org/10.1016/j.sajb.2015.05.005

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and e. al. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters.* **12**:351-366.

Choat, B., T. J. Brodribb, C. R. Brodersen, R. A. Duursma, R. López, and B. E. Medlyn. 2018. Triggers of tree mortality under drought. *Nature.* **558**:531-539. doi:10.1038/s41586-018-0240-x10.1038/s41586-018-0240-x

Choat, B., S. Jansen, T. J. Brodribb, H. Cochard, S. Delzon, R. Bhaskar, S. J. Bucci, T. S. Feild, S. M. Gleason, U. G. Hacke, A. L. Jacobsen, F. Lens, H. Maherali, J. Martínez-Vilalta, S. Mayr, M. Mencuccini, P. J. Mitchell, A. Nardini, J. Pittermann, R. B. Pratt, J. S. Sperry, M. Westoby, I. J. Wright, and A. E. Zanne. 2012. Global convergence in the vulnerability of forests to drought. *Nature.* **491**:752-755. doi:10.1038/nature1168810.1038/nature11688

Christensen, R. H. B. 2018. Cumulative link models for ordinal regression with the R package ordinal.

Christensen, R. H. B. 2019. ordinal - Regression models for ordinal data. https://CRAN.r-project.org/package=ordinal,

Clarke, H. D., S. R. Downie, and D. S. Seigler. 2000. Implications of Chloroplast DNA Restriction Site Variation for Systematics of *Acacia* (Fabaceae: Mimosoideae).

Clarke, P. J., and K. J. E. Knox. 2009. Trade-offs in resource allocation that favour resprouting affect the competitive ability of woody seedlings in grassy communities. *Journal of Ecology.* **97**:1374-1382. doi:https://doi.org/10.1111/j.1365-2745.2009.01556.xhttps://doi.org/10.1111/j.1365-2745.2009.01556.x

Clarke, P. J., K. J. E. Knox, K. E. Wills, and M. Campbell. 2005. Landscape patterns of woody plant response to crown fire: disturbance and productivity influence sprouting ability. *Journal of Ecology.* **93**:544-555. doi:https://doi.org/10.1111/j.1365-2745.2005.00971.xhttps://doi.org/10.1111/j.1365-2745.2005.00971.x

Clarke, P. J., M. J. Lawes, J. J. Midgley, B. B. Lamont, F. Ojeda, G. E. Burrows, N. J. Enright, and K. J. E. Knox. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist.* **197**:19-35. doi:https://doi.org/10.1111/nph.12001https://doi.org/10.1111/nph.12001

Coates Palgrave, K. 1983. *Trees of Southern Africa*. Second edition. C. Struik Publishers, Cape Town.

Coe, M., and C. Coe. 1987. Large herbivores, acacia trees and bruchid beetles. *South African Journal of Science.* **83**:624-635.

Coetsee, C., W. J. Bond, and E. C. February. 2010. Frequent fire affects soil nitrogen and carbon in an African savanna by changing woody cover. *Oecologia.* **162**:1027-1034. doi:10.1007/s00442-009-1490-y10.1007/s00442-009-1490-y

Comas, L., S. Becker, V. M. V. Cruz, P. F. Byrne, and D. A. Dierig. 2013. Root traits contributing to plant productivity under drought. *Frontiers in Plant Science.* **4** doi:10.3389/fpls.2013.0044210.3389/fpls.2013.00442

Cooper, S. M., and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia.* **68**:446-455.

Corrêa Scalon, M., F. Maia Chaves Bicalho Domingos, W. Jonatar Alves da Cruz, B. H. Marimon Júnior, B. Schwantes Marimon, and I. Oliveras. 2020. Diversity of functional trade-offs enhances survival after fire in Neotropical savanna species. *Journal of Vegetation Science.* **31**:139-150. doi:https://doi.org/10.1111/jvs.12823https://doi.org/10.1111/jvs.12823

Coverdale, T. C. 2020. Defence emergence during early ontogeny reveals important differences between spines, thorns and prickles. *Annals of Botany.* **124**:iii-iv. doi:10.1093/aob/mcz18910.1093/aob/mcz189

Cramer, M. D., A. Van Cauter, and W. J. Bond. 2010. Growth of N2-fixing African savanna *Acacia* species is constrained by below-ground competition with grass. *Journal of Ecology.* **98**:156-167. doi:https://doi.org/10.1111/j.1365-2745.2009.01594.xhttps://doi.org/10.1111/j.1365-2745.2009.01594.x

D'Onofrio, D., M. Baudena, F. D'Andrea, M. Rietkerk, and A. Provenzale. 2015. Tree-grass competition for soil water in arid and semi-arid savannas: The role of rainfall intermittency. *Water Resources Research.* **51**:169-181.

da Silva, D. M., and M. A. Batalha. 2008. Soil-vegetation relationships in cerrados under different fire frequencies. *Plant and Soil.* **311**:87-96.

Dai, A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change.* **3**:52-58.

Dantas, V. d. L., M. A. Batalha, and J. G. Pausas. 2013. Fire drives functional thresholds on the savanna–forest transition. *Ecology.* **94**:2454-2463. doi:https://doi.org/10.1890/12-1629.1https://doi.org/10.1890/12-1629.1

Dantas, V. d. L., M. Hirota, R. S. Oliveira, and J. G. Pausas. 2016. Disturbance maintains alternative biome states. *Ecology Letters.* **19**:12-19. doi:https://doi.org/10.1111/ele.12537https://doi.org/10.1111/ele.12537

Dantas, V. d. L., and J. G. Pausas. 2013. The lanky and the corky: fire-escape strategies in savanna woody species. *Journal of Ecology.* **101**:1265-1272. doi:https://doi.org/10.1111/1365-2745.12118https://doi.org/10.1111/1365-2745.12118

Davidson, L., and B. Jeppe. 1981. *A Field Guide to the Acacias of southern Africa*. Centaur Publishers, Johannesburg, South Africa.

Dayrell, R. L. C., A. J. Arruda, S. Pierce, D. Negreiros, P. B. Meyer, H. Lambers, and F. A. O. Silveira. 2018. Ontogenetic shifts in plant ecological strategies. *Functional Ecology.* **32**:2730-2741. doi:https://doi.org/10.1111/1365-2435.13221https://doi.org/10.1111/1365-2435.13221

Devine, A. P., R. A. McDonald, T. Quafie, and I. M. D. Maclean. 2017. Determinants of woody encroachment and cover in African savannas. *Oecologia.* **183**:939-951.

Dharani, N. 2006. *Field Guide to Acacias of East Africa*. Struik Publishers, Cape Town, South Africa.

Diatta, O., A. M. Diallo, D. Sanogo, L. R. Nielsen, A. Ræbild, E. D. Kjær, and J. K. Hansen. 2022. Variation in phenology of *Acacia senegal* (L.) Wild. in relation to origin and ploidy level: Implications for climatic adaptation. *Global Ecology and Conservation.* **33**:e01957. doi:https://doi.org/10.1016/j.gecco.2021.e01957https://doi.org/10.1016/j.gecco.2021.e01957

Diémé, J. S., C. Armas, G. M. Rusch, and F. I. Pugnaire. 2019. Functional responses of four Sahelian tree species to resource availability. *Flora.* **254**:181-187.

Ding, J., S. K. Travers, and D. J. Eldridge. 2021. Grow wider canopies or thicker stems: variable response of woody plants to increasing dryness. *Global Ecology and Biogeography.* **30**:183-195. doi:https://doi.org/10.1111/geb.13212https://doi.org/10.1111/geb.13212

Doran, J. C., J. W. Turnbull, D. J. Boland, and B. V. Gunn. 1983. Treatments to promote seed germinations. *Handbook on seeds of dry-zone acacias. A guide for collecting, extracting, cleaning, and storing the seed and for treatment to promote germination of dry-zone acacias*. FAO, Rome, Italy.

dos Santos Costa, A., J. Stropp, N. A. de Carvalho, F. Alves-Martins, R. J. Ladle, and A. C. M. Malhado. 2020. Environmental correlates of seed weight of tropical semi-arid woody species. *Plant and Soil.* **446**:369-378. doi:https://doi.org/10.1007/s11104-019-04341-1https://doi.org/10.1007/s11104-019-04341-1

Elias, T. S. 1981. Mimosoideae.In: R. M. Polhill and P. H. Raven, editors.eds *Advances in Legume Systematics*. Royal Botanic Gardens, Kew, UK. Pages 143-151

Erb, P. 2021. *Senegalia robynsiana*. iNaturalist.

Fairman, T. A., L. T. Bennett, and C. R. Nitschke. 2019. Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. *Journal of Environmental Management.* **231**:59-65. doi:https://doi.org/10.1016/j.jenvman.2018.10.021https://doi.org/10.1016/j.jenvman.2018.10.021

February, E. C., C. Coetsee, D. G. Cook, J. Ratnam, and B. Wigley. 2020. Physiological traits of savanna woody species: adaptations to resource availability.In: P. F. Scogings and M. Sankaran, editors.eds *Savanna Woody Plants and Large Herbivores*. John Wiley & Sons Ltd., Hoboken, NJ. Pages 311-323

February, E. C., and S. I. Higgins. 2010. The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. *South African Journal of Botany.* **76**:517-523. doi:https://doi.org/10.1016/j.sajb.2010.04.001https://doi.org/10.1016/j.sajb.2010.04.001

February, E. C., S. I. Higgins, W. J. Bond, and L. Swemmer. 2013. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology.* **94**:1155-1164. doi:https://doi.org/10.1890/12-0540.1https://doi.org/10.1890/12-0540.1

Fensham, R. J., R. J. Fairfax, and D. P. Ward. 2009. Drought-induced tree death in savanna. *Global Change Biology.* **15**:380-387.

Fensham, R. J., J. Fraser, H. J. MacDermott, and J. Firn. 2015. Dominant tree species are at risk from exaggerated drought under climate change. *Global Change Biology.* **21**:3777-3785. doi:https://doi.org/10.1111/gcb.12981https://doi.org/10.1111/gcb.12981

Fensham, R. J., B. Laffineur, and C. D. Allen. 2019. To what extent is drought-induced tree mortality a natural phenomenon? *Global Ecology and Biogeography.* **28**:365-373.

Fick, S. E., and R. J. Hijmans. 2017. Worldclim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology.* **37**:4302-4315.

Fictl, R., S. Dressler, M. Schmidt, and G. Zizka. 2014. African Plants - A Photo Guide. Forschungsinstitut Senckenberg, Germany. www.africanplants.seckenberg.de,

Fitter, A. 1996. Characteristics and functions of root systems.In: Y. Waisel, A. Eshel, and U. Kafkafi, editors.eds *Plant Roots: The Hidden Half*. Marcel Dekker, New York, USA. Pages 1-21

Fornara, D. A., and J. T. du Toit. 2008. Community-level interactions between ungulate browsers and woody plants in an African savanna dominated by palatable-spinescent Acacia trees. *Journal of Arid Environments.* **72**:534-545. doi:https://doi.org/10.1016/j.jaridenv.2007.07.010https://doi.org/10.1016/j.jaridenv.2007.07.010

Fox, J., S. Weisberg, B. Price, and e. al. 2019. Companion to Applied Regression. Pages Functions to Accompany J. Fox and S. Weisberg, An R Companion to Applied Regression. Sage.

Fréjaville, T., T. Curt, and C. Carcaillet. 2013. Bark flammability as a fire-response trait for subalpine trees. *Frontiers in Plant Science.* **4**:466. doi:10.3389/fpls.2013.0046610.3389/fpls.2013.00466

Friendly, M., and J. Fox. 2021. candisc: Visualising generalized canonical discriminant and canonical correlation analysis. https://CRAN.R-project.org/package=heplots, R package version 0.8-6

Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters.* **8**:1283-1290.

Furley, P. A. 2016. *Savannas: A Very Short Introduction*. Oxford University Press.10.1093/actrade/9780198717225.001.0001

Gaillard, C., L. Langan, M. Pfeiffer, D. Kumar, C. Martens, S. I. Higgins, and S. Scheiter. 2018. African shrub distribution emerges via a trade-off between height and sapwood conductivity. *Journal of Biogeography.* **45**:2815-2826.

Garnier, E., M.-L. Navas, K. Grigulis, E. Garnier, M.-L. Navas, and K. Grigulis. 2015. Trait-based ecology: definitions, methods, and a conceptual framework. *Plant Functional Diversity: Organism traits, community structure, and ecosystem properties*. Oxford University Press. Page 0 10.1093/acprof:oso/9780198757368.003.0002

Garnier, E., B. Shipley, C. Roumet, and F. Laurent. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology.* **15**:688-695. doi: https://doi.org/10.1046/j.0269-8463.2001.00563.x https://doi.org/10.1046/j.0269-8463.2001.00563.x

Gei, M., D. M. A. Rozendaal, L. Poorter, F. Bongers, J. I. Sprent, and e. al. 2018. Legume abundance along successional and rainfall gradients in Neotropical forests. *Nature Ecology & Evolution.* **2**:1104-1111.

Ghassali, F., A. K. Salkini, S. L. Petersen, A. A. Niane, and M. Louhaichi. 2012. Germination dynamics of *Acacia* species under different seed treatments. *Range Management and Agroforestry.* **33**:37-42.

Giglio, L., J. T. Randerson, G. R. van der Werf, P. S. Kasibhatla, G. J. Collatz, D. C. Morton, and R. S. DeFries. 2010. Assessing variability and long-term trends in burned area by merging multiple satellite fire products. *Biogeosciences.* **7**:1171-1186.

Gignoux, J., J. Clobert, and J.-C. Menaut. 1997. Alternate fire resistance strategies in savanna trees. *Oecologia.* **110**:576-583. doi:10.1007/s00442005019810.1007/s004420050198

Gignoux, J., S. Konaté, G. Lahoreau, X. Le Roux, and G. Simioni. 2016. Allocation strategies of savanna and forest tree seedlings in response to fire and shading: outcomes of a field experiment. *Scientific Reports.* **6**:38838. doi:10.1038/srep3883810.1038/srep38838

Gignoux, J., G. Lahoreau, R. Julliard, and S. Barot. 2009. Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology.* **97**:484-495. doi:https://doi.org/10.1111/j.1365-2745.2009.01493.xhttps://doi.org/10.1111/j.1365-2745.2009.01493.x

Gill, M. A. 1995. Stems and fires.In: B. L. Gartner, editor. *Plant Stems: Physiology and Functional Morphology*. Academic Press, San Diego. Pages 323-342 https://doi.org/10.1016/B978-012276460-8/50016-3

Gleason, S. M., M. Westoby, S. Jansen, B. Choat, U. G. Hacke, R. B. Pratt, R. Bhaskar, T. J. Brodribb, S. J. Bucci, K.-F. Cao, H. Cochard, S. Delzon, J.-C. Domec, Z.-X. Fan, T. S. Feild, A. L. Jacobsen, D. M. Johnson, F. Lens, H. Maherali, J. Martínez-Vilalta, S. Mayr, K. A. McCulloh, M. Mencuccini, P. J. Mitchell, H. Morris, A. Nardini, J. Pittermann, L. Plavcová, S. G. Schreiber, J. S. Sperry, I. J. Wright, and A. E. Zanne. 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist.* **209**:123-136. doi:https://doi.org/10.1111/nph.13646https://doi.org/10.1111/nph.13646

Glover, G. C., and J. P. M. Brenan. 1944. *Acacia zizyphispina* Chiov. [family Leguminosae-Mimosoideae] Herbarium Specimens. Royal Botanic Gardens, Kew, JSTOR Global Plants Initiative.

Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22(7):1-19.

Goss, M. J. 1977. Effect of mechanical impedance on growth of seedlings. *Journal of Experimental Botany.* **28**:96-111.

Götmark, F., E. Götmark, and A. M. Jensen. 2016. Why be a shrub? A basic model and hypotheses for the adaptive values of a common growth form. *Frontiers in Plant Science.* **7** doi:10.3389/fpls.2016.0109510.3389/fpls.2016.01095

Gotsch, S. G., E. L. Geiger, A. C. Franco, G. Goldstein, F. C. Meinzer, and W. A. Hoffmann. 2010. Allocation to leaf area and sapwood area affects water relations of co-occurring savanna and forest trees. *Oecologia.* **163**:291-301. doi:10.1007/s00442-009-1543-210.1007/s00442-009-1543-2

Gould, S. J., and E. S. Vrba. 1982. Exaptation - a missing term in the science of form. *Paleobiology.* **8**:4-15.

Grace, J., J. S. José, P. Meir, H. S. Miranda, and R. A. Montes. 2006. Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography.* **33**:387-400. doi:https://doi.org/10.1111/j.1365-2699.2005.01448.xhttps://doi.org/10.1111/j.1365-2699.2005.01448.x

Greenwood, S., P. Ruiz-Benito, J. Martínez-Vilalta, F. Lloret, T. Kitzberger, C. D. Allen, R. Fensham, D. C. Laughlin, J. Kattge, G. Bönisch, N. J. B. Kraft, and A. S. Jump. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters.* **20**:539-553. doi:https://doi.org/10.1111/ele.12748https://doi.org/10.1111/ele.12748

Greve, M., A. M. Lykke, A. Blach-Overgaard, and J.-C. Svenning. 2011. Environmental and anthropogenic determinants of vegetation distribution across Africa. *Global Ecology and Biogeography.* **20**:661-674. doi:https://doi.org/10.1111/j.1466-8238.2011.00666.xhttps://doi.org/10.1111/j.1466-8238.2011.00666.x

Greve, M., A. M. Lykke, C. W. Fagg, J. Bogaert, I. Friis, R. Marchant, and e. al. 2012. Continental-scale variability in browser diversity is a major driver of diversity patterns in acacias across Africa. *Journal of Ecology.* **100**:1093-1104.

Grime, J., K. Thompson, R. Hunt, J. Hodgson, J. Cornelissen, I. Rorison, G. Hendry, T. Ashenden, A. Askew, S. Band, R. Booth, C. Bossard, B. Campbell, J. Cooper, A. Davison, P. Gupta, W. Hall, D. Hand, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos.* **79**:259-281. doi:10.2307/354601110.2307/3546011

Groom, P. K., and B. B. Lamont. 1997. Fruit-seed relations in *Hakea*: serotinous species invest in more dry matter in predispersal seed protection. *Australian Journal of Ecology.* **22**:352-355.

Group, T. L. P. W. 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *TAXON.* **66**:44-77. doi:https://doi.org/10.12705/661.3https://doi.org/10.12705/661.3

Guy, P. R. 1989. The influence of elephants and fire on a *Brachystegia-Julbernardia* woodland in Zimbabwe. *Journal of Tropical Ecology.* **5**:215-226. doi:10.1017/S026646740000350310.1017/S0266467400003503

Gwynne, M. D. 1969. The nutritive values of *Acacia* pods in relation to *Acacia* seed distribution by ungulates. *East African Wildlife Journal.* **7**:176-178.

Hacke, U. G., J. S. Sperry, W. T. Pockman, S. D. Davis, and K. A. McCulloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia.* **126**:457-461. doi:10.1007/s00442010062810.1007/s004420100628

Hamilton, T., S. Archibald, and S. Woodborne. 2022. Historic changes in the fire-rainfall relationship at a woodland-savanna transition zone in southern Africa. *African Journal of Range and Forage Science.* **39**:70-81. doi:10.2989/10220119.2022.203040810.2989/10220119.2022.2030408

Hao, G.-Y., W. A. Hoffmann, F. G. Scholz, S. J. Bucci, F. C. Meinzer, A. C. Franco, K.-F. Cao, and G. Goldstein. 2008. Stem and leaf hydraulics of congeneric tree species from adjacent tropical savanna and forest ecosystems. *Oecologia.* **155**:405-415. doi:10.1007/s00442-007-0918-510.1007/s00442-007-0918-5

Harrison, S., and M. LaForgia. 2019. Seedling traits predict drought-induced mortality linked to diversity loss. *Proceedings of the National Academy of Sciences.* **116**:5576-5581. doi:doi:10.1073/pnas.1818543116doi:10.1073/pnas.1818543116

Hartmann, H., C. F. Moura, W. R. L. Anderegg, N. K. Ruehr, Y. Salmon, and e. al. 2018. Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytologist.* **218**:15-28.

Harvey, W. H. 1894. *Acacia horrida* Willd. [family Leguminosae-Mimosoideae]. Page 1 Flora Capensis. Royal Botanic Gardens, Kew, JSTOR Global Plants.

Hassan, A. S., and B. T. Styles. 1990. *A conspectus of Somali Acacias*. Natural Resources Institute, Chatham, UK.

Hean, J. W., and D. Ward. 2012. Fire and herbivory are not substitutable: evidence from regrowth patterns and changes in physical and chemical defences in *Acacia* seedlings. *Journal of Vegetation Science.* **23**:13-23. doi:https://doi.org/10.1111/j.1654-1103.2011.01330.xhttps://doi.org/10.1111/j.1654-1103.2011.01330.x

Hempson, G. P., S. Archibald, and W. J. Bond. 2015. A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science.* **350**:1056-1061. doi:doi:10.1126/science.aac7978doi:10.1126/science.aac7978

Hempson, G. P., S. Archibald, and C. Staver. 2019. Fire and Browsers in Savannas. *Savanna Woody Plants and Large Herbivores*. Pages 439-468 https://doi.org/10.1002/9781119081111.ch13

Hempson, G. P., S. Archibald, and C. Staver. 2020. Fire and browsers in savannas: traits, interactions and continent-level patterns.In: P. F. Scogings and M. Sankaran, editors.eds *Savanna Woody Plants and Large Herbivores*. John Wiley & Sons Ltd., Hoboken, New Jersey. Pages 439-468 https://doi.org/10.1002/9781119081111.ch13

Henery, M. L., and M. Westoby. 2001. Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos.* **92**:479-490. doi:https://doi.org/10.1034/j.1600-0706.2001.920309.xhttps://doi.org/10.1034/j.1600-0706.2001.920309.x

Hengst, G. E., and J. O. Dawson. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research.* **24**:688-696. doi:10.1139/x94-09210.1139/x94-092

Hervé, M. 2022. RVAideMemoire: Testing and plotting procedures for biostatistics. https://CRAN.R-project.org/package=RDAideMemoire, R package version 0.9-81-2

Higgins, S., M. Keretetse, and E. February. 2015. Feedback of trees on nitrogen mineralization to restrict the advance of trees in C4 savannas. *Biology letters.* **11** doi:10.1098/rsbl.2015.057210.1098/rsbl.2015.0572

Higgins, S. I. 2020. Field methods for plant ecology. Chair of Plant Ecology, University of Bayreuth, Universitätsstraße 30, Bayreuth, Germany.

Higgins, S. I., W. J. Bond, E. C. February, A. Bronn, D. I. W. Euston-Brown, B. Enslin, N. Govender, L. Rademan, S. O'Regan, A. L. F. Potgieter, S. Scheiter, R. Sowry, L. Trollope, and W. S. W. Trollope. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology.* **88**:1119-1125. doi:https://doi.org/10.1890/06-1664https://doi.org/10.1890/06-1664

Higgins, S. I., W. J. Bond, and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology.* **88**:213-229. doi:https://doi.org/10.1046/j.1365-2745.2000.00435.xhttps://doi.org/10.1046/j.1365-2745.2000.00435.x

Hijmans, R. J. 2022. raster: Geographic data analysis and modelling. https://CRAN.R-project.org/package=raster, R package version 3.5-15

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2021. dismo: Species distribution modelling. https://CRAN.R-project.org/package=dismo,

Hinckley, T., B. Lachenbruch, F. Meinzer, and T. Dawson. 2011. A lifespan perspective on integrating structure and function in trees.In: F. Meinzer, B. Lachenbruch, and T. Dawson, editors.eds *Size- and Age-Related Changes in Tree Structure and Function*. Springer. Pages 3-30 10.1007/978-94-007-1242-3_1

Hoffmann, W., E. Geiger, S. Gotsch, D. Rossatto, L. Silva, O. L. Lau, M. Haridasan, and A. Franco. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters.* **15**:759-768. doi:10.1111/j.1461-0248.2012.01789.x10.1111/j.1461-0248.2012.01789.x

Hoffmann, W., and O. Solbrig. 2003. The role of topkill in the differential response of savanna woody plants to fire. *Forest Ecology and Management.* **180**:273-286. doi:10.1016/S0378-1127(02)00566-210.1016/S0378-1127(02)00566-2

Hoffmann, W. A., R. Adasme, M. Haridasan, M. T. de Carvalho, E. L. Geiger, M. A. B. Pereira, S. G. Gotsch, and A. C. Franco. 2009. Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil. *Ecology.* **90**:1326-1337. doi:https://doi.org/10.1890/08-0741.1https://doi.org/10.1890/08-0741.1

Hoffmann, W. A., B. Orthen, and P. K. V. d. Nascimento. 2003. Comparative fire ecology of tropical savanna and forest trees. *Functional Ecology.* **17**:720-726. doi:https://doi.org/10.1111/j.1365-2435.2003.00796.xhttps://doi.org/10.1111/j.1365-2435.2003.00796.x

Högberg, P. 1986. Nitrogen-fixation and nutrient relations in savanna woodland trees (Tanzania). *Journal of Applied Ecology.* **23**:675-688.

Holdo, R. M., J. B. Nippert, and M. C. Mack. 2018. Rooting depth varies differentially in trees and grasses as a function of mean annual rainfall in an African savanna. *Oecologia.* **186**:269-280.

Huntley, B. J. 1982. Southern African savannas.In: B. J. Huntley and B. H. Walker, editors.eds *Ecology of tropical savannas*. Springer, Berlin. Pages 101-119

Illius, A. W., and I. J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia.* **89**:428-434. doi:10.1007/BF0031742210.1007/BF00317422

Jager, M. M., S. J. Richardson, P. J. Bellingham, M. J. Clearwater, and D. C. Laughlin. 2015. Soil fertility induces coordinated responses of multiple independent functional traits. *Journal of*

Ecology. **103**:374-385. doi:https://doi.org/10.1111/1365-2745.12366https://doi.org/10.1111/1365-2745.12366

Jakobsson, A., and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos.* **88**:494-502. doi:https://doi.org/10.1034/j.1600-0706.2000.880304.xhttps://doi.org/10.1034/j.1600-0706.2000.880304.x

James, J. J., T. J. Svejcar, and M. J. Rinella. 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology.* **48**:961-969.

Johnson, D. M., J. C. Domec, Z. C. Berry, A. M. Schwantes, K. A. McCulloh, and e. al. 2018. Co-occurring woody species have diverse hydraulic strategies and mortality rates during an extreme drought. *Plant, Cell and Environment.* **41**:576-588.

Jones, H. G. 1992. *Plants and microclimate: a quantitative approach to environmental plant physiology*. Second edition. Cambridge University Press, Cambridge.

Josse, J., and F. Husson. 2016. missMDA: A package for handling missing values in multivariate data analysis. *Journal of Statistical Software.* **70**:1-31. doi:doi:10.18637/jss.v070.i01doi:10.18637/jss.v070.i01

Joubert, D. F., A. Rothauge, and G. N. Smit. 2008. A conceptual model of vegetation dynamics in the semiarid highland savanna of Namibia, with particular reference to bush thickening by *Acacia mellifera*. *Journal of Arid Environments.* **72**:2201-2210.

Jurado, E., and M. Westoby. 1992. Germination biology of selected central Australian plants. *Australian Journal of Botany.* **17**:341-348.

Karavani, A., M. Boer, M. Baudena, C. Colinas, R. Diaz-Sierra, J. García, M. De Luis, A. Enríquez de Salamanca Sánchez-Cámara, and V. Resco de Dios. 2018. Fire-induced deforestation in drought-prone Mediterranean forests: drivers and unknowns from leaves to communities. *Ecological Monographs.* **88**:141-149. doi:10.1002/ecm.1285/full10.1002/ecm.1285/full

Kassa, A., R. Alía, W. Tadesse, V. Pando, and F. Bravo. 2010. Seed germination and viability in two African *Acacia* species growing under different water stress levels. *African Journal of Plant Science.* **4**:353-359.

Kassambara, A. 2020. Transform data to normal distribution in R. Statistical Tests and Assumptions. DataNovia. https://www.datanovia.com/en/lessons/transform-data-to-normal-distribution-in-r/,

Kaufman, Y. J., L. A. Remer, R. D. Ottmar, D. R. Ward, R. R. Li, and e. al. 1996. Relationship between remotely sensed fire intensity and rate of emission of smoke: SCAR-C experiment.In: J. S. Levine, editor. *Biomass Burning and Global Change*. MIT Press, Cambridge, MA. Pages 685-696

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science.* **16**:406-411. doi:https://doi.org/10.1016/j.tplants.2011.04.002https://doi.org/10.1016/j.tplants.2011.04.002

Khan, D., Z. A. Sahito, and M. J. Zaki. 2013. Parental investment of biomass in pod, seed, and seed packaging in a tree of wiry wattle (*Acacia coriacea* subsp. *pendens*) growing in Karachi, Pakistan. *International Journal of Biology and Biotechnology.* **10**:515-536.

Kheloufi, A., L. Mansouri, and Z. F. Boukhatem. 2017. Application and use of sulphuric acid pretreatment to improve seed germination of three acacia species. *REFORESTA.* **3**:1-10. doi:10.21750/REFOR.3.01.2510.21750/REFOR.3.01.25

Kirker, G., and P. F. Scogings. 2019. Savanna Ecosystem Models.In: P. F. Scogings and M. Sankaran, editors.eds *Savanna Woody Plands and Large Herbivores*. Wiley, Hoboken, NJ. Pages 661-682

Klimešová, J., J. Martínková, J. G. Pausas, M. G. de Moraes, T. Herben, F.-H. Yu, J. Puntieri, P. A. Vesk, F. de Bello, Š. Janeček, J. Altman, B. Appezzato-da-Glória, A. Bartušková, A. Crivellaro, J. Doležal, J. P. Ott, S. Paula, R. Schnablová, F. H. Schweingruber, and G. Ottaviani. 2019. Handbook of standardized protocols for collecting plant modularity traits. *Perspectives in Plant Ecology, Evolution and Systematics.* **40**:1-21. doi:https://doi.org/10.1016/j.ppees.2019.125485https://doi.org/10.1016/j.ppees.2019.125485

Kühner, A., and M. Kleyer. 2008. A parsimonious combination of functional traits predicting plant response to disturbance and soil fertility. *Journal of Vegetation Science.* **19**:681-692.

Kulmatiski, A., and K. H. Beard. 2013. Woody plant encroachment facilitated by increased precipitation intensity. *Nature Climate Change.* **3**:833-837. doi:https://doi.org/10.1038/nclimate1904https://doi.org/10.1038/nclimate1904

Kursar, T. A., B. M. J. Engelbrecht, A. Burke, M. T. Tyree, B. EI Omari, and J. P. Giraldo. 2009. Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology.* **23**:93-102. doi:https://doi.org/10.1111/j.1365-2435.2008.01483.xhttps://doi.org/10.1111/j.1365-2435.2008.01483.x

Kyalangalilwa, B., J. S. Boatwright, B. H. Daru, O. Maurin, and M. van der Bank. 2013. Phylogenetic position and revised classification of *Acacia* s.l. (Fabaceae: Mimosoideae) in Africa, including new combinations in *Vachellia* and *Senegalia*. *Botanical Journal of the Linnean Society.* **172**:500-523. doi:10.1111/boj.1204710.1111/boj.12047

Lagendijk, D. D. G., R. Mackey, B. R. Page, and R. Slotow. 2011. The effects of herbivory by a mega- and mesoherbivore on tree recruitment in sand forest, South Africa. *PLOS ONE.* **6**:1-9.

Lamont, B. B., D. C. Le Maitre, R. M. Cowling, and N. J. Enright. 1991. Canopy seed storage in woody plants. *The Botanical Review.* **57**:277-317. doi:10.1007/BF0285877010.1007/BF02858770

Lawes, M. J., J. J. Midgley, and P. J. Clarke. 2013. Costs and benefits of relative bark thickness in relation to fire damage: a savanna/forest contrast. *Journal of Ecology.* **101**:517-524. doi:https://doi.org/10.1111/1365-2745.12035https://doi.org/10.1111/1365-2745.12035

Lehmann, C. E. R., T. M. Anderson, M. Sankaran, S. I. Higgins, S. Archibald, and e. al. 2014. Savanna vegetation-fire-climate relationships differ among continents. *Science.* **343**:548-552.

Lehmann, C. E. R., S. A. Archibald, W. A. Hoffmann, and W. J. Bond. 2011. Deciphering the distribution of the savanna biome. *New Phytologist.* **191**:197-209. doi:https://doi.org/10.1111/j.1469-8137.2011.03689.xhttps://doi.org/10.1111/j.1469-8137.2011.03689.x

Leishman, M., I. Wright, A. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. *Seeds: The Ecology of Regeneration in Plant Communities.* **2** doi:10.1079/9780851994321.003110.1079/9780851994321.0031

Lens, F., A. Tixier, H. Cochard, J. S. Sperry, S. Jansen, and S. Herbette. 2013. Embolism resistance as a key mechanism to understand adaptive plant strategies. *Current Opinion in Plant Biology.* **16**:287-292. doi:https://doi.org/10.1016/j.pbi.2013.02.005https://doi.org/10.1016/j.pbi.2013.02.005

Levick, S. R., G. P. Asner, and I. P. J. Smit. 2012. Spatial patterns in the effects of fire on savanna vegetation three-dimensional structure. *Ecological Applications.* **22**:2110-2121.

Levick, S. R., A. E. Richards, G. D. Cook, J. Schatz, M. Guderle, R. J. Williams, P. Subedi, S. E. Trumbore, and A. N. Andersen. 2019. Rapid response of habitat structure and above-ground carbon storage to altered fire regimes in tropical savanna. *Biogeosciences.* **16**:1493-1503. doi:10.5194/bg-16-1493-201910.5194/bg-16-1493-2019

Lewis, G. P. 2005. Acacieae.In: G. P. Lewis, B. D. Schrire, B. Mackinder, and J. M. Lock, editors.eds *Legumes of the World*. Royal Botanic Gardens, Kew, UK. Pages 187-191

Li, F. L., and W. K. Bao. 2015. New insights into leaf and fine-root trait relationships: implications of resource acquisition among 23 xerophytic woody species. *Ecology and Evolution.* **5**:5344-5351. doi:10.1002/ece3.179410.1002/ece3.1794

Liyanage, G. S., and M. K. J. Ooi. 2018. Seed size-mediated dormancy thresholds: a case for the selective pressure of fire on physically dormant species. *Biological Journal of the Linnean Society.* **123**:135-143.

Lötter, M. C. 2018. Fabaceae: Mimosoideae.In: J. E. Burrows, S. Burrows, E. Schmidt, M. Lötter, and E. O. Wilson, editors.eds *Trees and Shrubs Mozambique*. Print Matters Heritage (Pty) Ltd, Nordhoek, Cape Town. Pages 180-223

Lucas, A. 2019. amap: Another Multidimensional Analysis Package. https://CRAN.R-project.org/package=amap,

Luckow, M. A., J. T. Miller, D. J. Murphy, and T. Livshultz. 2003. A phylogenetic analysis of the Mimosoideae (Leguminosae) based on chloroplast DNA sequence data.In: B. B. Klitgaard and A. Bruneau, editors.eds *Advances in Legume Systematics*. Royal Botanic Gardens, Kew, UK. Pages 197-220

Lumley, T. 2017. Regression Subset Selection. Based on Fortran code by Alan Miller

Maracahipes, L., M. B. Carlucci, E. Lenza, B. S. Marimon, B. H. Marimon, F. A. G. Guimarães, and M. V. Cianciaruso. 2018. How to live in contrasting habitats? Acquisitive and conservative strategies emerge at inter- and intraspecific levels in savanna and forest woody plants. *Perspectives in Plant Ecology, Evolution and Systematics.* **34**:17-25. doi:https://doi.org/10.1016/j.ppees.2018.07.006https://doi.org/10.1016/j.ppees.2018.07.006

Markesteijn, L., and L. Poorter. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology.* **97**:311-325.

Markham, C. G. 1970. Seasonality of precipitation in the United States. *Annals of the Association of American Geographers.* **60**:593-597.

Martin, R. E., and D. B. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. Pages 150-157 *in* Proceedings of the Conference on Biodiversity of Northwest California Ecosystems. Cooperative Extension, University of California: Berkeley, USA.

Martínez-Cabrera, H. I., C. S. Jones, S. Espino, and H. J. Schenk. 2009. Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. *American journal of botany.* **96**:1388-1398.

Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the Comparative Method: A General Approach to Incorporating Phylogenetic Information into the Analysis of Interspecific Data. *The American Naturalist.* **149**:646-667.

Materechera, E. K., and S. A. Materechera. 2001. Breaking dormancy to improve germination in seeds of *Acacia erioloba*. *South African Journal of Plant and Soil.* **18**:142-146.

McDowell, N., W. Pockman, C. Allen, D. Breshears, N. Cobb, T. Kolb, J. Plaut, J. Sperry, A. West, D. Williams, and E. Yepez. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *The New phytologist.* **178**:719-739. doi:10.1111/j.1469-8137.2008.02436.x10.1111/j.1469-8137.2008.02436.x

Mengel, R. 1994. Symbiotic dinitrogen fixation - Its dependence on plant nutrition and its ecophysiological impact. *Plant and Soil.* **337**:399-412.

Merino-Martín, L., C. Courtauld, L. Commander, S. Turner, W. Lewandrowski, and J. Stevens. 2017. Interactions between seed functional traits and burial depth regulate germination and seedling emergence under water stress in species from semi-arid environments. *Journal of Arid Environments.* **147**:25-33.

Midgley, J. J., M. A. Botha, and D. Balfour. 2001. Patterns of thorn length, density, type and colour in African Acacias. *African Journal of Range & Forage Science.* **18**:59-61. doi:10.2989/1022011010948575610.2989/10220110109485756

Midgley, J. J., L. M. Kruger, and R. Skelton. 2011. How do fires kill plants? The hydraulic death hypothesis and Cape Proteaceae "fire-resisters". *South African Journal of Botany.* **77**:381-386. doi:https://doi.org/10.1016/j.sajb.2010.10.001https://doi.org/10.1016/j.sajb.2010.10.001

Midgley, J. J., and M. J. Lawes. 2016. Relative bark thickness: towards standardised measurements and analysis. *Plant Ecology.* **217**:677-681. doi:doi:10.1007/s11258-016-0587-8doi:10.1007/s11258-016-0587-8

Midgley, J. J., M. J. Lawes, and S. Chamaillé-Jammes. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany.* **58**:1-11.

Miller, M. F. 1994. The costs and benefits of *Acacia* seed consumption by ungulates. *Oikos.* **71**:181-187.

Mlambo, D., and I. Mapaure. 2006. Post-fire resprouting of *Colospermum mopane* saplings in a southern African savanna. *Journal of Tropical Ecology.* **22**:231-234.

Moles, A. T. 2018. Being John Harper: Using evolutionary ideas to improve understanding of global patterns in plant traits. *Journal of Ecology.* **106**:1-18. doi:https://doi.org/10.1111/1365-2745.12887https://doi.org/10.1111/1365-2745.12887

Moles, A. T., B. Peco, I. R. Wallis, W. J. Foley, A. G. B. Poore, E. W. Seabloom, P. A. Vesk, A. J. Bisigato, L. Cella-Pizarro, C. J. Clark, P. S. Cohen, W. K. Cornwell, W. Edwards, R. Ejrnæs, T. Gonzales-Ojeda, B. J. Graae, G. Hay, F. C. Lumbwe, B. Magaña-Rodríguez, B. D. Moore, P. L. Peri, J. R. Poulsen, J. C. Stegen, R. Veldtman, H. von Zeipel, N. R. Andrew, S. L. Boulter, E. T. Borer, J. H. C. Cornelissen, A. G. Farji-Brener, J. L. DeGabriel, E. Jurado, L. A. Kyhn, B. Low, C. P. H. Mulder, K. Reardon-Smith, J. Rodríguez-Velázquez, A. De

Fortier, Z. Zheng, P. G. Blendinger, B. J. Enquist, J. M. Facelli, T. Knight, J. D. Majer, M. Martínez-Ramos, P. McQuillan, and F. K. C. Hui. 2013. Correlations between physical and chemical defences in plants: tradeoffs, syndromes, or just many different ways to skin a herbivorous cat? *New Phytologist.* **198**:252-263. doi:https://doi.org/10.1111/nph.12116https://doi.org/10.1111/nph.12116

Moles, A. T., and M. Westoby. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology.* **92**:372-383. doi:https://doi.org/10.1111/j.0022-0477.2004.00884.xhttps://doi.org/10.1111/j.0022-0477.2004.00884.x

Moles, A. T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. *Oikos.* **113**:91-105.

Morris, H., and S. Jansen. 2017. Bark: its anatomy, function and diversity. *International Dendrology Society.* **1**:51-61.

Munné-Bosch, S., and L. Alegre. 2004. Die and live: leaf senescence contributes to plant survival under drought stress. *Functional Plant Biology.* **31**:203-216.

Murphy, D. J. 2008. A review of the classification of *Acacia* (Leguminosae, Mimosoideae). *Muelleria: An Australian Journal of Botany.* **26**:10-26. doi:10.5962/p.29249010.5962/p.292490

Musch, T. p., S. Dressler, M. Schmidt, and G. Zizka. 2014. *Acacia ehrenbergia* Hayne. African Plants - A Photo Guide, Forschungsinstitut Senckenberg, Germany. www.africanplants.senckenberg.de, Location: Niger, NW of Bonkoukou, near Filingué

Nardini, A., and J. Luglio. 2014. Leaf hydraulic capacity and drought vulnerability: possible trade-offs and correlations with climate across three major biomes. *Functional Ecology.* **28**:810-818. doi:https://doi.org/10.1111/1365-2435.12246https://doi.org/10.1111/1365-2435.12246

Nishida, H., and T. Suzaki. 2018. Two negative regulatory systems of root nodule symbiosis: how are symbiotic benefits and costs balanced? *Plant and Cell Physiology.* **59**:1733-1738.

Nix, H. A. 1983. Climate of tropical savannas.In: F. Bourlière, editor. *Tropical Savannas*. Elsevier, Amsterdam. Pages 37-62

O'Connor, T. G., J. R. Puttick, and M. T. Hoffman. 2014. Bush encroachment in southern Africa: changes and causes. *African Journal of Range & Forage Science.* **31**:67-88. doi:10.2989/10220119.2014.93999610.2989/10220119.2014.939996

Oksanen, J., F. G. Blanchet, M. Frienfly, R. Kindt, P. Legendre, and e. al. 2019. Community Ecology Package. Pages Ordination methods, diversity analysis and other functions for community and vegetation ecologists. CRAN.

Oliver, P. 1871. *Acacia lahai* Steud. et Hochst. [family Leguminosae-Mimosoideae]. Page 1 Flora of Tropical Africa, JSTOR Global Plants. Royal Botanic Gardens, Kew, http://plants.jstor.org/stable/pdf/10.5555/al.ap.flora.flota002569,

Olson, M. E., D. Soriano, J. A. Rosell, T. Anfodillo, M. J. Donoghue, E. J. Edwards, C. León-Gómez, T. Dawson, J. J. C. Martínez, M. Castorena, A. Echeverría, C. I. Espinosa, A. Fajardo, A. Gazol, S. Isnard, R. S. Lima, C. R. Marcati, and R. Méndez-Alonzo. 2018. Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences.* **115**:7551-7556. doi:doi:10.1073/pnas.1721728115doi:10.1073/pnas.1721728115

Osborne, C. P., T. Charles-Dominique, N. Stevens, W. J. Bond, G. Midgley, and C. E. R. Lehmann. 2018. Human impacts in African savannas are mediated by plant functional traits. *New Phytologist.* **220**:10-24. doi:https://doi.org/10.1111/nph.15236https://doi.org/10.1111/nph.15236

Otieno, D. O., M. W. T. Schmidt, S. Adiku, and J. Tenhunen. 2005. Physiological and morphological responses to water stress in two *Acacia* species from contrasting habitats. *Tree physiology.* **25**:361-371.

Palmer, H., A. Denham, and M. Ooi. 2018. Fire severity drives variation in post-fire recruitment and residual seed bank size of *Acacia* species. *Plant Ecology.* **219** doi:10.1007/s11258-018-0815-510.1007/s11258-018-0815-5

Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics.* **35**:526-528.

Paul-Victor, C., and L. A. Turnbull. 2009. The effect of growth conditions on the seed size/number trade-off. *PLOS ONE.* **4**:1-10.

Pausas, J. G. 2015. Bark thickness and fire regime. *Functional Ecology.* **29**:315-327. doi:https://doi.org/10.1111/1365-2435.12372https://doi.org/10.1111/1365-2435.12372

Pausas, J. G., R. A. Bradstock, D. A. Keith, and J. E. Keeley. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology.* **85**:1085-1100. doi:https://doi.org/10.1890/02-4094https://doi.org/10.1890/02-4094

Pausas, J. G., J. E. Keeley, and D. W. Schwilk. 2017. Flammability as an ecological and evolutionary driver. *Journal of Ecology.* **105**:289-297.

Pausas, J. G., R. B. Pratt, J. E. Keeley, A. L. Jacobsen, A. R. Ramirez, and e. al. 2016. Towards understanding resprouting at the global scale. *New Phytologist.* **209**:945-954.

Pebesma, E. J., and R. S. Bivand. 2005. Classes and methods for spatial data in R. R News 5. https://cran.r-project.org/doc/Rnews/,

Pellegrini, A., A. Franco, and W. Hoffmann. 2015. Shifts in functional traits elevate risk of fire-driven tree dieback in tropical savanna and forest biomes. *Global Change Biology.* doi:10.1111/gcb.1311010.1111/gcb.13110

Pellegrini, A. F. A., W. R. L. Anderegg, C. E. T. Paine, W. A. Hoffmann, T. Kartzinel, and e. al. 2017. Convergence of bark investment according to fire and climate structures ecosystem to vulnerability change. *Ecology Letters.* **20**:307-346.

Pellegrini, A. F. A., A. C. Staver, L. O. Hedin, T. Charles-Dominique, and A. Tourgee. 2016. Aridity, not fire, favors nitrogen-fixing plants across tropical savanna and forest biomes. *Ecology.* **97**:2177-2183. doi:https://doi.org/10.1002/ecy.1504https://doi.org/10.1002/ecy.1504

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, W. K. Cornwell, J. M. Craine, D. E. Gurvich, C. Urcelay, E. J. Veneklaas, P. B. Reich, L. Poorter, I. J. Wright, P. M. Ray, L. Enrico, J. G. Pausas, A. C. d. Vos, N. Buchmann, G. Funes, F. Quétier, J. G. Hodgson, K. A. Thompson, H. D. Morgan, H. t. Steege, M. v. d. Heijden, L. Sack, B. Blonder, P. Poschlod, M. V. Vaieretti, G. Conti, A. C. Staver, S. O. d. Aquino, and J. H. C. Cornelissen. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany.* **61**:167-234.

Phillips, S. J. 2017. Fitting 'Maxent' species distribution models with 'glmet'. Pages Procedures to fit species distributions models from occurrence records and environmental variables, using 'glmnet' for model fitting. Model structure is the same as for the 'Maxent' Java package, version 3.4.0, with the same feature types and regularization options. CRAN.

Pittermann, J., J. Lance, L. Poster, A. Baer, and L. R. Fox. 2014. Heavy browsing affects the hydraulic capacity of *Caenothus rigidus* (Rhamnaceae). *Oecologia.* **175**:801-810.

Poorter, H., Ü. Niinemets, L. Poorter, I. J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist.* **182**:565-588. doi:https://doi.org/10.1111/j.1469-8137.2009.02830.xhttps://doi.org/10.1111/j.1469-8137.2009.02830.x

Poorter, L., and L. Markesteijn. 2008. Seedling traits that determine drought tolerance of tropical tree species. *Biotropica.* **40**:321-331.

Pratt, R. B., A. L. Jacobsen, F. W. Ewers, and S. D. Davis. 2007. Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist.* **174**:787-798.

Prins, H. H. T., and H. P. van der Jeugd. 1993. Herbivore population crashes and woodland structure in East Africa. *Journal of Ecology.* **81**:305-314.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins, and M. Sankaran. 2011. When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography.* **20**:653-660. doi:https://doi.org/10.1111/j.1466-8238.2010.00634.xhttps://doi.org/10.1111/j.1466-8238.2010.00634.x

Ratnam, J., C. Sheth, and M. Sankaran. 2020. African and Asian savannas: Comparisons of vegetation composition and drivers of vegetation structure and function.In: P. F. Scogings and M. Sankaran, editors.eds *Savanna Woody Plants and Large Herbivores*. Wiley, Hoboken, NJ. Pages 25-51

Renoult, D. 2008. Photo 3032994 - *Senegalia montis-usti*. iNaturalist.

Resco de Dios, V., C. Arteaga, J. Hedo, E. Pelegrín, and J. Voltas. 2018. A trade-off between embolism resistance and bark thickness in conifers: are drought and fire adaptations antagonistic? *Plant Ecology & Diversity.* **11**:1-6. doi:10.1080/17550874.2018.150423810.1080/17550874.2018.1504238

Robitzsch, A. 2020. Why ordinal variables can (almost) always be treated as continuous variables. Clarifying assumptions of robust continuous and ordinal factor analysis estimation methods. *Frontiers in Education.* doi:doi: 10.3389/feduc.2020.589965doi: 10.3389/feduc.2020.589965

Rohner, C., and D. Ward. 1997. Chemical and mechanical defense against herbivory in two sympatric species of desert *Acacia*. *Journal of Vegetation Science.* **8**:717-726.

Romero, C. 2014. Bark: structure and functional ecology. *Advances in Economic Botany.* **17**:5-25.

Rooke, T., K. Danell, R. Bergström, C. Skarpe, and J. Hjältén. 2004. Defensive traits of savanna trees - the role of shoot exposure to browsers. *Oikos.* **107**:161-171.

Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology.* **38**:268-280.

Rosell, J. A. 2016. Bark thickness across the angiosperms: more than just fire. *New Phytologist.* **211**:90-102.

Rosell, J. A. 2019. Bark in woody plants: understanding the diversity of a multifunctional structure. *Integrative and Comparative Biology.* **59**:535-547. doi:10.1093/icb/icz05710.1093/icb/icz057

Rosell, J. A., S. Gleason, R. Méndez-Alonzo, Y. Chang, and M. Westoby. 2014. Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist.* **201**:486-497.

Rosell, J. A., and M. E. Olson. 2014. The evolution of bark mechanics and storage across habitats in a clade of tropical trees. *American journal of botany.* **101**:764-777.

Rosell, J. A., M. E. Olson, and T. Anfodillo. 2017. Scaling of xylem vessel diameter with plant size: causes, predictions, and outstanding questions. *Current Forestry Reports.* **3**:46-59. doi:10.1007/s40725-017-0049-010.1007/s40725-017-0049-0

Ross, J. H. 1972. *The Acacia species of Natal*. 2nd edition. Natal branch, Wildlife Protection & Conservation Soc. of S.A, [S.l.].

Ross, J. H. 1979. *A Conspectus of the African Acacia Species*. Botanical Research Institue, Department of Agricultural Services, Republic of South Africa.

Rossatto, D. R., and A. C. Franco. 2017. Expanding our understanding of leaf functional syndromes in savanna systems: the role of plant growth form. *Oecologia.* **183**:953-962. doi:10.1007/s00442-017-3815-610.1007/s00442-017-3815-6

Rossatto, D. R., L. C. R. Silva, R. Villalobos-Vega, L. S. L. Sternberg, and A. César-Franco. 2012. Depth of water uptake in woody plants relates to groundwater level and vegetation structure along a topographic gradient in a neotropical savanna. *Environmental and Experimental Botany.* **77**:259-266.

Rueda, M., O. Godoy, and B. Hawkins. 2016. Spatial and evolutionary parallelism between shade and drought tolerance explains the distributions of conifers in the conterminous United States. *Global Ecology and Biogeography.* **26**:31-42. doi:10.1111/geb.1251110.1111/geb.12511

Rutherford, M. C., L. Mucina, M. C. Lötter, G. J. Bredenkamp, J. H. L. Smit, and e. al. 2006. Savanna biome: description of vegetation units.In: L. Mucina and M. C. Rutherford, editors.eds *The Vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria, South Africa. Pages 460-528

Sankaran, M. 2019. Drought and the ecological future of tropical savanna vegetation. *Journal of Ecology.* **107**:1531-1549.

Sankaran, M., N. Hanan, R. Scholes, J. Ratnam, D. Augustine, B. Cade, J. Gignoux, S. Higgins, X. Roux, F. Ludwig, J. Ardö, F. Banyikwa, A. Bronn, G. Bucini, K. Caylor, M. Coughenour, A. Diouf, W. Ekaya, C. Feral, and N. Zambatis. 2005. Determinants of woody cover in African Savannas. *Nature.* **438**:846-849. doi:10.1038/nature0407010.1038/nature04070

Sankaran, M., J. Ratnam, and N. Hanan. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography.* **17**:236-245. doi:https://doi.org/10.1111/j.1466-8238.2007.00360.xhttps://doi.org/10.1111/j.1466-8238.2007.00360.x

Sankaran, M., J. Ratnam, and N. P. Hanan. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters.* **7**:480-490. doi:https://doi.org/10.1111/j.1461-0248.2004.00596.xhttps://doi.org/10.1111/j.1461-0248.2004.00596.x

Sarmiento, G. 1984. *The Ecology of Neotropical Savannas*. Harvard University Press, Cambridge, MA 02138.

Schafer, J., B. Breslow, and W. Hoffmann. 2015. Relative bark thickness is correlated with tree species distributions along a fire frequency gradient. *Fire Ecology.* **11**:74-87. doi:10.4996/fireecology.110107410.4996/fireecology.1101074

Schmidt, M., S. Dressler, M. Schmidt, and G. Zizka. 2014. *Acacia macrostachya* Rchb. ex DC. African Plants - A Photo Guide, Forschungsinstitut Senckenberg, Germany. www.africanplants.seckenberg.de,

Schmitt, M. H., and A. M. Shrader. 2020. Browser population-woody vegetation relationships in savannas: from bites to landscapes.In: P. F. Scogings and M. Sankaran, editors.eds *Savanna Woody Plants and Large Herbivores*. John Wiley and Sons Ltd., Hoboken, NJ. Pages 245-279

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods.* **9**:671-675. doi:doi:10.1038/nmeth.2089doi:10.1038/nmeth.2089

Scholes, R. J. 1997. Savanna.In: R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors.eds *Vegetation of southern Africa*. Cambridge University Press, Cambridge. Pages 258-277

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics.* **28**:517-544. doi:10.1146/annurev.ecolsys.28.1.51710.1146/annurev.ecolsys.28.1.517

Scholes, R. J., P. R. Dowty, K. Caylor, D. A. B. Parsons, P. G. H. Frost, and H. H. Shugart. 2002. Trends in savanna structure and composition along an aridity gradient in the Kalahari. *Journal of Vegetation Science.* **13**:419-428. doi:https://doi.org/10.1111/j.1654-1103.2002.tb02066.xhttps://doi.org/10.1111/j.1654-1103.2002.tb02066.x

Scholes, R. J., and M. C. Scholes. 1997. Applications of biogeochemical modelling in southern Africa. *Progress in Physical Geography: Earth and Environment.* **21**:102-112. doi:10.1177/03091333970210010610.1177/030913339702100106

Scholes, R. J., and B. H. Walker. 2004. *An African savanna: synthesis of the Nylsvley study*. 1st pbk. edition. Cambridge University Press, Cambridge, UK.

Scholtz, R., V. M. Donovan, T. Strydom, C. Wonkka, U. P. Kreuter, W. E. Rogers, C. Taylor, I. P. J. Smit, N. Govender, W. Trollope, D. T. Fogarty, and D. Twidwell. 2022. High-intensity fire experiments to manage shrub encroachment: lessons learned in South Africa and the United States. *African Journal of Range & Forage Science.* **39**:148-159. doi:10.2989/10220119.2021.200800410.2989/10220119.2021.2008004

Scholz, F. G., S. J. Bucci, G. Goldstein, F. C. Meinzer, A. C. Franco, and F. Miralles-Wilhelm. 2007. Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant, Cell & Environment.* **30**:236-248. doi:https://doi.org/10.1111/j.1365-3040.2006.01623.xhttps://doi.org/10.1111/j.1365-3040.2006.01623.x

Sheffer, E., S. Batterman, S. Levin, and L. Hedin. 2015. Biome-scale nitrogen fixation strategies selected by climatic constraints on nitrogen cycle. *Nature Plants.* **1**:15182. doi:10.1038/nplants.2015.18210.1038/nplants.2015.182

Smit, N. 1999. *Guide to the Acacias of South Africa*. Briza Publications, Pretoria, South Africa.

Smith, A., and M. Wooster. 2005. Remote classification of head and backfire types from MODIS fire radiative power and smoke plume observations. *International Journal of Wildland Fire.* **14**:249.

Solbrig, O., E. Medina, and J. F. Silva. 1996. Biodiversity and Savanna Ecosystem Processes: a global perspective.In: H. A. Mooney, J. H. Cushman, E. Medina, O. E. Sala, and E.-D. Schulze, editors.eds *Functional Roles of Biodiversity: A Global Perspective*. John Wiley and Sons Ltd, Berlin, Heidelberg.10.1007/978-3-642-78969-4_3

Solbrig, O. T. 1991. The Origin and Function of Biodiversity. *Environment: Science and Policy for Sustainable Development.* **33**:16-38. doi:10.1080/00139157.1991.993139410.1080/00139157.1991.9931394

Song, M., G. Djagbletey, E. E. Nkrumah, and M. Huang. 2015. Patterns in leaf traits of leguminous and non-leguminous dominant trees along a rainfall gradient in Ghana. *Journal of Plant Ecology.* **9**:69-76. doi:10.1093/jpe/rtv03810.1093/jpe/rtv038

Song, W., S. Chen, Y. Zhou, and G. Lin. 2020. Rainfall amount and timing jointly regulate the responses of soil nitrogen transformation processes to rainfall increase in an arid desert ecosystem. *Geoderma.* **364**:1-11.

Spessa, A., B. McBeth, and C. Prentice. 2005. Relationships among fire frequency, rainfall and vegetation patterns in the wet-dry tropics of Northern Australia: an analysis based on NOAA-AVHRR data. *Global Ecology and Biogeography.* **14**:439-454.

Staver, A. C., S. Archibald, and S. Levin. 2011a. Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states. *Ecology.* **92**:1063-1072. doi:https://doi.org/10.1890/10-1684.1https://doi.org/10.1890/10-1684.1

Staver, A. C., S. Archibald, and S. A. Levin. 2011b. The global extent and determinants of savanna and forest as alternative biome states. *Science.* **334**:230-232. doi:doi:10.1126/science.1210465doi:10.1126/science.1210465

Staver, A. C., W. J. Bond, M. D. Cramer, and J. L. Wakeling. 2012. Top-down determinants of niche structure and adaptation among African acacias. *Ecology Letters.* **15**:673-679. doi:https://doi.org/10.1111/j.1461-0248.2012.01784.xhttps://doi.org/10.1111/j.1461-0248.2012.01784.x

Staver, A. C., W. J. Bond, and E. C. February. 2011c. History matters: tree establishment variability and species turnover in an African savanna. *Ecosphere.* **2**:1-12.

Staver, A. C., W. J. Bond, W. D. Stock, S. J. van Rensburg, and M. S. Waldram. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications.* **19**:1909-1919. doi:https://doi.org/10.1890/08-1907.1https://doi.org/10.1890/08-1907.1

Staver, A. C., and S. A. Levin. 2012. Integrating theoretical climate and fire effects on savanna and forest systems. *The American Naturalist.* **180**:211-224. doi:10.1086/66664810.1086/666648

Stevens, N., C. Lehmann, B. Murphy, and G. Durigan. 2016. Savanna woody encroachment is widespread across three continents. *Global Change Biology.* **23** doi:10.1111/gcb.1340910.1111/gcb.13409

Stevens, N., C. Seal, S. Archibald, and W. Bond. 2014. Increasing temperatures can improve seedling establishment in arid-adapted savanna trees. *Oecologia.* **175** doi:10.1007/s00442-014-2958-y10.1007/s00442-014-2958-y

Stovall, A. E. L., H. Shugart, and X. Yang. 2019. Tree height explains mortality risk during an intense drought. *Nature communications.* **10**:4385. doi:10.1038/s41467-019-12380-610.1038/s41467-019-12380-6

Strickland, C., A. C. Liedloff, G. D. Cook, G. Dangelmayr, and P. D. Shipman. 2016. The role of water and fire in driving tree dynamics in Australian savannas. *Journal of Ecology.* **104**:828-840.

Suleiman, M. K., K. Dixon, L. Commander, P. Nevill, N. R. Bhat, M. A. Islam, S. Jacob, and R. Thomas. 2018. Seed germinability and longevity influences regeneration of *Acacia gerrardii*. *Plant Ecology.* **219**:591-609. doi:10.1007/s11258-018-0820-810.1007/s11258-018-0820-8

Suzuki, R., Y. Terada, and H. Shimodaira. 2019. pvclust: Hierrchical clustering with p-values via multiscale bootstrap resampling. https://CRAN.R-project.org/package=pvclust,

Tang, G., and P. Bartlein. 2008. Simulating the climatic effects on vegetation: approaches, issues and challenges. *Progress in Physical Geography.* **5**:543-556. doi:https://doi.org/10.1177/0309133308100443https://doi.org/10.1177/0309133308100443

Teketay, D. 1998. Germination of *Acacia origena, A. pilispina* and *Pterolobium stellatum* in response to different presowing seed treatments, temperature and light. *Journal of Arid Environments.* **38**:551-560.

Telford, E. M., N. Stevens, G. F. Midgley, and C. E. R. Lehmann. 2021. Nodulation alleviates water stress in *Vachellia sieberiana. PREPRINT (Version 1) available at Research Square.*https://doi.org/10.21203/rs.21203.rs-522345/v522341.

Thiele, K. R., V. A. Funk, K. Iwatsuki, P. Morat, C.-I. Peng, P. H. Raven, J. Sarukhán, and O. Seberg. 2011. The controversy over the retypification of *Acacia* Mill. with an Australian type: A pragmatic view. *TAXON.* **60**:194-198.

Thulin, M. 1993. *Flora of Somalia*. Royal Botanic Gardens, Kew.

Timberlake, J. 1980. *Handbook of Botswana Acacias*. Ministry of Agriculture, Botswana, Gaborone, Botswana.

Trenberth, K. E., A. Dai, G. Van Der Schrier, P. D. Jones, J. Barichivich, K. R. Briffa, and J. Sheffield. 2014. Global warming and changes in drought. *Nature Climate Change.* **4**:17-22. doi:https://doi.org/10.1038/nclimate2067https://doi.org/10.1038/nclimate2067

Trollope, W. S. W. 1984. Fire in savanna.In: P. V. de Booysen and N. M. Tainton, editors.eds *Ecological Effects of Fire in South African Ecosystems*. Springer, Berlin, Heidelberg. Pages 149-175 https://doi.org/10.1007/978-3-642-69805-7_7

Trugman, A. T., M. Detto, M. K. Bartlett, D. Medvigy, W. R. L. Anderegg, C. Schwalm, B. Schaffer, and S. W. Pacala. 2018. Tree carbon allocation explains forest drought-kill and recovery patterns. *Ecology Letters.* **21**:1552-1560. doi:https://doi.org/10.1111/ele.13136https://doi.org/10.1111/ele.13136

Tsvuura, Z., and D. Ward. 2022. Does a reciprocal transplant experiment of neighboring *Vachellia karroo* populations demonstrate local adaptation? *South African Journal of Botany.* **144**:316-324. doi:https://doi.org/10.1016/j.sajb.2021.09.012https://doi.org/10.1016/j.sajb.2021.09.012

Tybirk, K. 1993. Pollination, breeding system and seed abortion in some African acacias. *Botanical Journal of the Linnean Society.* **112**:107-137.

Van Langevelde, F., C. A. D. M. Van De Vijver, L. Kumar, J. Van De Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology.* **84**:337-350. doi:https://doi.org/10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2https://doi.org/10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2

Varma, V., A. M. Catherin, and M. Sankaran. 2018. Effects of increased N and P availability on biomass allocation and root carbohydrate reserves differ between N-fixing and non-N-fixing savanna tree seedlings. *Ecology and Evolution.* **8**:8467-8476.

Venter, F., and J.-A. Venter. 1996. *Making the most of indigenous trees*. Briza Publications, Pretoria, South Africa.

Venter, F. J., R. J. Scholes, and H. C. Eckhardt. 2003. The abiotic template and its associated vegetation pattern.In: J. T. Du Toit and H. C. Biggs, editors.eds *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington. Pages 83-129

Vitousek, P. M., D. N. L. Menge, S. C. Reed, and C. C. Cleveland. 2013. Biological nitrogen fixation: rates, patterns and ecological controls in terrstrial ecosystems. *Philosophical transactions of the Royal Society B.* **368**:1-9.

Voisin, A. S., N. G. Munier-Jolain, and C. Salon. 2010. The nodulation process is tightly adjucted to plant growth. An analysis using environmentally and genetically induced variation of nodule number and biomass in pea. *Plant and Soil.* **337**:399-412.

Voisin, A. S., C. Salon, C. Jeudy, and F. R. Warembourg. 2003. Symbiotic N_2 fixation activity in relation to C economy of *Pisum sativum* L. as a function of plant phenology. *Journal of Experimental Botany.* **54**:2733-2744.

Vozzo, J. A., and U. S. F. Service. 2002. *Tropical Tree Seed Manual*. U.S. Department of Agriculture, Forest Service.

Vu, V. Q. 2011. ggbiplot: A ggplot2 based biplot. https://github.com/vqv/ggbiplot, R package version 0.55

Wakeling, J. L., A. C. Staver, and W. J. Bond. 2011. Simply the best: the transition of savanna saplings to trees. *Oikos.* **120**:1448-1451. doi:https://doi.org/10.1111/j.1600-0706.2011.19957.xhttps://doi.org/10.1111/j.1600-0706.2011.19957.x

Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science.* **22**:101-105.

Werner, P. A., and L. D. Prior. 2013. Demography and growth of subadult savanna trees: interactions of life history, size, fire season, and grassy understory. *Ecological Monographs.* **83**:67-93.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil.* **199**:213-227. doi:10.1023/A:100432722472910.1023/A:1004327224729

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics.* **33**:125-159. doi:10.1146/annurev.ecolsys.33.010802.15045210.1146/annurev.ecolsys.33.010802.150452

Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution.* **21**:261-268. doi:https://doi.org/10.1016/j.tree.2006.02.004https://doi.org/10.1016/j.tree.2006.02.004

White, F. 1983. *The Vegetation of Africa: a descriptive memoir to accompany the UNESCO/ AETFAT/ UNSO/ vegetation map of Africa*, Paris.

Whittaker, R. H. 1975. *Communities and Ecosystems*. Second edition. Collier Macmillan, London.

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer, New York. https://ggplot2.tidyverse.org,

Wigley, B., T. Charles-Dominique, G. Hempson, N. Stevens, S. Archibald, W. Bond, K. Bunney, C. Coetsee, J. Donaldson, A. Fidelis, X. Gao, J. Gignoux, C. Lehmann, T. Massad, J. Midgley, M. Millan, D. Schwilk, F. Siebert, C. Solofondranohatra, and L. Kruger. 2020. A handbook for the standardised sampling of plant functional traits in disturbance-prone ecosystems, with a focus on open ecosystems. *Australian Journal of Botany.* **68** doi:10.1071/BT2004810.1071/BT20048

Wigley, B. J., W. J. Bond, H. Fritz, and C. Coetsee. 2015. Mammal browsers and rainfall affect *Acacia* leaf nutrient content, defense, and growth in South African savannas. *Biotropica.* **47**:190-200. doi:https://doi.org/10.1111/btp.12192https://doi.org/10.1111/btp.12192

Wigley, B. J., C. Coetsee, D. J. Augustine, J. Ratnam, D. Hattas, and M. Sankaran. 2019. A thorny issue: woody plant defence and growth in an East African savanna. *Journal of Ecology.* **107**:1839-1851. doi:https://doi.org/10.1111/1365-2745.13140https://doi.org/10.1111/1365-2745.13140

Wigley, B. J., C. Coetsee, K. A. Mawoyo, and H. Fritz. 2022. No evidence for the simultaneous induction of structural and chemical defences in spiny southern African savanna trees. *Austral Ecology.* **47**:1415-1426. doi:https://doi.org/10.1111/aec.13223https://doi.org/10.1111/aec.13223

Wigley, B. J., H. Fritz, and C. Coetsee. 2018. Defence strategies in African savanna trees. *Oecologia.* **187**:797-809. doi:https://doi.org/10.1007/s00442-018-4165-8https://doi.org/10.1007/s00442-018-4165-8

Wigley, B. J., J. A. Slingsby, S. Diaz, W. J. Bond, H. Fritz, and C. Coetsee. 2016. Leaf traits of African woody savanna species across climate and soil fertility gradients: evidence for conservative versus acquisitive resource-use strategies. *Journal of Ecology.* **104**:1357-1369.

Williams, R. J., B. R. A., C. Geoffrey, J. G. A. M., L. A. C., L. C., W. R. J., A. A. N., B. D. M. J. S., C. P. J., C. G. D., H. K. J., and Y. Alan. 2009. *Interactions between climate change, fire regimes and biodiversity in Australia : a preliminary assessment*. CSIRO, [Canberra, A.C.T.].

Wright, I. J., D. S. Falster, M. Pickup, and M. Westoby. 2006. Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics. *Physiologia Plantarum.* **127**:445-456. doi:https://doi.org/10.1111/j.1399-3054.2006.00699.xhttps://doi.org/10.1111/j.1399-3054.2006.00699.x

Wright, I. J., P. B. Reich, and M. Westoby. 2001. Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. *Functional Ecology.* **15**:423-434.

Wright, I. J., and M. Westoby. 2001. Understanding seedling growth relationship through specific leaf area and leaf nitrogen concentration: generalisations across growth forms and growth irradiance. *Oecologia.* **127**:21-29.

Wright, I. J., and M. Westoby. 2002. Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytologist.* **155**:403-416.

Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Díaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2010. Functional traits and the growth–

mortality trade-off in tropical trees. *Ecology.* **91**:3664-3674. doi:https://doi.org/10.1890/09-2335.1https://doi.org/10.1890/09-2335.1

Zeppel, M. J. B., S. P. Harrison, H. D. Adams, D. I. Kelley, G. Li, D. T. Tissue, and e. al. 2015. Research review: Drought and resprouting plants. *New Phytologist.* **206**:583-589.

Zhang, Y.-J., F. C. Meinzer, G.-Y. Hao, F. G. Scholz, S. J. Bucci, F. S. C. Takahashi, R. Villalobos-Vega, J. P. Giraldo, K.-F. Cao, W. A. Hoffmann, and G. Goldstein. 2009. Size-dependent mortality in a Neotropical savanna tree: the role of height-related adjustments in hydraulic architecture and carbon allocation. *Plant, Cell & Environment.* **32**:1456-1466. doi:https://doi.org/10.1111/j.1365-3040.2009.02012.xhttps://doi.org/10.1111/j.1365-3040.2009.02012.x

Zinn, A., D. Ward, and K. Kirkman. 2007. Inducible defences in *Acacia sieberiana* in response to giraffe browsing. *African Journal of Range and Forage Science.* **24**:123-129.

Zirka, A., N. Govender, and S. I. Higgins. 2014. How to tell a shrub from a tree: a life-history perspective from a South African savanna. *Austral Ecology.* **39**:767-778.

Chapter six

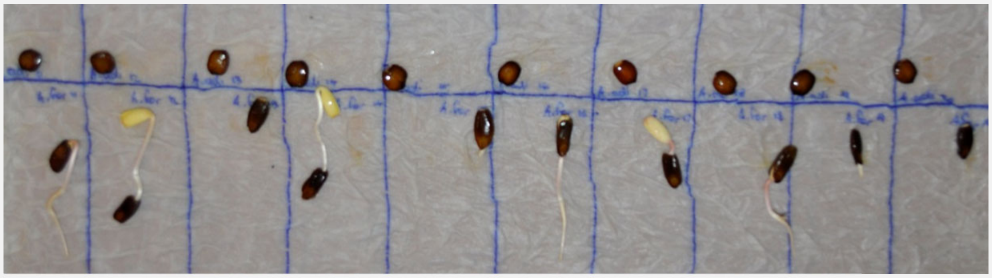
Appendix

Appendix Methods A.

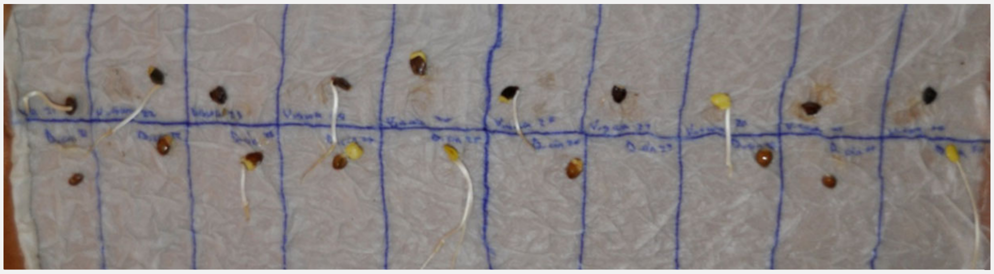
Germination and seedling development patterns – Paper doll experiment

Seed germinations and seedling development patterns were investigated using paper dolls. Acacia seeds are "hard-seeded" because the seed coat prevents water uptake and results in seed dormancy (Smit 1999). The most common method of breaking seed dormancy is to soak seed in boiling water (Venter and Venter 1996). Recent research suggests mechanical scarification may be more effective (Suleiman et al. 2018). For each species, 30 seeds were scarified using two scarification techniques to promote germination (Doran et al. 1983, Ghassali et al. 2012, Suleiman et al. 2018). Mechanically scarified seeds had a small section of the seed testa opposite the hilium to minimise embryo damage (Suleiman et al. 2018) removed using sandpaper (Materechera and Materechera 2001). Boiled seeds were soaked in boiling water to increase seed coat permeability (Teketay 1998, Abari et al. 2012). After scarification, seed were soaked in water for 12-24 hours prior to placement in paper dolls, to allow seeds to fully imbibe (Kheloufi et al. 2017).

Within a paper doll, seeds were placed in a grid-like system of two rows; each row contained ten seeds of a given species and three sets of paper dolls were used per species pair (Figure A1). The paper dolls were moistened with approximately 100ml of water and rolled into cylinders that were placed vertically in clear plastic bags; six paper dolls were stored in a plastic bag which was then tied closed. A propamocarb-based fungicide was sprayed over the opened paper dolls daily and seed germination was monitored for 28 days. The date of germination was recorded once the radicle emerged from the seed or the plumule became visible (Vozzo and Service 2002, Kassa et al. 2010, Bewley et al. 2013). The average germination percentage was then derived for each species for each scarification technique. Results are shown in Table A1.

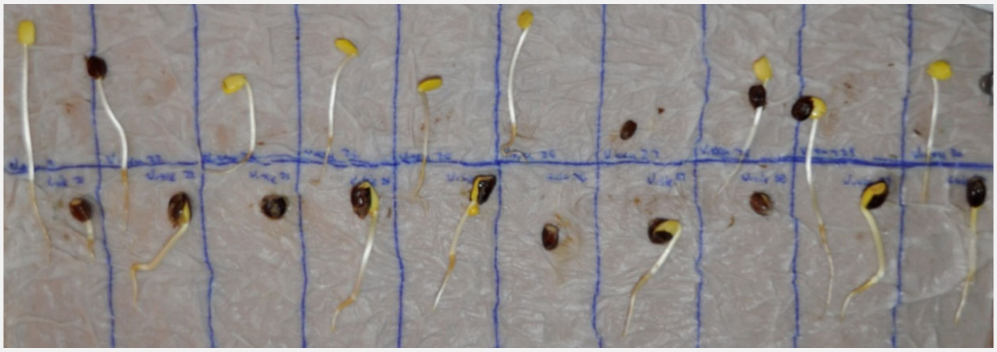


Albizia adianthifolia (Top) and *Albizia forbesii* (Bottom)



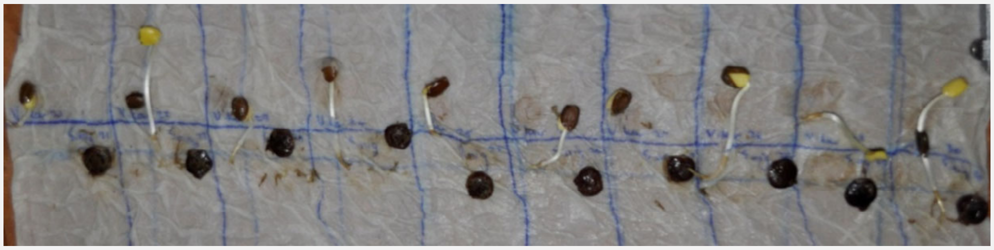
Vachellia swazica (Top) and *Dichrostachys cinerea* (Bottom)

Vachellia erioloba (Top) and *Senegalia galpinii* (Bottom)

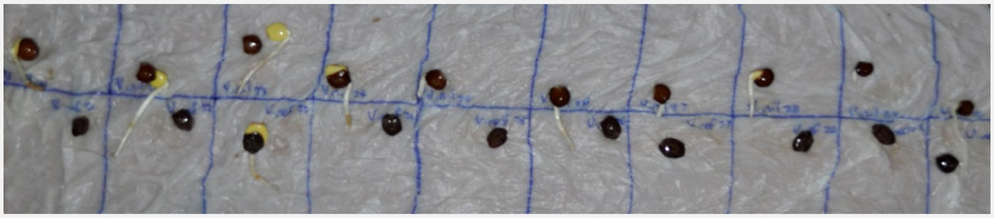


Vachellia exuvialis (Top) and *Vachellia sieberiana* (Bottom)

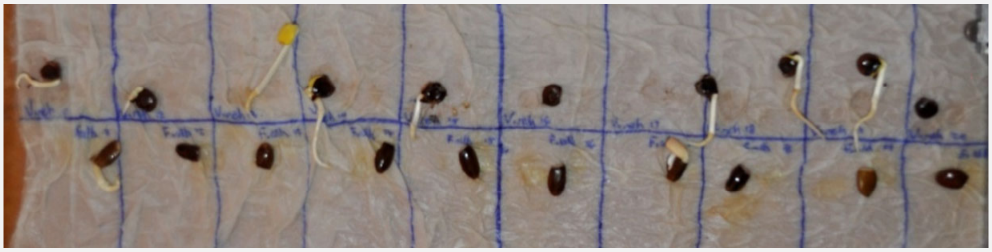
Figure A1: *Images from the germination experiment captured on 11 November 2019, using a tripod and constant magnification for individuals 1-10, 11-20 or 21-30 of a species.*



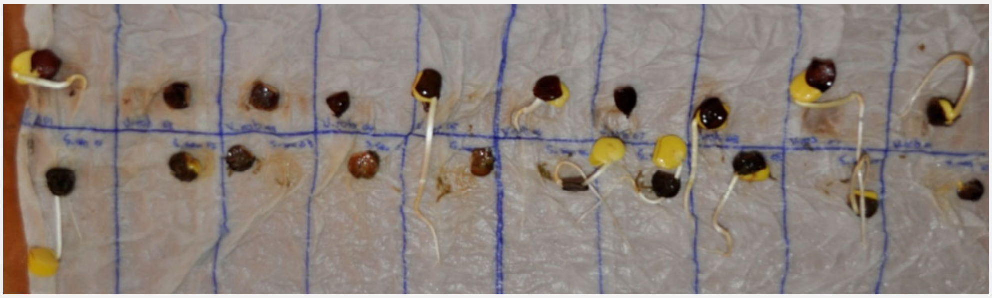
Vachellia karroo (Top) and *Senegalia nigrescens* (Bottom)



Vachellia nilotica (Top) and *Vachellia reficiens* (Bottom)



Vachellia rehmanniana (Top) and *Faidherbia albizia* (Bottom)



Vachellia robusta (Top) and *Senegalia Senegal* (Bottom)

Figure A1 (continued): Images (continued) from the germination experiment captured on 11 November 2019, using a tripod and constant magnification for individuals 1-10, 11-20 or 21-30 of a species.

Table A1: The germination successes from paper doll experiments that were achieved for the two scarification techniques are shown.

Species	Germination success (Mechanical, %)	Germination success (Boiled, %)
Albizia forbesii Benth.	80	*47*
Dichrostachys cinerea (L.) Wight & Arn.	*41*	*7*

Senegalia galpinii (Burtt Davy) Seigler & Ebinger	*53*	*43*
Senegalia Senegal var. rostrata (Brenan) Kyal. & Boatwr.	*37*	*43*
Vachellia erioloba (E.Mey.) Seigler & Ebinger	*97*	*13*
Vachellia exuvialis (I.Verd.) Kyal. & Boatwr.	*77*	*38*
Vachellia karroo (Hayne) Banfi & Galasso	*80*	*31*
Vachellia nilotica (L.) P.J.H.Hurter & Mabb.	*87*	*20*
Vachellia rehmanniana (Schinz) Kyal. & Boatwr.	*63*	*0*
Vachellia robusta (Burch.) Kyal. & Boatwr.	*50*	*27*
Vachellia sieberiana (DC.) Kyal. & Boatwr.	*63*	*83*
Vachellia swazica (Burtt Davy) Kyal. & Boatwr.	*73*	*14*

Table A2: Ceptometer readings performed at three different locations per greenhouse were recorded using the Photosynthetically Active Radiation (PAR) output in µmols/m^{2} s. The average PAR reading per greenhouse is also shown.

Greenhouse number	**Ceptometer reading (Photosynthetically Active Radiation,** µmols/m^{2}s**)**			
	1	**2**	**3**	**Average per greenhouse**
1	1154	1222	1342	1239
2	1294	1424	1249	1322
3	1260	1349	1408	1339
4	1283	1258	1315	1285

Table A3: Citations for downloaded GBIF occurrence records

Species	Citation
Albizia forbesii Benth.	Bijmoer R, Scherrenberg M, Creuwels J (2021). Naturalis Biodiversity Center (NL) - Botany. Naturalis Biodiversity Center. Occurrence dataset https://doi.org/10.15468/ib5ypt accessed via GBIF.org on 2021-02-19. Datizua C, Massingue A (2019). Colecção do Herbário da Universidade Eduardo Mondlane. Version 1.4. Herbário da Universidade Eduardo Mondlane (LMU). Occurrence dataset https://doi.org/10.15468/aywock accessed via GBIF.org on 2021-02-19. Figueira R (2017). IICT Herbário LISC. Version 4.2. Instituto de Investigação Científica Tropical. Occurrence dataset https://doi.org/10.15468/iinlqm accessed via GBIF.org on 2021-02-19. Odorico D (2020). Colecção Botânica do Instituto de Investigação Agrária de Moçambique. Version 1.3. Herbarium LMA: Agricultural Research Institute of Mozambique. Occurrence dataset https://doi.org/10.15468/hsez7x accessed via GBIF.org on 2021-02-19.
Dichrostachys cinerea(L.) Wight & Arn.	Akpene K, KAKPO S B (2019). Plan d'Aménagement participative de la Forêt Classée d'Alédjo (Togo). Version 1.6. Network of African Leaders for Biodiversity Conservation and Environment (NALBCE). Occurrence dataset https://doi.org/10.15468/xtukrj accessed via GBIF.org on 2021-03-01. Amahowe O I, Affoukou C, Natta A K (2016). Species composition in twelve (12) *Afzelia africana* Sm & Pers populations in Benin. GBIF Benin. Occurrence dataset https://doi.org/10.15468/9wycdn accessed via GBIF.org on 2021-03-01. Amidou D (2020). Distribution de quelques espèces de plantes et *de Mimusops andongensis* au Bénin. Laboratoire d'Ecologie Appliquée/Université d'Abomey-Calavi (LEA/UAC). Occurrence dataset https://doi.org/10.15468/xlqzzt accessed via GBIF.org on 2021-03-01. Bakayoko A, Chatelain C, Kone M W, Kone I, Ouattara D, Yao K, Gautier L (2020). Occurrences des échantillons de plantes de l'Herbier du Centre Suisse de Recherches Scientifiques (CSRS) en Côte d'Ivoire. Version 1.2. Centre Suisse de Recherches Scientifiques en Côte d'Ivoire. Occurrence dataset https://doi.org/10.15468/gdbrsj accessed via GBIF.org on 2021-03-01. Bijmoer R, Scherrenberg M, Creuwels J (2021). Naturalis Biodiversity Center (NL) - Botany. Naturalis Biodiversity Center. Occurrence dataset https://doi.org/10.15468/ib5ypt accessed via GBIF.org on 2021-03-01. Bissiengou P, Wieringa J, Creuwels J, Engone Obiang N L (2019). Herbier National du Gabon. Version 1.4. Herbier National du Gabon. Occurrence dataset https://doi.org/10.15468/sgxokl accessed via GBIF.org on 2021-03-01.

Catarino L (2017). Dados de ocorrência de espécies da flora da Guiné-Bissau. Version 1.2. Centre for ecology, evolution and environmental change. Occurrence dataset https://doi.org/10.15468/xsp4ka accessed via GBIF.org on 2021-03-01.

Datizua C, Massingue A (2019). Colecção do Herbário da Universidade Eduardo Mondlane. Version 1.4. Herbário da Universidade Eduardo Mondlane (LMU). Occurrence dataset https://doi.org/10.15468/aywock accessed via GBIF.org on 2021-03-01.

de Vries H, Lemmens M. Observation.org, Nature data from around the World. Observation.org. Occurrence dataset https://doi.org/10.15468/5nilie accessed via GBIF.org on 2021-03-01.

Dossa Gbo C F, Vitoekpon I, Gbo F C (2020). Census of plant species in Benin as part of several research projects. ONG Rêve développement. Occurrence dataset https://doi.org/10.15468/9w3pr5 accessed via GBIF.org on 2021-03-01.

Doumbouya S, Diabate M (2018). Espèces menacées de la Guinée forestière extraites dans la base de données de CRRA Sérédou Macenta, IRAG (BID-AF2015-0066-REG). Version 1.4. Institut de Recherche Agronomique de Guinée (IRAG). Occurrence dataset https://doi.org/10.15468/irkrku accessed via GBIF.org on 2021-03-01.

Essou F (2020). Diversity and distribution of multipurpose species in Benin. Laboratoire d'Ecologie Appliquée/Université d'Abomey-Calavi (LEA/UAC). Occurrence dataset https://doi.org/10.15468/i7nkmo accessed via GBIF.org on 2021-03-01.

Favi F, Wabi F, Aikpon G (2017). Distribution de quelques espèces de plantes agroforestières et médicinales au Bénin. Faculté des Sciences et Techniques (FAST). Occurrence dataset https://doi.org/10.15468/kpwam2 accessed via GBIF.org on 2021-03-01.

Figueira R (2017). IICT Herbário LISC. Version 4.2. Instituto de Investigação Científica Tropical. Occurrence dataset https://doi.org/10.15468/iinlqm accessed via GBIF.org on 2021-03-01.

Gagnibo C N, Gbètoho A J (2016). Census of plant species in Monts-Kouffè regions, center Benin. Version 1.1. GBIF Benin. Occurrence dataset https://doi.org/10.15468/9tfduu accessed via GBIF.org on 2021-03-01.

Gangnibo C N, Gbètoho A J (2016). Census of plant species in Pahou forest reserve. Version 1.2. GBIF Benin. Occurrence dataset https://doi.org/10.15468/yr534j accessed via GBIF.org on 2021-03-01.

Gangnibo C, Gbetoho A J (2019). Medicinal plant species found in protected areas and riparian lands in Sudano-Guinean and Sudanian agroecological zones. Data mobilized in the framework of BID National project BID-AF2015-

0065-NAC and funded by EU. Version 1.3. GBIF Benin. Occurrence dataset https://doi.org/10.15468/qbb7sg accessed via GBIF.org on 2021-03-01

Gaston A S, Direction D G F E D R N (2016). The census of national forest of Benin. Version 1.2. GBIF Benin. Occurrence dataset https://doi.org/10.15468/5cdfgv accessed via GBIF.org on 2021-03-01.

Gbetoho J (2018). Distribution de quelques espèces végétales du Bénin. Version 1.2. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/5j9fd4 accessed via GBIF.org on 2021-03-01.

Herbarium of the University of Aarhus. The AAU Herbarium Database. Occurrence dataset https://doi.org/10.15468/7uigwo accessed via GBIF.org on 2021-03-01.

Houessou L G, Kakpo S (2016). Plant inventory of W Biosphere reserve (North-Benin). Data mobilized in the framework of JRS Biodiversity Foundation project. Version 1.2. GBIF Benin. Occurrence dataset https://doi.org/10.15468/jbp1u9 accessed via GBIF.org on 2021-03-01.

Hounsa M, Gbetoho A (2019). Biodiversité végétale de quelques écosystèmes au Bénin. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/a1cdnr accessed via GBIF.org on 2021-03-01.

Hounsa M, Gbetoho J (2018). Espèces envahissantes et menacées des pâturages naturels de la zone soudano-guinéenne, données mobilisées dans le cadre du projet BID. Version 1.1. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/uul0mj accessed via GBIF.org on 2021-03-01.

Kakpo S B, Akpene K (2019). Inventaire floristique dans le cadre le cadre de l'Aménagement de la forêt classé de l'Amou-Mono (Togo). Version 1.4. Network of African Leaders for Biodiversity Conservation and Environment (NALBCE). Occurrence dataset https://doi.org/10.15468/7jsx76 accessed via GBIF.org on 2021-03-01.

Kingbo A, Ganglo J (2017). Census of the species of Benin. Data mobilized in the framework of JRS Benin project and funded by JRS Biodiversity Foundation. Version 1.5. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/uhrfuc accessed via GBIF.org on 2021-03-01.

Kingbo A, Kiki P, Ganglo J (2019). Census of medicinal plants of Benin. Version 1.7. GBIF Benin. Occurrence dataset https://doi.org/10.15468/p4cwmb accessed via GBIF.org on 2021-03-01.

Kouassi A F, Ake-Assi A E, Yao K, N'Goran B (2018). Liste de quelques espèces envahissantes de l'herbier du Centre National de Floristique (CNF) en

Côte d'Ivoire. Version 1.2. Institut Botanique Ake-Assi D'andokoi (IBAAN). Occurrence dataset https://doi.org/10.15468/0aoqi5 accessed via GBIF.org on 2021-03-01.

Koura K (2017). Agroforestry species in Parkia biglobosa's parklands in Northern Benin. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/iokuu0 accessed via GBIF.org on 2021-03-01.

Magill B, Solomon J, Stimmel H (2021). Tropicos Specimen Data. Missouri Botanical Garden. Occurrence dataset https://doi.org/10.15468/hja69f accessed via GBIF.org on 2021-03-01.

Magloe G A, Tohinnou C (2020). Ethnobotanique et diversité floristique des écosystèmes temporairement inondés et fragiles du Bénin. Laboratoire d'Ecologie Appliquée/Université d'Abomey-Calavi (LEA/UAC). Occurrence dataset https://doi.org/10.15468/zccksy accessed via GBIF.org on 2021-03-01.

Masinde S, Matheka K, Atieno D, Odhiambo K, Nyange M, Kamau P (2019). Plant species occurrences recorded from selected sites in the upper Tana River Basin, Kenya. National Museums of Kenya. Occurrence dataset https://doi.org/10.15468/a5iokr accessed via GBIF.org on 2021-03-01.

Moussa D (2018). Les plantes forestières utiles en Guinée Forestière. Inventaire des espèces et usages (BID-AF2015-0066-REG). Version 1.2. Institut de Recherche Agronomique de Guinée (IRAG). Occurrence dataset https://doi.org/10.15468/c2mh0c accessed via GBIF.org on 2021-03-01.

Moussa D (2018). Relevé floristique dans les bassins du fleuve Niger à Faranah (BID-AF2015-0066-REG). Version 1.1. Institut de Recherche Agronomique de Guinée (IRAG). Occurrence dataset https://doi.org/10.15468/hbcxet accessed via GBIF.org on 2021-03-01.

Moussa D, Diabate M (2018). Relevé floristique dans les bassins du fleuve Milo à Kankan (CESP2016-022). Version 1.1. Institut de Recherche Agronomique de Guinée (IRAG). Occurrence dataset https://doi.org/10.15468/sc2xod accessed via GBIF.org on 2021-03-01.

Moussa D, Doumbouya S (2018). Bassins versants de vere et nalon (BID-AF2015-0066-REG). Version 1.1. Centre d'Observation de Surveillance et d'Information Environnementales (COSIE). Occurrence dataset https://doi.org/10.15468/zdeoud accessed via GBIF.org on 2021-03-01.

Moussa D, Doumbouya S (2018). Inventaires des adventices dans les bas-fonds rizicoles de Sérédou (CESP16-0022-Guinea). Version 1.3. Institut de Recherche Agronomique de Guinée (IRAG). Occurrence dataset https://doi.org/10.15468/yqjcbi accessed via GBIF.org on 2021-03-01.

Natural History Museum (2021). Natural History Museum (London) Collection Specimens. Occurrence dataset https://doi.org/10.5519/0002965 accessed via GBIF.org on 2021-03-01.

Nnabude P, Egboka T, Ugbogu O, Osiyemi O (2019). Plants Of Nnamdi Azikiwe University Herbarium (NAUH) Awka. Version 1.5. Forestry Research Institute of Nigeria. Occurrence dataset https://doi.org/10.15468/qqzpfc accessed via GBIF.org on 2021-03-01.

Odorico D (2020). Colecção Botânica do Instituto de Investigação Agrária de Moçambique. Version 1.3. Herbarium LMA: Agricultural Research Institute of Mozambique. Occurrence dataset https://doi.org/10.15468/hsez7x accessed via GBIF.org on 2021-03-01.

Orrell T, Informatics Office (2021). NMNH Extant Specimen Records. Version 1.41. National Museum of Natural History, Smithsonian Institution. Occurrence dataset https://doi.org/10.15468/hnhrg3 accessed via GBIF.org on 2021-03-01.

Oyedokou E A E N, Hounsa M A F (2020). Plant species from Mono Delta transboundary biosphere reserve. Faculté des Sciences et Techniques (FAST). Occurrence dataset https://doi.org/10.15468/dj9mv4 accessed via GBIF.org on 2021-03-01.

Ramirez J, Tulig M, Watson K, Thiers B (2021). The New York Botanical Garden Herbarium (NY). Version 1.31. The New York Botanical Garden. Occurrence dataset https://doi.org/10.15468/6e8nje accessed via GBIF.org on 2021-03-01.

Rakotondrajaona R, Rakotoarisoa M, Ranaivo J, Rakotonandrasana S, Randriambanona H (2019). Database on reference specimens for medicinal plants of the Fabaceae family, conserved at the CNARP herbarium. Version 1.3. Madagascar Biodiversity Information Facility (MadBIF). Occurrence dataset https://doi.org/10.15468/bznvdf accessed via GBIF.org on 2021-03-01.

Sales F, Santos J (2020). Herbarium of University of Coimbra (COI). Herbarium of University of Coimbra (COI). Occurrence dataset https://doi.org/10.15468/7x9xtx accessed via GBIF.org on 2021-03-01.

Sidibe S, Akbaraly M (2016). Phanérogames recensés aux Monts Nimba. Version 3.1. Centre d'Observation de Surveillance et d'Information Environnementales (COSIE). Occurrence dataset https://doi.org/10.15468/nu7rmc accessed via GBIF.org on 2021-03-01.

Telenius A, Shah M (2018). Botany (UPS). GBIF-Sweden. Occurrence dataset https://doi.org/10.15468/ufmslw accessed via GBIF.org on 2021-03-01.

Telenius A, Shah M (2020). Phanerogamic Botanical Collections (S). GBIF-Sweden. Occurrence dataset https://doi.org/10.15468/yo3mmu accessed via GBIF.org on 2021-03-01.

Togni Y (2017). Data on medicinal plants of Benin. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/lhlwfx accessed via GBIF.org on 2021-03-01.

Toko Imorou I, Sogbossi E, Biaou S, Gobi Mohamed A (2018). Distribution géographique de quelques espèces invasives du Bénin (Afrique de l'Ouest).. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/xmucap accessed via GBIF.org on 2021-03-01.

Traore I (2016). Inventory of Penessoulou forest (North West Benin). Version 1.1. GBIF Benin. Occurrence dataset https://doi.org/10.15468/2a9ebc accessed via GBIF.org on 2021-03-01.

Tushabe H (2020). National Biodiversity Data Bank. Observation records, 1900-2014. Version 1.5. National Biodiversity Data Bank. Occurrence dataset https://doi.org/10.15468/djzgie accessed via GBIF.org on 2021-03-01.

Ugbogu O, Osiyemi O, Chukwuma E, Adeniji K, Odewo A, Okanlawon T, Soyewo T, Oyebola T, Aina S (2019). Capture of Primary Biodiversity Data for West African Plants. Version 1.6. Forestry Research Institute of Nigeria. Occurrence dataset https://doi.org/10.15468/9czcig accessed via GBIF.org on 2021-03-01.

Umurungi Y, Gashakamba F (2020). Rwanda's wetlands biodiversity data from different inventories that were conducted between year 2008 and 2017. Version 1.5. Centre of Excellence in Biodiversity and Natural Resources Management. Occurrence dataset ttps://doi.org/10.15468/cfmjjf accessed via GBIF.org on 2021-03-01.

Wittzell H, Shah M (2021). Lund Botanical Museum (LD). Lund Botanical Museum (LD). Occurrence dataset https://doi.org/10.15468/c4w4co accessed via GBIF.org on 2021-03-01.

Wouyou H, Houngbedji M (2020). Study of the floristic diversity of some habitats of *Cercopithecus erythrogaster erythrogaster*, the red-bellied monkey in South Benin. Organisation pour le Développement Durable et la Biodiversité. Occurrence dataset https://doi.org/10.15468/qftf1p accessed via GBIF.org on 2021-03-01.

Yêhouénou Tessi D R (2017). Census of medicinal and agroforestry plants of Benin. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/y8jm57 accessed via GBIF.org on 2021-03-01.

Yehouenou Tessi D R (2017). List of medicinal and agroforestry plants found in various ecosystems of Benin. Laboratory of Forest Sciences (University of Abomey-Calavi). Occurrence dataset https://doi.org/10.15468/wojfbp accessed via GBIF.org on 2021-03-01.

Table A4: Correlation matrix of all trait and environmental variables considered for the study. Darker red cells indicate values close to one; darker blue cells indicate values close to negative one and light shades indicate values close to zero. Trait abbreviations are given in Table 1. Environmental variables are shown in bold. Highly correlated variables (>|0.65|) that were removed from analyses are italicised. Variables that were transformed using '$\frac{1}{[log(max(x+1)-x)+1]}$' are indicated using 'Kassambara'.

	Leaf area	Stem length	Stem diameter	Xylem diameter	IBT	AG mass	BG mass	RBT	D5th root	SLA	Root length	Nodule mass	Stem LDR	Root LDR	Seed mass	Root diameter
Leaf area	1.00															
Stem length	0.28	1.00														
Stem diameter	0.02	*0.82*	1.00													
Xylem diameter	0.25	0.93	0.88	1.00												
IBT	-0.38	0.05	0.04	0.05	1.00											
AG mass	0.18	*0.76*	0.65	0.88	0.18	1.00										
BG mass	0.22	0.49	0.43	0.61	0.16	*0.81*	1.00									
RBT	-0.31	-0.54	-0.29	-0.32	-0.23	-0.11	0.08	1.00								
D5th root	-0.67	-0.36	-0.14	-0.27	0.05	0.00	0.03	0.56	1.00							
SLA	0.00	0.13	0.27	0.00	0.05	-0.21	-0.25	-0.51	-0.31	1.00						
Root length	0.22	0.47	0.55	0.58	-0.44	0.41	0.44	0.02	-0.16	-0.07	1.00					
Nodule mass	0.25	0.58	0.33	0.68	0.25	*0.71*	0.53	-0.08	-0.41	-0.36	0.34	1.00				
Stem LDR	0.46	*0.68*	0.22	0.53	0.12	0.50	0.43	-0.62	-0.55	-0.10	0.10	0.58	1.00			
Root LDR	-0.27	-0.21	-0.19	-0.35	-0.34	-0.57	-0.40	-0.04	-0.08	0.17	0.31	-0.29	-0.17	1.00		
Seed mass	-0.02	0.58	0.66	0.61	0.39	0.54	0.48	-0.20	0.00	-0.05	0.28	0.27	0.30	-0.38	1.00	
Root diameter	0.28	0.61	0.63	0.80	0.23	*0.90*	*0.73*	-0.06	0.00	-0.21	0.35	0.58	0.31	*-0.75*	0.66	1.00
SRS	-0.08	-0.10	0.04	-0.12	-0.04	-0.16	0.33	0.14	-0.12	0.24	0.23	-0.13	-0.05	0.46	-0.14	-0.28
SLS	0.33	-0.65	-0.85	-0.61	-0.19	-0.31	-0.02	0.39	0.02	-0.45	-0.31	-0.06	-0.05	-0.06	-0.57	-0.27
DSRT	0.14	0.64	0.51	0.50	0.16	0.45	0.40	-0.45	0.00	-0.02	0.01	0.03	0.58	-0.34	0.70	0.43
H lowest bud	0.35	0.63	0.44	0.45	-0.24	0.30	0.13	-0.40	-0.33	0.47	0.23	0.14	0.38	-0.06	0.29	0.17
Total mass	0.21	0.59	0.51	0.72	0.20	*0.91*	*0.98*	0.02	0.01	-0.23	0.44	0.62	0.46	-0.48	0.51	*0.82*
Nodule count	0.51	0.36	0.21	0.50	0.10	0.48	0.45	-0.09	-0.49	-0.44	0.33	0.74	0.44	-0.27	0.10	0.52
Precipitation	0.28	-0.25	-0.31	-0.31	-0.41	-0.57	-0.54	0.00	-0.62	0.17	0.01	-0.03	-0.02	0.45	-0.39	-0.55
Rain Seasonality	0.05	0.48	0.52	0.39	-0.26	0.14	0.33	-0.18	-0.24	0.14	0.47	0.04	0.34	0.42	0.22	-0.05
Drought	0.25	0.67	0.58	0.63	0.05	0.58	0.40	-0.59	-0.04	0.10	0.42	0.18	0.39	-0.17	0.36	0.55
Fire intensity	-0.09	-0.42	-0.44	-0.33	0.04	0.00	-0.06	0.39	0.58	-0.48	-0.55	-0.19	-0.25	-0.49	-0.33	0.08
Browser	0.09	-0.51	-0.32	-0.59	-0.36	-0.80	-0.71	0.09	-0.19	0.41	-0.38	-0.67	-0.44	0.24	-0.37	-0.63
Precipitation^{Kassambara}	0.31	0.00	-0.23	-0.06	-0.14	-0.24	-0.32	-0.13	-0.66	-0.08	-0.05	0.32	0.36	0.16	-0.06	-0.25
Fire interval	-0.63	0.39	0.50	0.45	0.28	0.51	0.41	0.07	0.51	-0.16	0.23	0.21	0.06	0.04	0.29	0.29

	SRS	SLS	DSRT	H lowest bud	Total mass	Nodule count	**Precipitation**	**Rain Seasonality**	**Drought**	**Fire intensity**	**Browser**	**Precipitation**$^{\text{Kassambara}}$	**Fire interval**
Leaf area													
Stem length													
Stem diameter													
Xylem diameter													
IBT													
AG mass													
BG mass													
RBT													
D5th root													
SLA													
Root length													
Nodule mass													
Stem LDR													
Root LDR													
Seed mass													
Root diameter													
SRS	1.00												
SLS	0.06	1.00											
DSRT	-0.08	-0.42	1.00										
H lowest bud	-0.11	-0.41	0.36	1.00									
Total mass	0.19	-0.11	0.41	0.19	1.00								
Nodule count	0.01	0.15	0.03	-0.24	0.48	1.00							
Precipitation	0.08	0.22	-0.47	0.11	-0.58	-0.01	**1.00**						
Rain Seasonality	0.66	-0.41	0.45	0.23	0.26	0.14	**0.03**	**1.00**					
Drought	-0.15	-0.43	0.54	0.21	0.47	0.32	**-0.60**	**0.24**	**1.00**				
Fire intensity	-0.38	0.50	-0.04	-0.46	-0.04	0.01	**-0.44**	**-0.51**	**-0.05**	**1.00**			
Browser	0.09	0.13	-0.27	0.04	-0.78	-0.45	***0.66***	**-0.04**	**-0.57**	**-0.06**	**1.00**		
Precipitation$^{\text{Kassambara}}$	-0.18	0.18	-0.18	0.18	-0.32	0.15	***0.84***	**-0.06**	**-0.50**	**-0.41**	**0.33**	**1.00**	
Fire interval	0.16	-0.53	0.32	-0.15	0.45	0.03	***-0.67***	**0.38**	**0.40**	**0.05**	***-0.65***	**-0.56**	**1.00**

Appendix Results A

Table A5: Non-significant results of OLS models investigating the influence of seed size on seedling growth patterns. Model estimates and p-values are shown. All trait variables were log-transformed, scaled, and centred.

	Fixed effects:	Estimate	Std. error	t-value	p-value	Multiple R^2
log(Aboveground mass)	log(Seed mass)	0.541	0.266	2.035	0.069	0.293
log(Belowground mass) ×	log(Seed mass)	0.486	0.386	1.259	0.244	0.165
log(Total mass) ×	Log(Seed mass)	0.466	0.357	1.307	0.227	0.176

× *D. cinerea* and *V. erioloba* were removed as influential outliers.

Table A6: R^2 and p-values of the ordinary least squares (OLS) regression models used to evaluate the trade-offs and potential constraints in trait investment strategies.

Equation	Multiple R^2	Adjusted R^2	Model p-value
BG mass ~ log(stem length) + AG mass	0.935	0.911	<0.001
Stem length ~ Stem diameter + Seed mass	0.681	0.610	0.005
Root length ~ Root diameter + Seed mass	0.126	-0.068	0.545
Nodule mass ~ Nodule count + Seed mass	0.549	0.504	0.006
Total mass ~ log(SLA) + log(Seed mass)	0.167	-0.041	0.482
Xylem conduit diameter ~ log(Stem length) + log(Seed mass)	0.864	0.834	<0.001
Relative bark thickness ~ log(Xylem conduit diameter)	0.100	0.01	0.317

Table A7: Non-significant results of the significant best subset OLS regression models depict potential trade-offs and constraints in trait resource allocation. P-values highlighted by an asterisk (*) remained significant after performing the Benjamini-Hochberg correction. All trait variables were log-transformed, scaled, and centred. Model R^2 and p-values are shown in Appendix Table A5.

	Fixed effects:	Estimate	Std. error	t-value	p-value
Root length	Root diameter	0.297	0.415	0.717	0.492
	Seed mass	0.798	0.415	0.192	0.852
Total mass	log(SLA)	-0.318	0.402	-0.793	0.451
	log(Seed mass)	0.341	0.310	1.097	0.304
Relative bark thickness	log(Xylem conduit diameter)	0.316	0.300	-1.052	0.317

Table A8: The results of phylogenetic least squares (PGLS) regression models and ordinary least squares (OLS) regression models analysing the relationships between environmental variables and species traits are shown: PGLS or OLS model coefficients, significance and lambda (λ) branch length transformations. Differences in Akaike information criterion (AIC) values and Bayesian information criterion (BIC) values for PGLS vs. OLS models are shown if ΔAIC > 0.2 and ΔBIC > 0.25; indicating that the PGLS model should be used (ǂ). SLA = Specific leaf area, MAP = mean annual precipitation (rainfall), Fire intensity = fire radiative power (FRP), Browser = browser biomass index (browser pressure), SPEI = standardized evapotranspiration index (drought severity), XC diameter = xylem conduit diameter, DSRT = depth of the stem-root transition, D5th root = depth of the fifth lateral root, AG mass = aboveground mass, SRS ratio = seedling root-shoot ratio, SLS ratio = seedling leaf-shoot ratio. Variables corrected by 1/(log(max(x+1)-x)+1) are indicated by 'Kassambara'.

Equation	**Multiple R²**	**Adjusted R²**	**Model p-value**	
SLA ~ Log(MAP) + Fire intensity + Log(Browser)	0.682	0.563	0.022	λ=0.000
Stem length ~ SPEI + Fire intensity	0.600	0.499	0.018	λ=0.000
Stem diameter ~ log(SPEI) + log(Fire intensity)	0.513	0.405	0.039	λ=0.000
XC diameter ~ log(SPEI) + log(Fire intensity)	0.541	0.438	0.030	λ=0.000
log(IBT) ~ Rain seasonality + log(Browser)	0.284	0.125	0.223	λ=0.000
RBT ~ Log(MAP) + SPEI	0.595	0.505	0.017	λ=0.000
HLB ~ log(MAP) + SPEI ǂ	0.166	-0.019	0.442	λ=0.796 ΔAIC=4.502 ΔBIC=4.987
log(DSRT) ~ Rain seasonality + log(SPEI)	0.344	0.499	0.150	λ=0.000
log(D5th root) ~ Log(MAP) + log(SPEI)	0.566	0.469	0.023	λ=0.000
log(Root length) ~ log(SPEI) + log(Fire intensity)	0.289	0.131	0.215	λ=0.000
log(Root diameter) ~ SPEI + Browser	0.454	0.333	0.066	λ=0.000
AG mass ~ SPEI + Browser	0.595	0.505	0.017	λ=0.000
log(BG mass) ~ log(Rain seasonality) + log(Browser)	0.501	0.390	0.043	λ=0.000
log(Total mass) ~ log(Rain seasonality) + Browser	0.679	0.608	0.006	λ=0.000
log(SRS ratio) ~ Rain seasonality + SPEI ×[1]	0.838	0.792	0.002	λ=0.000
log(SLS ratio) ~ log(MAP) + log(Fire intensity) + Browser	0.885	0.836	0.001	λ=0.000
log(Nodule count) ~ Rain seasonality + log(Fire intensity) ×[3]	0.620	0.512	0.034	λ=0.000
Total nodule mass ~ MAP + Browser	0.755	0.701	0.002	λ=0.000
log(Seed mass) ~ Rain seasonality + log(Fire intensity)	0.545	0.444	0.029	λ=0.000

×[1] *V. karroo* and *V. rehmanniana* removed as influential outliers; ×[2] *V. rehmanniana* removed as an influential outlier; ×[3] *A. forbesii* and *V. sieberiana* removed as influential outliers.

Table A9: Results of non-significant ordinary least-squared regression models (OLS) depicting relationships between a trait and selected environmental variables based on the best subset model with the lowest Bayesian Information Criterion (BIC) values. MAP = Mean annual precipitation, Fire intensity = Fire radiative power, Browser = Browser biomass index (Browser pressure), SPEI = Standardized precipitation evapotranspiration index (Drought severity). Variables that were transformed using '$\frac{1}{[log(max(x+1)-x)+1]}$' are indicated using 'Kassambara'. P -values highlighted by an asterisk (*), remained significant after performing the Benjamini-Hochberg correction. Model R^2 and p-values are shown in Appendix Table A6.

	Fixed effects:	**Estimate**	**Std. error**	**t-value**	**p-value**
log(Stem diameter)	log(SPEI)	1.170	0.454	2.574	0.030
	log(Fire intensity)	-0.731	0.482	-1.519	0.163
log(Inner bark thickness)	Rain seasonality	-0.196	0.285	-0.689	0.508
	log(Browser)	-0.516	0.312	-1.654	0.132
log(Height of the lowest bud) ‡	$(\text{MAP})^{\text{Kassambara}}$	1.470	1.548	0.950	0.367
	SPEI	0.578	0.461	1.252	0.242
log(Depth of the stem-root transition)	Rain seasonality	0.320	0.286	1.118	0.293
	log(SPEI)	0.773	0.558	1.384	0.200
log(Root length)	log(SPEI)	-0.310	0.220	-1.410	0.192
	log(Fire intensity)	0.292	0.246	1.190	0.264
log(Root diameter)	Browser	-0.472	0.300	-1.572	0.150
	SPEI	0.282	0.300	0.937	0.373

Table A10: Results of the Welch two-sample t-test comparing the mean trait value for species Cluster A and Cluster B. All trait variables were log-transformed. P-values highlighted by an asterisk (*) remained significant after performing the Benjamini-Hochberg correction.

	t	df	p-value	Mean	95% Confidence Interval	
					Lower	Upper
Seed mass	-2.319	9.871	0.043	A = -0.566 B = 0.566	-2.221	-0.043
SLA	-0.083	9.838	0.935	A = -0.025 B = 0.025	-1.402	1.301
log(Stem length)	-4.47	9.989	0.001*	A = -0.782 B = 0.782	-2.343	-0.784
log(Stem diameter)	-5.550	9.083	<0.001*	A = -0.832 B = 0.832	-2.341	-0.987
log(Xylem conduit diameter)	-9.003	9.923	<0.001*	A = -0.903 B = 0.903	-2.254	-1.360
log(IBT)	-0.676	9.999	0.5146	A = -0.200 B = 0.200	-1.720	0.919
RBT	0.932	8.307	0.378	A = 0.271 B = -0.271	-0.790	1.872
log(Height of the lowest bud)	-0.892	7.491	0.400	A = -0.260 B = 0.260	-1.880	0.840
log(Depth of the stem-root transition)	-1.377	5.311	0.2236	A = -0.382 B = 0.382	-2.167	0.638
log(Depth of the fifth lateral root)	0.591	6.212	0.5756	A = 0.176 B = -0.176	-1.093	1.796
Root length	-1.689	9.895	0.1224	A = -0.451 B = 0.451	-2.094	0.290
log(Root diameter)	-5.234	8.837	<0.001*	A = -0.819 B = 0.819	-2.349	-0.929
log(Aboveground mass)	-5.000	9.817	<0.001*	A = -0.809 B = 0.809	-2.341	-0.895
log(Belowground mass)	-2.004	9.029	0.07597	A = -0.512 B = 0.512	-2.181	0.132
log(Total mass)	-2.803	9.484	0.01963	A = -0.635 B = 0.635	-2.287	-0.253
log(Seedling root-shoot ratio)	0.643	7.010	0.5406	A = 0.191 B = -0.191	-1.021	1.784
log(Seedling leaf-shoot ratio)	2.521	9.635	0.03117	A = 0.597 B = -0.597	0.133	2.254

log(Nodule count)	-2.023	9.654	0.07168	A = -0.516 B = 0.516	-2.174	0.110
log(Nodule mass)	-2.515	5.894	0.04627	A = -0.596 B = 0.596	-2.357	-0.027

Table A11: Results of the Welch two-sample t-test comparing the average environmental variable estimates for species Cluster A and Cluster B. P-values highlighted by an asterisk (*) remained significant after performing the Benjamini-Hochberg correction.

Environmental variable	T	df	p-value	Mean	95% Confidence Interval	
					Lower	Upper
Log(MAP)	0.676	6.508	0.522	A = 0.670 B = 0.606	-0.162	0.288
Rain seasonality	-0.666	9.855	0.521	A = -0.197 B = 0.197	-1.717	0.929
SPEI	-2.789	8.235	0.023*	A = -0.633 B = 0.633	-2.309	-0.224
log(Fire intensity)	0.609	8.851	0.558	A = 0.181 B = -0.181	-0.986	1.711
Browser	2.250	7.555	0.056	A = 0.555 B = -0.555	-0.039	2.260

Appendix Methods B

Table B1: List of the African acacia species used to obtain trait estimates of each species, and with sufficient locality records to extract environmental variables. The final sample size represents the number of locality records after subsampling to control for sampling bias.

Species	Habit	Final sample size
Senegalia		
Senegalia adenocalyx (Brenan & Exell) Kyal. & Boatwr.	Shrub/Tree	21
Senegalia asak (Forssk.) Kyal. & Boatwr.	Shrub/Tree	18
Senegalia ataxacantha (DC.) Kyal. & Boatwr.	Climber/Tree	243
Senegalia brevispica (Harms) Seigler & Ebinge	Shrub/Tree	130
Senegalia burkei (Benth.) Kyal. & Boatwr	Tree	35
Senegalia caffra (Thunb.) P.J.H.Hurter & Mabb.	Shrub/Tree	55
Senegalia caraniana (Chiov.) Kyal. & Boatwr	Tree	2
Senegalia chariessa (Milne-Redh.) Kyal. & Boatwr.	Shrub	7
Senegalia cheilanthifolia (Chiov.) Kyal. & Boatwr	Shrub	11
Senegalia ciliolata (Brenan & Exell) Kyal. & Boatwr.	Liane	4
Senegalia condyloclada (Chiov.) Kyal. & Boatwr	Tree	7
Senegalia dudgeonii (Craib) Kyal. & Boatwr.	Shrub/Tree	72
Senegalia eriocarpa (Brenan) Kyal. & Boatwr.	Shrub/Tree	10
Senegalia erubescens (Welw. Ex Oliv.) Kyal. & Boatwr.	Shrub/Tree	101
Senegalia erythrocalyx (Brenan) Kyal. & Boatwr	Shrub	46
Senegalia fleckii (Schinz) Boatwr.	Shrub/Tree	70
Senegalia galpinii (Burtt Davy) Seigler & Ebinger	Tree	59
Senegalia goetzei (Harms) Kyal. & Boatwr.	Tree	119
Senegalia gourmaensis (A.Chev.) Kyal. & Boatwr.	Shrub/Tree	31
Senegalia hamulosa (Benth.) Boatwr.	Shrub	19
Senegalia hecatophylla (Steud. Ex A.Rich.) Kyal. & Boatwr	Tree	17
Senegalia hereroensis (Engl.) Kyal. & Boatwr.	Shrub/Tree	32
Senegalia kamerunensis (Gand.) Kyal. & Boatwr.	Shrub/Liane	74
Senegalia kraussiana (Meisn. Ex Benth.) Kyal. & Boatwr	Scrambling Shrub/Liane	15
Senegalia laeta (R.Br. ex Benth.) Seigler & Ebinger	Shrub/Tree	73
Senegalia latistipulata (Harms) Kyal. & Boatwr.	Scrambling Shrub	14
Senegalia lujae (De Wild. & T.Durand) Kyal. & Boatwr.	Liane	23
Senegalia macrostachya (Rchb. Ex DC.) Kyal. & Boatwr.	Shrub/Tree	86
Senegalia mellifera (Benth.) Seigler & Ebinger	Shrub/Tree	239
Senegalia montigena (Brenan & Exell) Kyal. & Boatwr.	Shrub	29
Senegalia montis-usti (Merxm. & A.Schreib.) Kyal. & Boatwr.	Shrub/Tree	5
Senegalia nigrescens (Oliv.) P.J.H.Hurter	Tree	103
Senegalia ogadensis (Chiov.) Kyal. & Boatwr.	Tree	8
Senegalia pentagona (Schumach.) Kyal. & Boatwr.	Liane	118
Senegalia persiciflora (Pax) Kyal. & Boatwr.	Tree	25
Senegalia polyacantha (Willd.) Seigler & Ebinger	Tree	279

Senegalia robynsiana (Merxm. & A.Schreib.) Kyal. & Boatwr.	Shrub/Tree	5
Senegalia rovumae (Oliv.) Kyal. & Boatwr	Tree	13
Senegalia schweinfurthii var. sericea (Brenan & Exell) Kyal. & Boatwr.	Scrambling Shrub/Tree	79
Senegalia senegal (Brenan) Kyal. & Boatwr.	Shrub/Tree	350
Senegalia tanganyikensis (Brenan) Kyal. & Boatwr	Tree	7
Senegalia thomasii (Harms) Kyal. & Boatwr.	Straggling Shrub/Tree	4
Senegalia welwitschii (Oliv.) Kyal. & Boatwr.	Tree	27
Vachellia		
Vachellia abyssinica (Hochst. Ex Benth.) Kyal. & Boatwr.	Tree	61
Vachellia amythethophylla (Steud. Ex A.Rich.) Kyal. & Boatwr.	Tree	108
Vachellia ancistroclada (Brenan) Kyal. & Boatwr.	Shrub/Tree	7
Vachellia arenaria (Schinz) Kyal. & Boatwr.	Shrub/Tree	40
Vachellia borleae (Burtt Davy) Kyal. & Boatwr.	Shrub/Tree	16
Vachellia burttii (Baker f.) Kyal. & Boatwr.	Shrub/Small Tree	4
Vachellia bussei (Harms ex Y.Sjöstedt) Kyal. & Boatwr.	Tree	37
Vachellia davyi (N.E.Br.) Kyal. & Boatwr.	Shrub/Tree	16
Vachellia dolichocephala (Harms) Kyal. & Boatwr.	Tree	16
Vachellia drepanolobium (Harms ex Y.Sjöstedt) P.J.H.Hurter	Shrub/Tree	52
Vachellia edgeworthii (T.Anderson) Kyal. & Boatwr.	Shrub	36
Vachellia elatior (Brenan) Kyal. & Boatwr.	Tree	20
Vachellia erioloba (E.Mey.) Seigler & Ebinger	Shrub/Tree	127
Vachellia etbaica (Schweinf.) Kyal. & Boatwr.	Tree	68
Vachellia exuvialis (I.Verd.) Kyal. & Boatwr.	Shrub/Tree	7
Vachellia fischeri (Harms) Kyal. & Boatwr.	Shrub/Tree	7
Vachellia flava (Forssk.) Kyal. & Boatwr.	Shrub/Tree	129
Vachellia gerrardii (Benth.) P.J.H.Hurter	Shrub/Tree	177
Vachellia grandicornuta (Gerstner) Seigler & Ebinger	Tree	25
Vachellia haematoxylon (Willd.) Seigler & Ebinger	Shrub/Tree	28
Vachellia hebeclada (DC.) Kyal. & Boatwr.	Shrub/Tree	93
Vachellia hockii (De Wild.) Seigler & Ebinger	Shrub/Tree	217
Vachellia horrida (L.) Kyal. & Boatwr.	Shrub	42
Vachellia karroo (Hayne) Banfi & Galasso	Tree	185
Vachellia kirkii (Oliv.) Kyal. & Boatwr.	Shrub/Tree	65
Vachellia lahai (Steud. & Hochst. Ex Benth.) Kyal. & Boatwr.	Tree	25
Vachellia lasiopetala (Oliv.) Kyal. & Boatwr	Tree	8
Vachellia luederitzii (Engl.) Kyal. & Boatwr	Shrub/Tree	64
Vachellia nebrownii (Burtt Davy) Seigler & Ebinger	Shrub/Tree	33
Vachellia negrii (Pic.Serm.) Kyal. & Boatwr.	Shrub/Tree	5
Vachellia nilotica (L.) P.J.H.Hurter & Mabb.	Tree	449
Vachellia oerfota (Forssk.) Kyal. & Boatwr.	Shrub	83
Vachellia paolii (Chiov.) Kyal. & Boatwr.	Shrub/Tree	18

Vachellia permixta (Burtt Davy) Kyal. & Boatwr.	Shrub/Tree	10
Vachellia pilispina (Pic.Serm.) Kyal. & Boatwr.	Shrub/Tree	34
Vachellia pseudofistula (Harms) Kyal. & Boatwr.	Shrub/Tree	11
Vachellia reficiens (Wawra & Peyr.) Kyal. & Boatwr.	Shrub/Tree	68
Vachellia rehmanniana (Schinz) Kyal. & Boatwr.	Shrub/Tree	31
Vachellia robusta (Burch.) Kyal. & Boatwr.	Tree	147
Vachellia seyal (Delile) P.J.H.Hurter	Tree	242
Vachellia sieberiana (DC.) Kyal. & Boatwr.	Tree	351
Vachellia stuhlmannii (Taub.) Kyal. & Boatwr.	Shrub/Tree	38
Vachellia swazica (Burtt Davy) Kyal. & Boatwr.	Shrub/Tree	3
Vachellia tenuispina (I.Verd.) Kyal. & Boatwr	Shrub	12
Vachellia tortilis (Forssk.) Galasso & Banfi	Tree	421
Vachellia turnbulliana (Brenan) Kyal. & Boatwr.	Shrub	5
Vachellia xanthophloea (Benth.) Banfi & Galasso	Tree	40
Vachellia zanzibarica (S.Moore) Kyal. & Boatwr.	Shrub/Tree	31

Table B2a: *Vachellia* correlation matrix of all trait and environmental variables considered for the study. Darker red cells indicate values close to one; darker blue cells indicate values close to negative one and light shades indicate values close to zero. Environmental predictors are shown in bold. Fire interval = fire return interval.

	Leaf area	Height	Canopy Height	Canopy shape	Bark texture	Spine leaf ratio	Pod investment	Pod glands	**Precipitation**	**Rain Seasonality**	**Drought**	**Fire interval**	**Fire intensity**	**Browser**
Leaf area	1.00													
Height	0.11	1.00												
Canopy Height	0.10	0.82	1.00											
Canopy shape	-0.18	0.12	0.35	1.00										
Bark texture	0.31	0.23	0.27	-0.11	1.00									
Spine leaf ratio	-0.42	-0.01	-0.08	-0.11	-0.29	1.00								
Pod investment	0.05	0.09	0.05	0.29	0.26	-0.08	1.00							
Pod glands	-0.11	-0.17	-0.15	-0.17	-0.10	0.09	-0.01	1.00						
Precipitation	**0.56**	**0.20**	**0.32**	**0.05**	**0.10**	**-0.52**	**-0.19**	**-0.23**	**1.00**					
Rain seasonality	**-0.12**	**-0.02**	**-0.07**	**0.35**	**-0.18**	**0.18**	**0.19**	**-0.16**	**-0.43**	**1.00**				
Drought	**-0.34**	**-0.13**	**-0.07**	**0.19**	**-0.17**	**0.10**	**0.01**	**-0.25**	**-0.23**	**0.07**	**1.00**			
Fire interval	**-0.52**	**-0.02**	**-0.05**	**0.31**	**-0.14**	**0.27**	**0.14**	**-0.17**	**-0.55**	**0.29**	**0.72**	**1.00**		
Fire intensity	**-0.11**	**0.03**	**-0.07**	**-0.26**	**0.24**	**0.14**	**0.22**	**0.54**	**-0.38**	**-0.10**	**-0.56**	**-0.17**	**1.00**	
Browser	**-0.24**	**-0.11**	**-0.23**	**-0.35**	**-0.01**	**0.37**	**-0.20**	**0.13**	**-0.27**	**-0.43**	**0.01**	**-0.08**	**0.25**	**1.00**

Table B2b: *Senegalia* correlation matrix of all trait and environmental variables considered for the study. Darker red cells indicate values close to one; darker blue cells indicate values close to negative one and light shades indicate values close to zero. Environmental predictors are shown in bold. Fire interval = fire return interval.

	Leaf area	Height	Canopy height	Canopy shape	Bark texture	Pod investment	Pod glands	**Precipitation**	**Rain Seasonality**	**Drought**	**Fire interval**	**Fire intensity**	**Browser**
Leaf area	1.00												
Height	0.39	1.00											
Canopy height	0.35	0.85	1.00										
Canopy shape	-0.02	-0.02	0.22	1.00									
Bark texture	0.31	0.72	0.64	0.07	1.00								
Pod investment	-0.11	0.22	0.16	-0.16	0.17	1.00							
Pod glands	-0.12	-0.27	-0.05	0.63	-0.15	-0.19	1.00						
Precipitation	**0.44**	**0.13**	**0.13**	**0.17**	**0.17**	**0.13**	**0.18**	**1.00**					
Rain Seasonality	**-0.43**	**-0.21**	**-0.32**	**-0.37**	**-0.17**	**0.05**	**-0.42**	**-0.67**	**1.00**				
Drought	**-0.10**	**-0.25**	**-0.32**	**-0.10**	**-0.25**	**-0.17**	**-0.02**	**0.26**	**-0.30**	**1.00**			
Fire interval	**-0.62**	**-0.13**	**-0.16**	**-0.01**	**-0.09**	**-0.17**	**0.03**	**-0.57**	**0.30**	**0.34**	**1.00**		
Fire intensity	**0.21**	**0.14**	**0.11**	**0.28**	**0.27**	**0.08**	**0.42**	**0.17**	**-0.29**	**-0.41**	**-0.35**	**1.00**	
Browser	**-0.01**	**0.05**	**-0.03**	**0.10**	**0.11**	**-0.19**	**0.04**	**0.10**	**-0.06**	**0.15**	**0.02**	**0.40**	**1.00**

Appendix Results B

Table B3: The models and model results of best subset ordinary least squares (OLS) regression models analysing the relationships between environmental variables and species traits. Significant model outputs are reported in the main text.

***Vachellia* – Equation**	**Multiple R^2**	**Adjusted R^2**	**Model p-value**
Leaf area ~ Precipitation + sqrt(Rain seasonality)+ log(Fire interval)	0.378	0.336	<0.001
Height ~ sqrt(Precipitation) + log(Fire interval) + sqrt(Fire intensity)	0.239	0.184	0.008
Canopy height ~ sqrt(Precipitation) + log(Fire interval) + Fire intensity	0.209	0.155	0.015
sqrt(Canopy shape) ~ Precipitation + Rain seasonality + Fire interval	0.305	0.258	0.001
sqrt(Spine:leaf ratio) ~ sqrt(Precipitation) + Browser	0.252	0.219	0.001
***Senegalia* – Equation**	**Multiple R^2**	**Adjusted R^2**	**Model p-value**
log(Leaf area) ~ Rain seasonality + Drought severity	0.437	0.410	<0.001
log(Height) ~ Rain seasonality + Drought severity	0.270	0.234	0.002
Canopy height ~ log(Fire interval) + Fire intensity	0.066	-0.006	0.414
sqrt(Canopy shape) ~ Rain seasonality + Fire intensity	0.062	-0.010	0.433

Table B4: The estimate table of non-significant OLS regression models investigating the relationships between a species trait and the best subset of environmental variables. Results of significant models are shown in the main text.

	Coefficients:	**Estimate**	**Std. error**	**t-value**	**p-value**
Canopy height *Senegalia*	Intercept	0.042	0.196	0.212	0.833
	log(Fire interval)	-0.461	0.212	-2.177	0.0354
	Browser	-0.362	0.262	-1.383	0.144
Canopy shape *Senegalia*	Intercept	-0.149	0.198	-0.753	0.456
	Precipitation	0.168	0.155	1.085	0.285
	log(Fire intensity)	0.280	0.240	1.164	0.251

Table B5: Analysis of deviance table based on the results of the cumulative link models analysing the relationships between environmental variables and ordinal species traits. df = degrees of freedom, logLik = log likelihood at the estimated optimum and cond. H = condition number of the Hessian matrix at the optimum. Significant model outputs are reported in the main text.

Equation - *Vachellia*	**df**	**logLik**	**cond. H**
Bark texture ~ Precipitation + Fire intensity	6	-56.74	$8.9e^{+01}$
Pod investment ~ Precipitation + Browser	4	-46.35	$6.2e^{+01}$
od glands ~ Precipitation + Fire intensity + Browser	5	-28.99	$1.2e^{+01}$
Equation - *Senegalia*	**df**	**logLik**	**cond. H**
Bark texture ~ Drought severity + Fire intensity	38	-53.19	$1.5e^{+01}$
Pod investment ~ log(MAP) + log(Browser)	39	-36.08	$5.6e^{+00}$
Pod glands ~ Rain seasonality + log(Fire intensity)	39	-23.66	$3.4e^{+02}$

Table B6: Non-significant results of the cumulative link models investigating the relationships between ordinal traits and environmental variables

Vachellia	**Coefficients:**	**Estimate**	**Std. error**	**2.5% CI**	**97.5% CI**	**Odds ratio**	χ^2	**p-value**
Bark texture	Precipitation	0.336	0.280	-0.208	0.904	1.399	1.461	0.227
	Fire intensity	0.516	0.290	-0.039	1.110	1.675	3.311	0.069
Pod investment	Precipitation	-0.586	0.322	-1.251	0.022	0.556	3.198	0.074
	Browser	-1.083	0.871	-2.874	0.571	0.339	1.544	0.214

Senegalia	**Coefficients:**	**Estimate**	**Std. error**	**2.5% CI**	**97.5% CI**	**Odds ratio**	χ^2	**p-value**
Bark texture	Drought severity	0.190	0.371	-0.542	0.939	1.209	0.263	0.608
	Fire intensity	0.481	0.365	-0.210	1.249	1.618	1.837	0.175
Pod investment	Precipitation	0.537	0.323	-0.080	1.199	1.710	2.898	0.089
	Browser	-0.641	0.331	-1.343	-0.024	0.527	4.152	0.042

Table B7: The results of OLS regression models analysing the relationship between plant height and leaf area as a potential trade-off in survival strategies

	Coefficients:	**Estimate**	**Std. error**	**t-value**	**p-value**	**Multiple R^2**	**Adjusted R^2**	**Model p-value**
Height (*Vachellia*)	sqrt(Leaf area)	0.437	0.446	0.979	0.333	0.028	0.015	0.530
	log(Spine-leaf ratio)	0.279	0.300	0.930	0.357			
Height (*Senegalia*)	Leaf area	0.466	0.172	2.708	0.010	0.152	0.152	0.010

Table B8: The results of CLM models investigating a trade-off between bark investment and plant height

	Coefficients:	**Estimate**	**Std. error**	**2.5% CI**	**97.5% CI**	**Odds ratio**	**z-value**	**p-value**	**logLik**	**AIC**	**cond. H**
Bark texture (*Vachellia*)	Height	2.692	1.966	-1.094	6.763	14.765	1.370	0.171	-55.89	123.79	1.1e^{+03}
	Height^2	-3.318	1.957	-7.202	0.627	0.036	-1.695	0.090			
Bark texture (*Senegalia*)	Height	0.721	0.331	0.107	1.431	2.056	2.178	0.029	-52.48	114.96	6.7e^{+01}