Limited Impact of Severe Drought on Plant Dynamics in African Savanna

Minor Dissertation presented in partial fulfilment of the requirements for the degree of Master of Science in Conservation Biology.

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Plagiarism Declaration

I, Huyam Abbas, know the meaning of plagiarism and declare that all of the work in the thesis, save for that which is properly acknowledged, is my own.

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Abstract

Severe drought is defined as rainfall deficiency over an extended period of successive years. The impacts of such droughts on savanna dynamics are not well studied resulting in widely divergent views. Opportunities to study severe drought are scarce because multi-year rainfall deficits are naturally rare and occur at unpredictable intervals. South Africa experienced multi-year rainfall deficit in 2014-2016. A drought index analysis indicated that it was the worst drought in 35 years. Here we explored the response of a South African savanna ecosystem to this drought focussing on savanna tree dynamics and changes in perennial grass composition and abundance. We used open long term monitoring plots established in 2000 and distributed across broad rainfall gradients in the Hluhluwe-iMfolozi Park in KwaZulu-Natal. They are characterised by a variety of herbivore use intensity, fire frequency and soil type. We compared records of tree size and density and grass biomass and composition in 2016 (after the drought) with 2012 (before the drought). Data analysis showed a massive increase (around seven fold) in the tree population especially among the small size classes (0.1m-0.3m) in 2016 relative to 2012. Tree mortality due to drought was negligible (0.03%) and there was no substantial change in tree composition. Although grass biomass and cover decreased, drought effects on veld conditions were minor. Grass showed rapid recovery by resprouting. The decreaser species and the increaser IIb were favoured by droughts. In contrast, the increaser I species have declined while the increaser IIc species have experienced a slight decrease. In addition, drought caused a shift to palatable grazing lawn species and a decline in unpalatable grasses such as *Sporobolus pyramidalis*. This suggests that this South African ecosystem is resilient to severe drought. The implication is that drought might facilitate woody encroachment by reducing the competitive effect of grass and by reducing the fuel load of grass for fire.

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Contents

To Haifaa

Chapter 1

Introduction

Savanna is characterized by the co-dominance of a scattered mixed tree layer with a continuous C4 grass layer (Frost et al. 1986; Scholes & Archer 1997; Higgins et al. 2000; Jurena & Archer 2003; Sankaran et al. 2005; Wiegand et al. 2006; Riginos 2009; February et al. 2013). Savanna systems are generally considered to occur in a non-equilibrium state (Wiegand et al. 2006; Bond & Midgley 2012; Case & Staver 2016). Large-scale fluctuations of tree-grass ratios in savanna systems can lead to the transition between the open grassy state and a closed forest state (Staver et al. 2011; Bond & Midgley 2012). The switch of these biomes as a consequence of woody plant encroachment in the grasslands, can have a negative impact on biodiversity and integrity of ecosystem functions (Hulme 2005; Wiegand et al. 2006; Case & Staver 2016). For instance, many herbivores and wildlife species restricted to open habitat may be endangered (Wiegand et al. 2006; Wigley et al. 2009). Thus woody encroachment is a big concern to land managers and conservationists (Jurena & Archer 2003; Wigley et al. 2009; Case & Staver 2016). A number of factors govern the fluctuation in tree-grass ratio interacting in ways that are poorly understood (Scholes & Archer 1997; Sankaran et al. 2005; Staver et al. 2009; February et al. 2013).

Tree-grass coexistence has intrigued many ecologists (Scholes & Archer 1997; Jurena & Archer 2003; Baldocchi et al. 2004; Wiegand et al. 2006). Understanding the coexistence of these contrasting life forms is essential for maintaining savanna functions and for projecting its response to all the drivers that change and shape tree- grass ratios (Higgins et al. 2000; Staver et al. 2009; Hoffmann et al. 2012). Resource-based hypotheses and disturbance-based hypotheses are proposed to explain tree-grass coexistence (Baldocchi et al. 2004; Sankaran et al. 2005; Wiegand et al. 2006; February et al. 2013). Walter (1971) was the first to develop a resource-based hypothesis arguing that tree-grass coexistence is due to niche partitioning in the soil profile. Grass roots, he argued, occupy the superficial soil layer and adult tree roots occupy the deeper layers thus they are not competing directly. Critics claimed that the hypothesis explained the coexistence of grasses with adult trees, in which trees possess well-developed root systems, but did not explain the early demographic stages of seedling establishment where grass and tree seedlings compete directly as their roots occupy the same soil profile (Scholes & Archer 1997; Higgins et al. 2000; Jurena & Archer 2003; Wiegand et al. 2006; February et al. 2013; Wakeling et al. 2012).

Disturbance-based hypotheses have recently emerged that emphasise tree demographic bottlenecks as a response to disturbance or environmental variables (Higgins et al. 2000; February et al. 2013). Seedling establishment, and sapling release into adult trees are the critical demographic stages that determine tree relative abundance in savanna (Hoffmann 1999; Higgins et al. 2000; Bond & Midgley 2000; February et al. 2013). Demographic transitions in life history stages are constrained by resource availability (bottom up), and fire and herbivory (top down effect) (Bond 2008; Staver & Bond 2014). Savanna structure and distribution are influenced by many complex interactive factors (Scholes & Archer 1997; Jurena & Archer 2003; Wiegand et al. 2006; Wakeling et al. 2011, 2012; Case & Staver 2016). These include global factors (such as CO_2, temperature and rainfall), and local factors (such as fire, land use, biotic interactions and herbivory) (Scholes & Archer 1997; Fensham & Holman 1999; Higgins et al. 2000; Jurena & Archer 2003; Sankaran et al. 2005; Bond & Midgley 2012), and they vary at both spatial and temporal scales (Walker et al. 1987; Scholes & Archer 1997).

Despite insights into the effects of these complex factors in determining savanna structure and distribution (Higgins et al. 2000; Bond 2008; Staver et al. 2011; Hirota et al. 2011; Hoffmann et al. 2012), our understanding of their relative and multiple impacts on savannas dynamics and distribution remains unclear (Bond 2008; Staver et al. 2011; Hoffmann et al. 2012; February et al. 2013; Case & Staver 2016). Amongst the local factors, fire is known to play a significant role in structuring tree cover in many savannas (Bond et al. 2005; Wakeling et al. 2011; Bond & Midgley 2012) by reducing tree cover and suppressing sapling release into adult trees (Hoffmann et al. 2012). This is through the direct top-kill of juveniles which obstructs their growth and release and hence their contribution to tree cover (Bond 2008; Wakeling et al. 2011; Bond & Midgley 2012). For individual trees to avoid stem death by fire it is necessary for them to accumulate sufficient thick bark (Hoffmann et al. 2012) and to reach a critical size that is no longer susceptible to aboveground kills (Bond & Midgley 2000). And for the ecosystem to reach the fire-suppression threshold it requires sufficient tree cover to suppress fire by excluding grass (Hoffmann et al. 2012).

The effect of herbivory is idiosyncratic (Staver et al. 2009) differing for browsers and grazers. Browsing acts in analogous manner to fire reducing rates of transition to larger size classes by heavy pruning of the stems and paralyzing their growth into adult trees (Bond & Midgley 2000). Grazing contrasts with browsing and fire (Riginos 2009; Staver et al. 2009). It promotes woody plant recruitment by reducing the competitive impact of grass and mitigating the effect of fire owing to reduction of fuel (Bond & Midgley 2000; Hulme 2005; Fensham et al. 2009; Case & Staver 2016).

Considering the global drivers, there is increasing evidence that elevated carbon dioxide favours woody plant encroachment in savannas and grassland(Archer et al. 1995; Bond & Midgley 2000; Bond et al. 2005; Higgins & Scheiter 2012). This is through boosting plant physiological processes, including enhancing photosynthesis rate for C3 plants over C4 grasses, increased water use efficiency due to carbon fertilization and reduction of the transpiration rate by the plant (Bond & Midgley 2000; Hulme 2005). Although woody plant encroachment is associated with elevated CO2 and overgrazing, fire and intensive browsing in contrast suppress tree seedling establishment and sapling release, and hinder their recruitment into adult trees (Fensham et al. 2009; Hoffmann et al. 2012). Inter-annual rainfall variability determines grass growth, fuel loads and fire frequency and intensity (Scholes & Archer 1997; Bond & Midgley 2000; Balfour & Howison 2002). Rainfall also promotes tree growth rate so that wet years might be expected to shorten the duration for the tree to reach the threshold size where it is no longer susceptible to aboveground kills by fire or herbivory (Bond & Midgley 2000; Hoffmann et al. 2012). However high rainfall induces frequent and intense fire by promoting grass fuel productivity leading to the opposite effect on trees (Balfour & Howison 2002).

It is widely known that extreme climatic events are predicted to occur frequently due to anthropogenic-induced climate change (Easterling et al. 2000; Solomon

2007; Twidwell et al. 2014). Observed trends are an increase of 0.6°C in the global mean temperature and increase in land surface precipitation since the start of the 20 century (Easterling et al. 2000). Models project increased frequencies of extreme events for future climates, such as frequent extreme precipitation and temperature events (Easterling et al. 2000; Burke et al. 2006; Fensham et al. 2009). The impending global changes of precipitation pattern will enhance the importance of rainfall variability in governing the structure of the savanna community (Wilson & Mitchell 1987; O'Connor 1994; Engelbrecht et al. 2009).

Recently South Africa experienced multi-year rainfall deficit during 2014-2015, The last two severe droughts were documented in the early 1980s and in the early 1990s. In the 90s multi-year drought in Kruger National Park caused negligible rates of tree dieback with the least mortality, surprisingly, in the arid savanna (Viljoen 1995). Despite the pervasiveness of severe drought on savanna dynamics (Walker et al. 1987), the response of plant community to severe drought in influencing savanna dynamics has barely been studied (Fensham & Holman 1999), especially in comparison to the role of fire and herbivory (Staver et al. 2009). Opportunities to study drought are scarce, because multi-year rainfall deficits are naturally rare and occur at unpredictable intervals (Fensham & Holman 1999). Tree mortality as a consequence of severe drought has been observed globally (McDowell et al. 2008). Examples include, extensive tree mortality as a result of drought in both deciduous and conifer species, in North America (Swetnam & Betancourt 1998), forest tree mortality in the temperate zone of Europe (Lloret et al. 2004), temperate *Nothofagus* and *Austrocedrus* forests in South America (Villalba & Veblen 1998), *Terminalia* forests in Venezuela (Dezzeo et al. 1997), eucalyptus trees in Australia (Fensham & Holman 1999) and *Nothofagus* in New Zealand (Wardle & Allen 1983), the tropical moist forest of Borneo (Clark 2004) as well as the tropical regions of Africa (Gonzalez 2001). Previous studies suggested that severe drought causes major shifts in species composition in all biomes and all regions (Fensham & Holman 1999; Fensham et al. 2005; McDowell et al. 2008).

Severe drought has the potential to induce tree mortality in all demographic stages (Roques et al. 2001), whereas herbivory and fire primarily suppress sapling growth rather than causing sapling mortality or preventing seedling establishment (Scholes & Archer 1997; Bond et al. 2005; Sankaran et al. 2005). In contrast, given that drought may cause grass mortality, it may alternatively facilitate tree recruitment by reducing the competitive effect of grass. Low grass biomass in a drought may also reduce the frequency and the intensity of fire allowing release of juvenile trees. The effect of drought has long been a concern for land managers because of threats to the economy, and its adverse effect on grass productivity and livestock carrying capacity, thus threatening the sustainability of pastoral, subsistence and commercial livestock grazing (Fensham et al. 2009). We do not yet understand the role of drought on savanna dynamics. According to Fensham et al. (2009) mortality of large trees in severe droughts is the main cause of the open structure of savannas, not constraints on recruitment. In complete contrast, droughts may cause the release of saplings and an increase in mature trees because of there is little or no grass to fuel fires or to compete with woody plants (February et al. 2013). As regards grasses, some studies suggest that it takes many decades for a grass sward to recover from severe drought (e.g. O'Connor 2015), whereas others suggest recovery is on the order of a year or two (Danckwerts & StuartHill 1988). Clearly there is an urgent need to explore the impact of severe drought on the vegetation dynamics in African savanna. Understanding the role of rainfall variability in influencing savanna vegetation dynamics is crucial for predicting the drivers and dynamics of savannas (Roques et al. 2001), and for developing an effective implementation of strategies to cope with the negative consequences associated with severe drought (Fensham & Holman 1999). For instance, drought can have great repercussions for conservation and the economy. Drought raises an important issue of whether to cull or not to cull, whether to open or close dams, and/or other sources of water (Fensham et al. 2009). Drought has adverse effects on agriculture, food production, grazing and communal land Walker et al. (1987). Therefore, understanding drought effect is crucial for informative management for conservation and the economy (Walker et al. 1987).

This study aimed to investigate the effect of severe drought on savanna vegetation dynamics, by using data from long-term field records from the same research sites to address the following questions: First, does drought cause tree mortality or rather facilitate tree recruitment? Second, does drought cause perennial grass mortality? Third, what is the relative impact of drought on woody plant and perennial grass demography across a rainfall gradient (mesic vs semi-arid savannas)?

Chapter 2

Methods

2.1 Study Area

The study was carried out in the Hluhluwe-iMfolozi Park (HiP), located in the northern part of Kwazulu Natal, South Africa (28°0′ - 28°26′ S; 31°43′ - 32°9′ E). The park is fenced and the area of the park is about 900 km^2 (Whateley & Porter 1983; Balfour & Howison 2002). The topography of the study area is rolling hills and valleys consisting predominantly of sloping monocline toward the East, characterised by undulating lowland and steeper uplands in the West (Balfour & Howison 2002). Soil types belong to bedrock geology which is dominated by shale and sandstone (Whateley & Porter 1983; Graham 1992; Staver et al. 2009). Hluhluwe Reserve contains sandstone-derived soils with some shales and dolerite while iMfolozi Reserve contains largely dolerite-derived soils (Whateley & Porter 1983; Staver et al. 2009).

The park experiences mean minimum temperature of 13°C and mean maximum temperature of 35°C (Greyling & Huntley 1984; Balfour & Howison 2002). Average daily temperatures range between $\sim$ 40 to 14 °C during summer and $\sim$ 34 to 6°C during winter (Staver et al. 2009). Frosts are rare (Balfour & Howison 2002) and have been recorded very occasionally in some river valleys (Whateley & Porter 1983). The park has a wide range of rainfall (Archibald et al. 2010). The mean annual rainfall varies between $<$ 600 mm in the low lying southern regions up to 990mm in the north- western hills (Balfour & Howison 2002; Archibald et al. 2010). Hluhluwe Game Reserve is dominated by mesic savanna in the north (225 km^2, higher rainfall, higher altitude) and the iMfolozi Game Reserve is dominated by semi-arid savanna in the south (447 km^2, lower rainfall, lower altitude) (Whateley & Porter 1983; Archibald et al. 2010; Gray & Bond 2013). Fire frequency in the park is positively correlated with rainfall (Balfour & Howison 2002; Staver et al. 2009). Most mesic areas experienced high fire frequency and have burned more than ten times during 1956-1996, while arid areas have a lower fire frequency and some areas have scarcely burned once in the same period (Balfour & Howison 2002; Staver et al. 2009). The park contains forest, savanna (mesic and semi arid savannas), grassland and thickets (Whateley & Porter 1983). The park hosts many large mammal species, densities of which vary according to their habitat preference (Staver & Bond 2014). The study area provides an unique opportunity to study drought impact on plant dynamics along a rainfall gradient and to compare drought impact on the mesic savanna in Hluhluwe Game Reserve with the semi arid savanna in iMfolozi Game Reserve.

2.2 Data Collection

Ten sites were previously established in 1999 across a broad altitudinal gradient with five in the Hluhluwe Game Reserve and five in iMfolozi Game Reserve to study the interaction of fire and herbivory on tree dynamics (Staver 2008). Each transect consisted of a minimum of three and up to five plots (40 × 40 m), subjected to different herbivory treatments. Treatments common to all sites consisted of fences designed to exclude all herbivores larger than a hare, a cable designed to exclude rhinos and a control that gave access to all mammal herbivores. Fences were removed in 2012. All these plots were annually monitored from 2000 to 2012 (Staver et al. 2009). Data included identification of trees and grass species and measuring tree heights and grass biomass. Since then drought has taken place and this provided a unique opportunity to investigate the role of drought in savanna dynamics.

To study drought impact, the control plots open to all herbivores were selected (see figure 2.1) to investigate tree and perennial grass responses to severe drought. All the control plots are exposed to different grazing and browsing pressure (Staver et al. 2009). Plots were censused in December 2016 after rains had commenced. The historical records of control plots were used to assess plant community structure pre (2012) and post (2016) drought. Each plot as divided into (40 m × 2 m) 20 transects, by placing a pair of ropes with a length of 40 m in parallels. The survey was performed by walking systematically across the transect.Tree species were identified and tree heights were measured of all woody stems throughout the control plots. Tree death and the causes of tree death were recorded. Tree mortality and survival were monitored across different size classes: small (< 1 m), medium (1 to < 2 m), and large trees (> 2 m), to detect if they can respond to drought differently. Tree death and tree death causes were recorded. Tree dieback was recorded for each tree by identifying trees as undisturbed (no sign of damage by disturbance), disturbed (top-killed), or dead. Top-kill was attributed to fire if there were signs of having been burned and these were corroborated by local fire records. Herbivory was attributed if the stem was broken or pruned. Tree death was attributed to drought only or the combination of drought, fire and/or herbivory if there was sign of burning and no re- sprouting. The heights of total/partial dead skeletons were measured as was re-sprout height. Tree death or top kill (= stem death) might be caused by either drought, fire or herbivory.

Perennial grass recovery was investigated by determining whether grass re-sprouted from tussock or recruited from seeds. The rain started at the beginning of October, sampling took place at the end of the drought (Dec 1st to 10th/2016) but before significant summer rains or growth. Therefore it was relatively obvious as to whether a plant was a seedling or a re-sprout. Thus re-sprouting was confirmed by noting plant size and the presence of underground roots or tussocks. For each plot, 20 DPM readings were recorded. At every two meter intervals along the middle of the plot, grass biomass was measured by using a Disk Pasture Meter (DPM). This consists of an aluminium disk of radius (diameter 45cm) dropped from a standard height. The settling height is proportional to herbaceous biomass and is referred to as a DPM reading. Under the DPM, the most common Four grass species were recorded, and they were listed if they are emerged from seeds or re-sprouted from tussocks. The DPM values were multiplied by 1 for the most common grass species, 0.5 for the second common, 0.33 for the third common and 0.25 for the least common grass species. Grass species were recorded as was the percentage of grass cover beneath the disk area estimated in every DPM reading. DPM readings were used to obtain grass biomass via the following equation: grass biomass in [g m^{-2}] $= 12.6 + 26.1 \times$ DPM (Waldram et al. 2008).

2.3 Data Analysis

2.3.1 Drought intensity

There are several ways to compute the drought index. We choose to present our analysis using two methods: Foleys index and the Standardized Precipitation Index (SPI). Foleys drought index was used to compare drought intensity in South Africa during 2014-2016 with a global analysis of drought in savannas worldwide by Fensham et al. (2009). Foleys index is the total rainfall deficit normalized by the mean annual rainfall which can be written as:

$$D_{m,y} = \sum_{t=y-x+1}^{y} \frac{a_{m,y} - A}{A}, \tag{2.1}$$

where $a_{m,y}$ is the total rainfall over a year y for all months m and A is the long-term annual average rainfall. The x represents the chosen deficit period which is set to three years for our analysis following Fensham et al. (2009). Foleys index requires long-term monthly data which can be only calculated for Hluhluwe dam station due to the lack of data in other sites. Standardized Precipitation Index (SPI) was developed by Mckee et al. (1993) to quantify the intensity of drought over a given time scale. It is essentially a standardized transformation of the probability (expected frequency of events) of the actual rainfall over time scale (Guttman 1998; Naresh Kumar et al. 2009). SPI was chosen over other drought indices because it can be calculated for any desired duration. It also gives a better representation of wet and dry events than the other indices (Guttman 1998). The SPI has been widely used due to simplicity, ease of interpretation and because it allows a direct comparison between different rainfall zones (Guttman 1998; Heim & Richard 2002; Naresh Kumar et al. 2009; Spinoni et al. 2014). The SPI for a given duration can be calculated as the following:

$$SPI = (X - \bar{X})/\sigma, \tag{2.2}$$

where X is the annual rainfall, $\bar{X}$ is the mean annual rainfall and σ is the standard deviation of the long term mean.

2.3.2 Drought impact on tree demography and composition

To assess the impact of drought on tree dynamics, tree surveys were performed in our ten plots in order to identify different tree mortality drivers. Our collected data in 2016 were compared with the most recent record from 2012 in order to establish a comparison with prior to, and after the drought. The comparison was done for all sites except Sokwazela due to the lack of its 2012 data. Tree heights records for 2012 and 2016 were used to test drought impact on the following:

- Changes in tree number distribution for each height class before and after the drought.
- The distribution of Weighted Mean Number Tree Density (WMNTD) of trees that is weighted according to the cover area (A) and multiplied by the density of each size class. The weight of each size class (h) is estimated as follows:
  - Very small: $0.1 \text{ m} < \text{h} \leqslant 0.3 \text{ m}$, $\text{A} = 0.1 \text{ m}^2$.
  - Small: $0.3 \text{ m} < \text{h} \leqslant 2 \text{ m}$, $\text{A} = 0.2 \text{ m}^2$.
  - Medium: $2 \text{ m} < \text{h} \leqslant 4 \text{ m}$, $\text{A}=1.0 \text{ m}^2$.
  - Large: $\text{h} > 4 \text{ m}$, $\text{A}=2.0 \text{ m}^2$.

The χ^2 test also was used to assess the significance of changes of the weighted mean of tree density. Tree compositional change was determined by comparing the total number of individual tree species in 2012 with 2016 for all sites.

2.3.3 Drought impact on grass community

Changes in grass biomass and grass cover were determined by comparing the records of 2016 with that of 2012. Weighted Palatability Composition Method (WPCM) was used to assess how drought changed grass palatability composition (Barnes et al. 1987; Tainton 1999). Grass species were classified according to their palatability rating using Guide to grasses of South Africa (Van Oudtshoorn 1992) as summarized in table A.1. Classes were described as class 1: highly palatable grass species (HP), class 2: medium palatable grass species (MP), and class

3: unpalatable grass species (UP) and these classes then are weighted as 3, 2, and 1 respectively. The biomass for each grass species was weighted and multiplied by its palatability score. The palatability composition rating (PC) was calculated as the total weighted relative abundance of all species. The PC was converted to percentages to develop a scale ranging from 33.3 (all species in class 3) to 100 (all species in class 1). The PC values can be expressed as WPC values as the following:

$$WPC = (PC - 33.3) \times 100 \div 66.7. \tag{2.3}$$

The Ecological Index Method (EIM) was used to assess grass condition along the successional pathway varying from poor pioneer state to excellent state as assessed for livestock or wild grazers (Westoby et al. 1989; Tainton 1999). We then categorized grass species (see definitions summary in A) as decreaser (weighted as 10), increaser Ia and increaser IIa (weighted as 7), increaser Ib and increaser IIb (weighted as 4), and increaser IIc (weighted as 1) as summarized in table A.1. The veld condition was calculated as the sum of the multiplied relative abundance of each grass species by its weighting (Tainton 1999)

(A) Gqoyeni

(B) Nombali

(C) Mbuzani

(D) Ledube

(E) Mona

(F) Kalazana

(G) Thoboti

(H) Seme

(I) Sokwazela

(J) Maqanda

FIGURE 2.1: The long-term monitering sites. Left column shows our study sites in iMfolozi, whereas right column shows those of Hluhluwe.

Chapter 3

Results

3.1 Drought intensity

The rainfall of Hluhluwe dam station was at its minimum average rainfall of 526.7mm and 382.6 mm in the early 1980s and 2014-2016 respectively, as shown in figure 3.1. These minima can be regarded as severe droughts according to Fensham et al. (2009) analysis for savannas worldwide. However, these rainfall records strongly indicate that the recent 2014-2016 years witnessed the lowest precipitation as compared to previous years.

Foleys index reveals major drought events in the early 1980s and 2014-2016 as shown in figure 3.2. The drought of 2014-2016 may be regarded as the most intense drought of the entire rainfall record with Foleys index dropping below -1.5. The Standardized Precipitation Index (SPI) for eight stations in HiP in figure 3.3 showed similar rainfall history and similar pattern of rainfall events with slight differences in Memorial and Mpila stations. All stations showed a conspicuous severe drought during 2014-2016 with an average SPI of -1.3. The SPI for each station showed severe drought and ranged from dry (-1.0) to very dry (-1.8) (Spinoni et al. 2014).

3.2 Drought impact on tree demography

The total number of trees surveyed in all sites in 2016 was 2825, including 2218 undisturbed trees, 584 top-killed, and 23 dead trees. Despite the similarity between

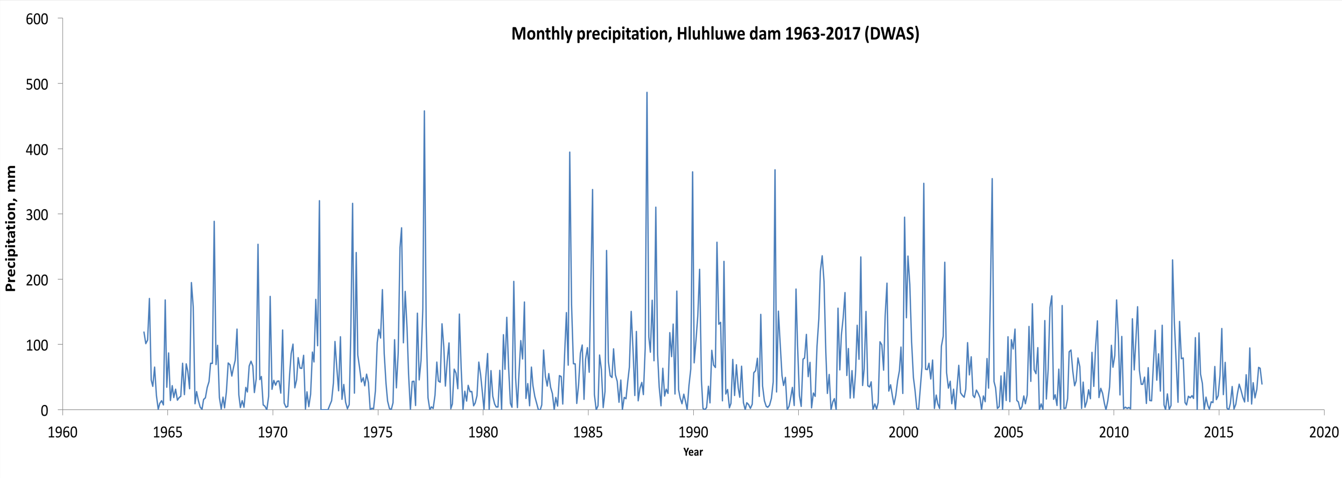

Figure 3.1: Rainfall records plotted as monthly sums for Hluhluwe dam from 1963-2017. It is evident that the precipitation was at its minimum during early 1980 and 2014.

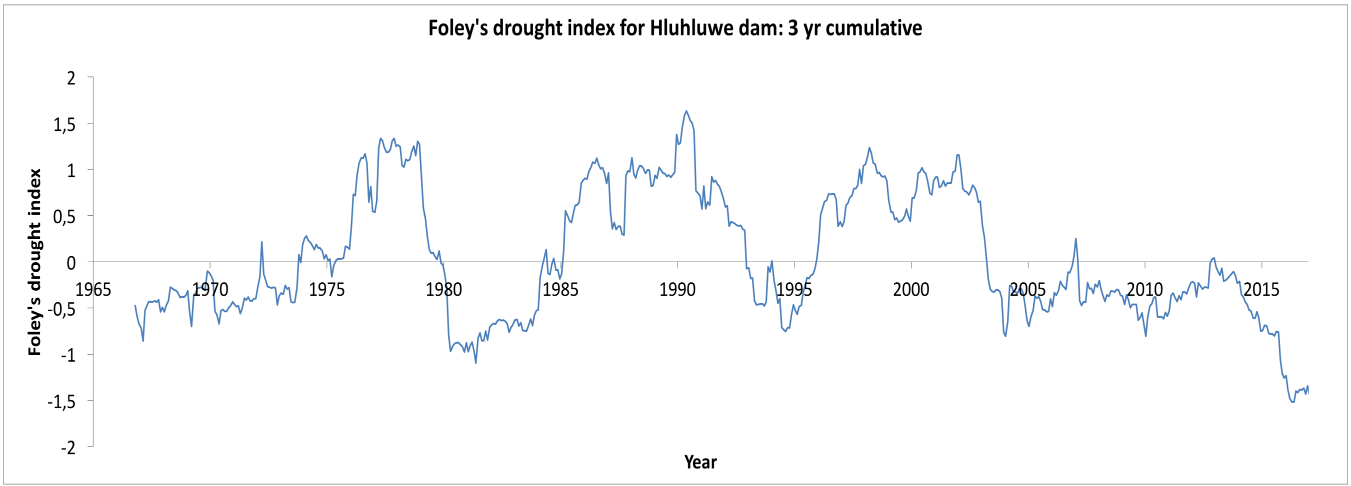

Figure 3.2: Foleys drought index calculated from the rainfall data in Figure 3.1 using a three year running mean. Major droughts occurred during the early 1980s and 2014-2016 where the drought index drops below -1. The recent drought can be regarded as the worst drought in the period of record as the drought index during 2014-2016 dropped below -1.5.

South Africa and Australia in the intensity of the drought (Foleys index dropped below -1) we found that the recent drought in South Africa had negligible effects on tree mortality (0.03% mortality). The multiple impact of fire and drought resulted only in 0.5% of woody mortality while the combination of fire droughts and elephants caused 0.03% mortality. The total top-killed trees represent 20.7%. Fire contributed to 17.45% of top-killed trees while elephants contributed to 3.22%. The total dead trees (whether by fire, drought or elephants) represents 0.81 % and there was no direct sign of tree mortality caused by the drought. A summary of

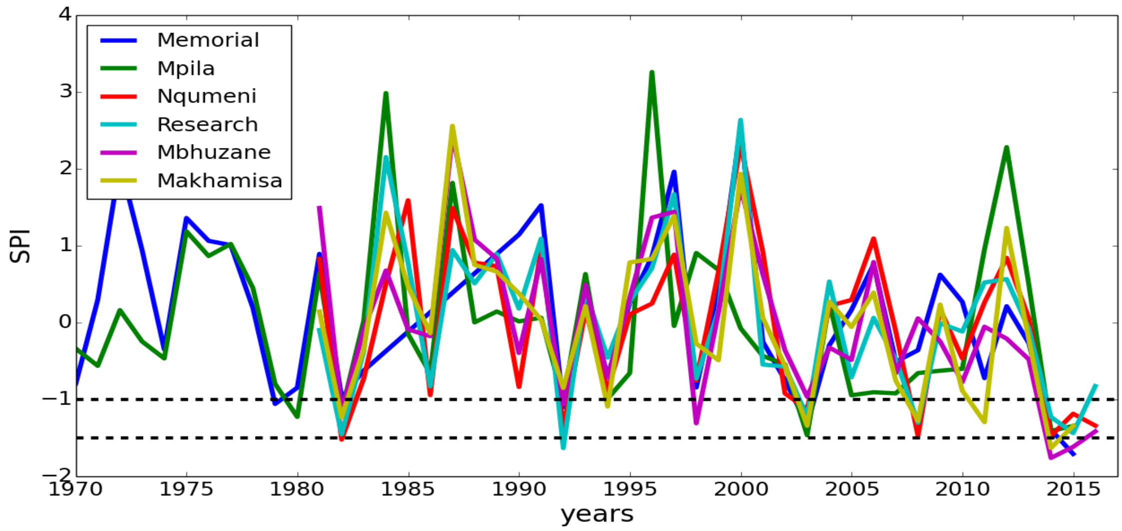

FIGURE 3.3: The annual Standardized precipitation!index (SPI) for Hilltop, Memorial, Mpila, Nqumeni, Research, Mbhuzane, Masinda, Makhamisa stations in HiP. All stations show similar SPI evolution as a function of time. The average SPI for all stations = -1.33 in 2014-2016.

these results is presented in table 3.1.

In comparing the number of trees in different height classes for each site in 2016 relative to 2012, the tree populations increased remarkably from 1585 to 2825 trees, especially across the small size classes in 2016 relative to 2012 see figure 3.4. In all sites, the Weighted Mean Number Tree Density (WMNTD), whether or not the disturbance effect is included, only increased significantly across the very small size (0.1 m $< h \leq 0.3$ m) class in 2016 relative to 2012. The corresponding χ^2 analysis across the very small size class shows: $\chi^2 = 10.9$, df = 1, p-value = 0.0009. This confirms the significant increase among the small size class as shown in figure 3.5. A similar result was found when WMNTD is computed only in Hluhluwe or iMfolozi sites as shown in figure 3.6, 3.7. However, the change across the small, medium and large classes are minor where WMNTD error bars overlap as seen in figures 3.5, 3.6, 3.7. This also consistent with our previous finding of the marked increase across the small trees in number count tree distribution in figure 3.4.

Damaged by	**Trees Number**	**Top-killed Trees**	**Dead Trees**
Drought	1		1 (0.03%)
Elephant	98	91 (3.22%)	7 (0.25%)
Fire	493	493 (17.45%)	
Fire+Drought	14		14 (0.50%)
Fire+Drought+Elephant	1		1 (0.03%)
No damage	2218		
Total tree number	2825	584 (20.67%)	23 (0.81%)

TABLE 3.1: Summary of different mortality drivers on trees in 2016 for all sites in HiP. The percentage is taken out of total trees number.

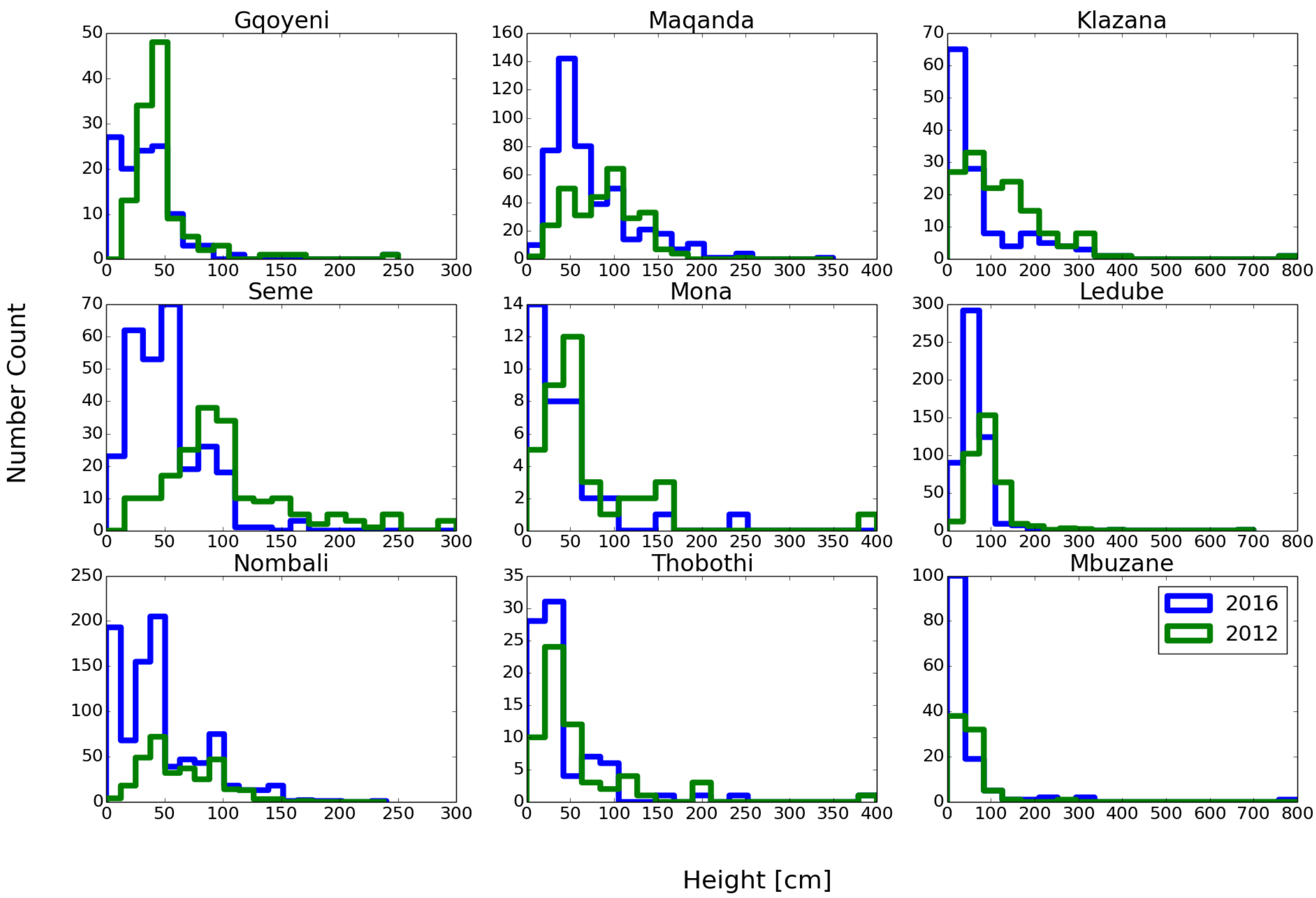

FIGURE 3.4: Frequency distribution of tree heights in 2012 (green) and 2016 (blue) for each site. Each title on top quotes the site name. The 2016 distribution shows higher numbers of small size class (< 100 cm) as compared with that of 2012 in all sites except the site of Sokwazela due to lack of its 2012 data.

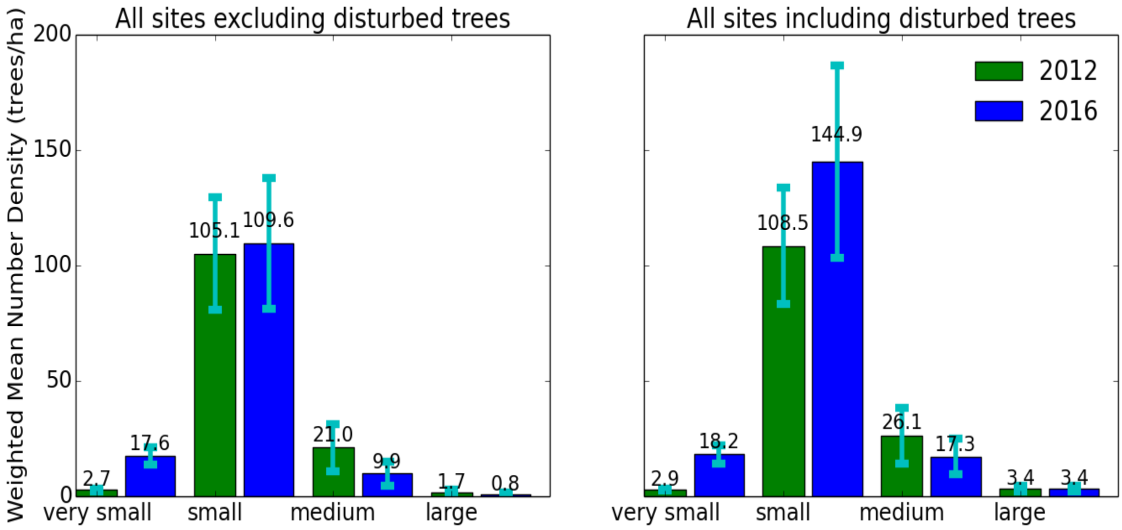

FIGURE 3.5: Weighted Mean Number Tree Density (WMNTD) (mean number count per hectare) in all sites. Left: excluding trees top-killed by fire or herbivores in all sites. Right: including trees top-killed by fire or herbivores in all sites. The comparison is between 2012 (green) and 2016 (blue) for different size classes (very small: 0.1 m $<$ h $\leq$ 0.3 m; small: 0.3 m $<$ h $\leq$ 2 m; medium: 2 m $<$ h $\leq$ 4 m; large: h $>$ 4 m) with the corresponding standard error as shown by the error bars. The weighted mean tree density in all sites is significantly increased in 2016 as compared with 2012 in the very small class.

3.2.1 Drought impact on tree species composition

Tree species composition remained unaffected due to drought where relative changes in 2016 as compared with 2012 are very small as seen in figure 3.8. Most common tree species abundance increased. Among tree species, *Ormocarpum trichocarpum* showed a sharp increase from 40 to 228 stems ($\chi^2 = 131.88$, df = 1, p-value $<$ 0.001), while *Dombeya rotundifolia* has declined considerably from 21 to 4 ($\chi^2 = 11.56$, df = 1, p-value = 0.001). These are the only species that experienced a major change by a factor of more than or equal to 4.

3.3 Drought impact on grass demography

During drought years, grass mortality in our study area is difficult to quantify as the ground is bare. After the drought broke, grasses re-sprouted vigorously. This indicates a rapid grass recovery from the drought in HiP. The veld condition prior to drought was 91% whereas after drought the percentage was 87%. This indicates

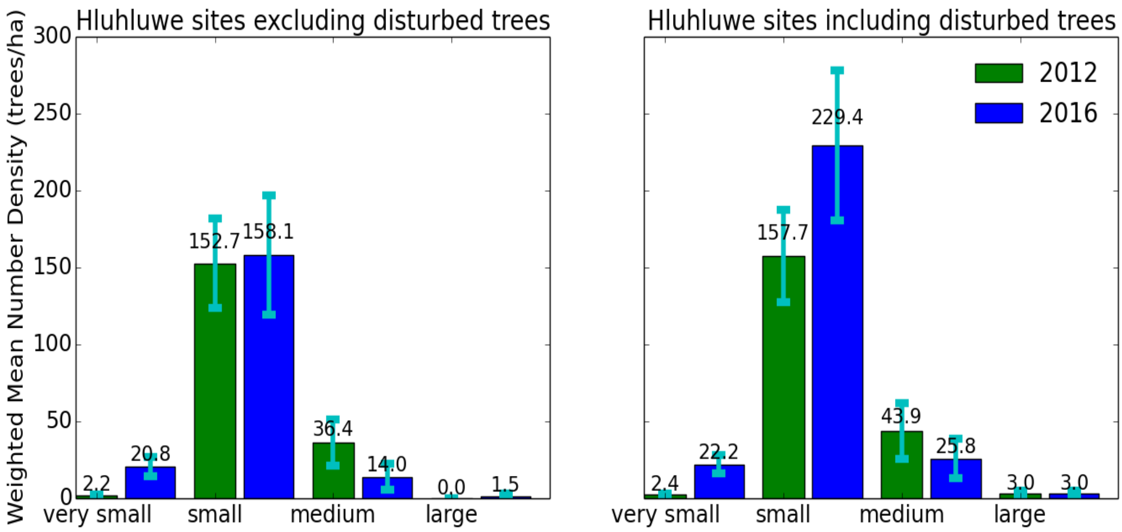

FIGURE 3.6: Weighted mean number tree density (mean number count per hectare) in Hluhluwe. Left: excluding trees top-killed by fire or herbivores. Right: including trees top-killed by fire or herbivores. The comparison is between 2012 (green) and 2016 (blue) for different size classes (very small: 0.1 m $< h \leq$ 0.3 m; small: 0.3 m $< h \leq 2$ m; medium: 2 m $< h \leq$ 4 m; large: $h >$ 4 m) with the corresponding standard error as shown by the error bars. The weighted mean tree density in Hluhluwe is significantly increased in 2016 as compared with 2012 in the very small class.

that the drought impact on veld condition is minor ($\chi^2 = 0.09$, df $= 1$, p-value $=$ 0.76). Grass biomass and grass cover displayed a strong decline from 2012 to 2016 in all sites (especially Maqanda) except Mona site, as the grass biomass and grass cover showed slight decline and increase respectively (see figure 3.9, 3.10). Drought clearly favoured the decreaser species and the increaser IIb (see figure 3.11). In contrast, the increaser I species declined and the increaser IIc experienced a slight decrease as seen in figure 3.11.

In terms of Weighted Palatability Composition (WPC), the highly palatable and moderately palatable grass species responded to severe drought by a slight increase, whereas the unpalatable grass exhibited a marked decline ($\chi^2 = 3.7692$, df $= 1$, p-value $= 0.05$) in 2016 relative to 2012 as figure 3.12 shows. The effect of drought on grass composition can be determined using relative change in their biomass. The most marked effects were a conspicuous surge of the grazing lawn perennial species such as the highly palatable and the increaser IIc, perennial *Urochloa mosambicensis* ($\chi^2 = 343.76$, df $= 1$, p-value < 0.001), and in contrast the dramatic decline ($\chi^2 = 496.96$, df $= 1$, p-value < 0.001) of the common increaser IIc and the unpalatable perennial *Sporobolus pyramidalis* (only occurs in Hluhluwe) as seen in

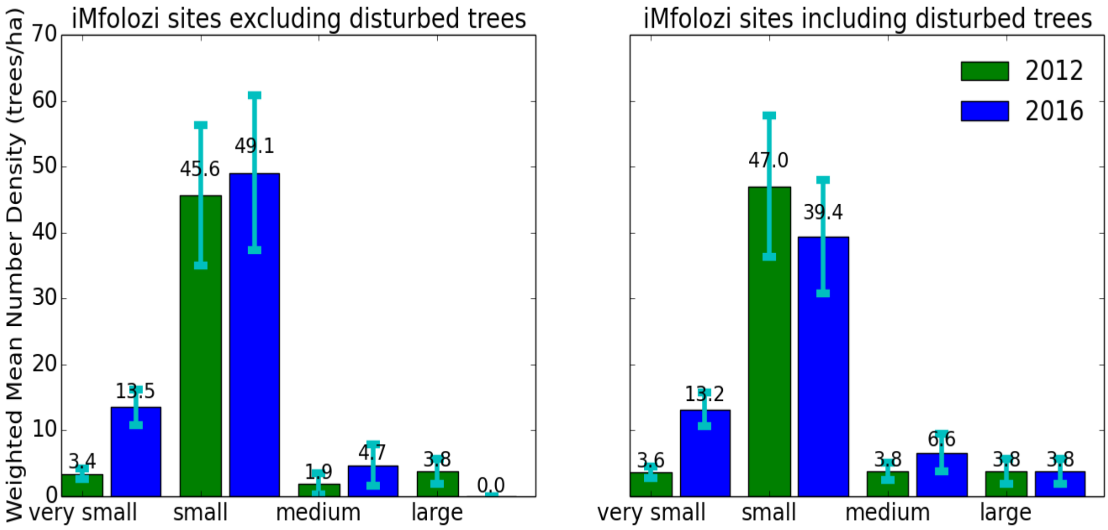

FIGURE 3.7: Weighted mean number tree density (mean number count per hectare) in iMfolozi. Left: excluding trees top-killed by fire or herbivores. Right: including trees top-killed by fire or herbivores. The comparison is between 2012 (green) and 2016 (blue) for different size classes (very small: 0.1 m $< h \leq$ 0.3 m; small: 0.3 m $< h \leq$ 2 m; medium: 2 m $< h \leq$ 4 m; large: $h >$ 4 m) with the corresponding standard error as shown by the error bars. The weighted mean tree density in iMfolozi is significantly increased in 2016 as compared with 2012 in the very small class.

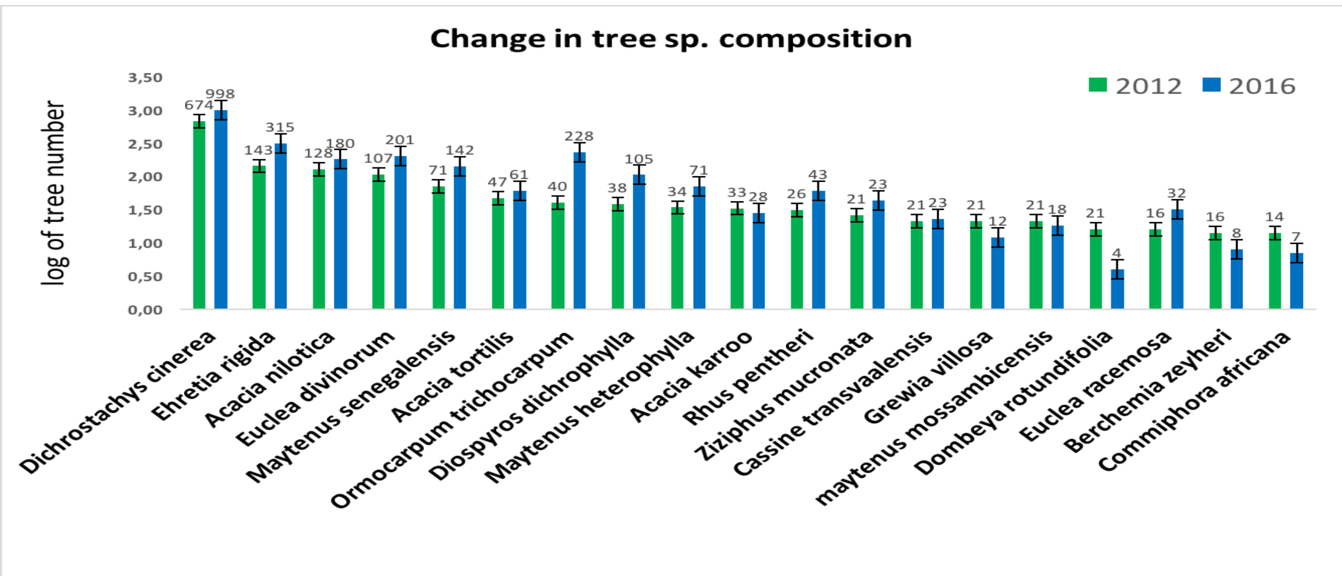

FIGURE 3.8: Change in tree species composition for the most common species and for all size classes in HiP during 2012 and 2016.

figure 3.13. Additionally, the annual *Tragus berteronianus*, that is classified as an increaser IIc and medium palatable, was absent before the drought but appeared,

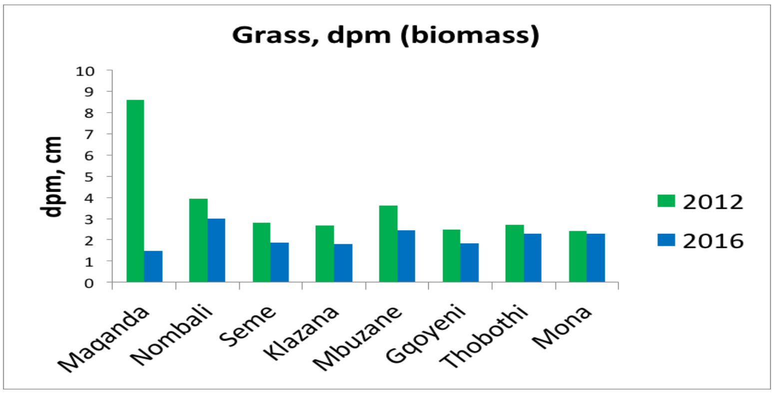

FIGURE 3.9: Changes in DPM as a surrogate for grass biomass from 2012 to 2016 for all sites except Ledube and Sokwazela due to the lack of adequate data in 2012. Sites ranked from least to most grazed with first four in Hluhluwe and last four in iMfolozi respectively.

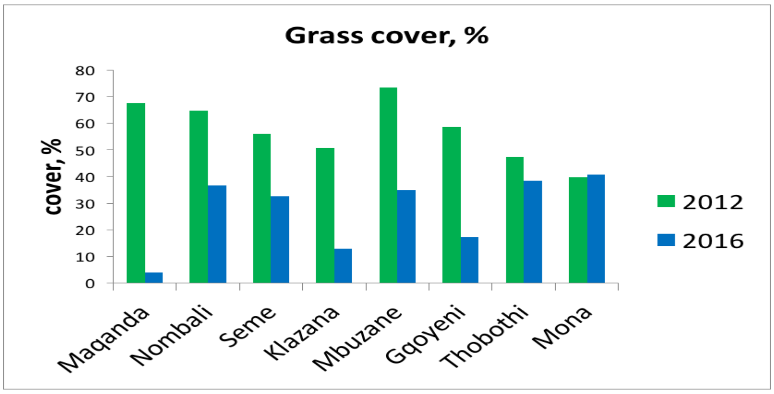

FIGURE 3.10: Changes in grass cover from 2012 to 2016 for all sites except Ledube and Sokwazela due to the lack of adequate data in 2012. Sites ranked from least to most grazed with first four in Hluhluwe and last four in Imfolozi respectively.

probably from a seedbank, after the drought but only in sites in iMfolozi.

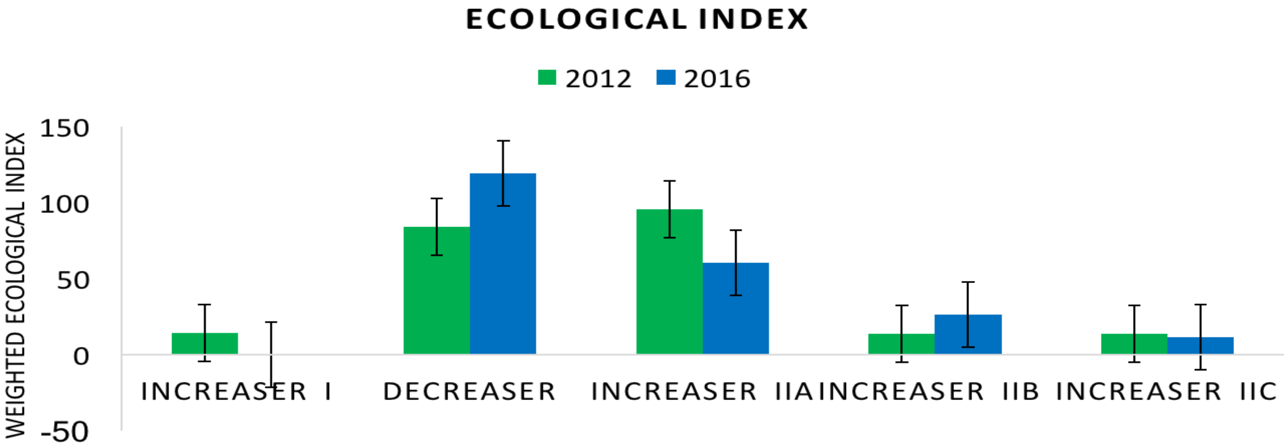

FIGURE 3.11: Change in the INCREASER IA, DECREASER, INCREASER IIA, INCREASER IIB, and INCREASER IIC grass species, based on their weighted ecological index from 2012 to 2016.

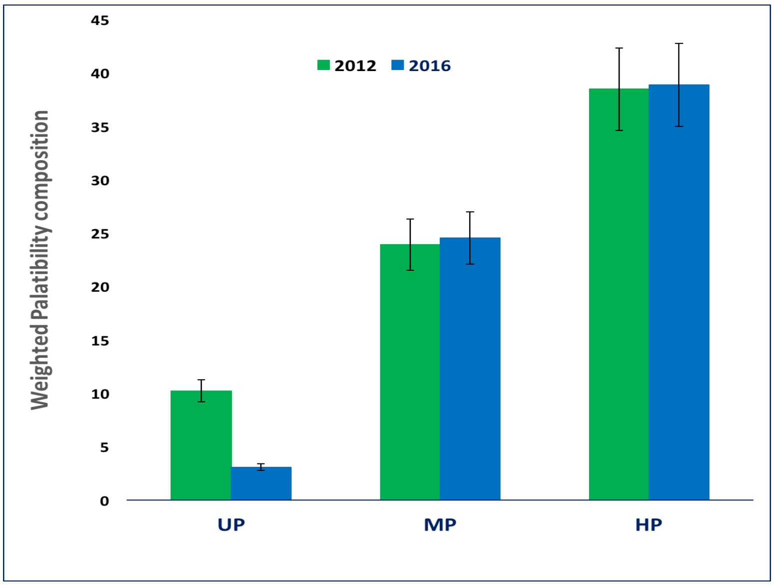

FIGURE 3.12: Change in Weighted Palatability Composition (WPC) from 2012 to 2016. UP, MP and HP represent unpalatable, medium palatable, highly palatable grass species, respectively.

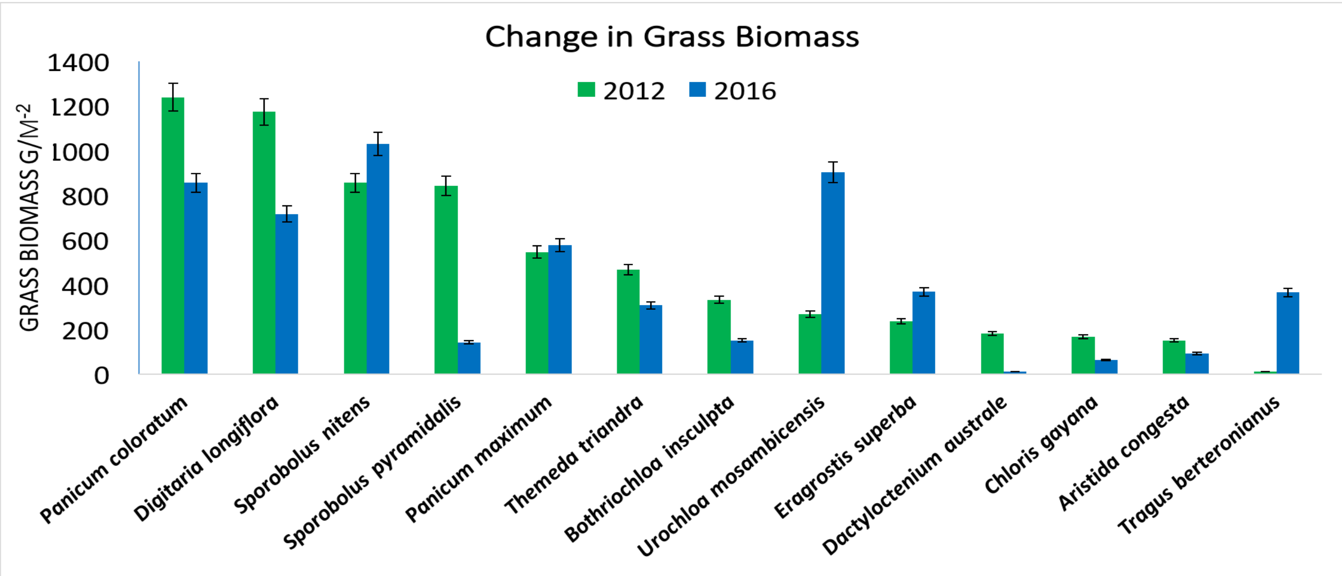

FIGURE 3.13: Changes in individual grass species biomass for the most dominant grasses from 2012 to 2016 for all sites except Ledube and Sokwazela due to the lack of adequate data in 2012.

Chapter 4

Discussion

4.1 Drought index

With both Foley's and SPI indices, the drought evolution as a function of time is somewhat similar, particularly over the last decade, as shown in figure 3.2, 3.3. The drought index analysis, and also the corresponding rainfall deficit data (figure 3.1), represent two major drought episodes in the history of South Africa, namely during the early 1980s and recently in 2014-2016. The Foley's drought index value during 2014-2016 in Hluhluwe dam is -1.52, suggesting that this was the worst drought with the highest intensity in the region as compared to the early 1980s. Fensham et al. (2009) demonstrated that Australian savanna regions can witness extensive tree death when the drought index drops below -1. Therefore, the recent South African drought was quite severe according to the drought world scale as quoted by Fensham et al. (2009). Although our drought index analysis shows an intense drought, nevertheless the tree mortality rate was minimal in contrast to findings by Fensham et al. (2009).

4.2 The effect of the drought on tree demography

Most of past studies in the literature (Auclair 1993; McDowell et al. 2008; Fensham et al. 2009) have concluded that severe drought causes woody plant mortality in all biomes. For instance, tree mortality in savanna as a consequence of drought has been documented in North America, Asia, Australia and Africa (McDowell et al. 2008; Fensham et al. 2009). In addition, a suite of studies in the savanna biome had demonstrated that tree mortality occurred when the drought index dropped below -1 for an extended period (Fensham & Fairfax 2007). In contrast, our findings show exactly the opposite scenario in the South African savanna, where drought does not seem to contribute to tree mortality. This indicates that the South African savanna system is strikingly different from other savannas worldwide, or at least the examples selected by Fensham et al. (2009). The recent intense drought in South Africa did not have any substantial negative effect on tree demography in HiP as the mortality rate was negligible (0.03 %) as summarised in table 3.1. This finding coincides with Viljoen (1995) study where he also found low tree mortality (7 %) after the 1990s droughts in the Kruger National Park (Fensham et al. 2009).

We here show that severe drought impact on savanna tree dynamics is far from universal. For instance, similar studies in Australia have revealed that extensive tree death (29%) occurred owing to severe drought in Eucalyptus savanna in north Queensland (Fensham & Holman 1999). But this Australian savanna may have a distinct ecology (Bond 2008; Staver et al. 2011) as opposed to our study area in South Africa. In Australian savanna, the eucalypt cover is largely constrained by the mean annual precipitation (Williams et al. 1996) suggesting that, the distinct physiology and genetics of eucalypts may drive their sensitivity to rainfall variability (Fensham & Fairfax 2007; Bond 2008). In contrast, the tree cover in Africa increases asymptotically with mean annual precipitation (Bond 2008), and is mainly constrained by fire at higher rainfall (Bond & Keeley 2005). In addition tree community structure remained unaffected by the recent drought (figure 3.8). This suggests that the tree community in HiP possesses high resistance against water stress. Among woody species, *Ormocarpum trichocarpum* exhibited a major increase from 40 to 228 stems, while *Dombeya rotundifolia* declined considerably from 16 to 4 as a consequence of drought. This raises the question of why do different species respond to severe drought differently?. The heterogeneity of species response to water stress may be attributed to different rooting architecture, physiological features between species and soil conditions (Oconnor 1998; Fensham & Fairfax 2007; McDowell et al. 2008).

According to the world scale, this recent drought was strong and intense enough to cause extensive tree mortality. We find that woody plants were able to overcome this severe drought very easily in HiP. Surprisingly, there was rather a massive increase in the tree population especially in small size classes (see figure 3.4). Tree number density has also increased largely over small size class, even though this recent drought was very intense and likely to prevent any increase (figure 3.5, 3.6, 3.7). To check whether this increase of small size class is attributed to disturbance, we have excluded any tree with burned or pruned skeleton from the tree number density analysis. We find that the tree frequency still shows the same increase over small size class whether or not the disturbance effect is included.

This increase suggests that drought may have promoted re-sprouting ability and growth rate in juvenile trees, allowing for higher escaping probability from fire and herbivory. February et al. (2013) had conducted an experimental study of how rainfall manipulation (rainfall reduction and addition) influences the competitive interaction between tree and grass. This study showed that rainfall addition positively influenced grass biomass, and tree presence did not have a significant effect on grass biomass, but grass removal significantly served to favour high tree growth rate. This study emphasises how rainfall is critical to modulate the competitive effect of the grass. Thus, the competitive interaction of the grass would constrain the extent to which high rainfall promotes tree recruitment. Our data appears to supports the hypothesis proposed by February et al. (2013) where drought may benefit juvenile tree growth by reducing grass productivity and thereby also the fuel for fires. In addition, we find the opposite pattern to the assumption for the demographic bottleneck suggested by Higgins et al. (2000). They suggested that a sequence of high rainfall years would heighten the probability for juvenile trees to reach the fire and herbivory resistant height by promoting high growth rates into adult trees (Higgins et al. 2000).

Over the previous years during 2007-2014, the encroachment of woody plants represents a huge concern in HiP (Wigley et al. 2009; Case & Staver 2016). The increase of the woody component has been generally attributed to elevated carbon dioxide, intensive grazing and reduced fire (Wigley et al. 2009; Fensham et al. 2009). The strong decline in grass cover, woody plant resistance to extended rainfall deficit and the consequent flourishing of woody plants, would suggest that severe drought may be one of the additional drivers prompting woody encroachment into grassland (Bá ez et al. 2013), and eventually will lead to closed savanna in HiP. Nevertheless, fire is considered as a fundamental tool in controlling woody encroachment and maintaining open savanna (Bond 2008). In addition, the role of tree-grass competition is also essential for offsetting this encroachment (Scholes & Archer 1997). Moreover, the grass traits such that the ability to explore soil (Partel & Wilson 2002), higher response to resource flux (Scholes & Walker 1993) and faster recovery from disturbance (Bond 2008), all together make grasses superior competitor to trees, and enable them to influence the bottom-up effect directly and top-down effect indirectly (Bond 2008). In contrast, the combination of grazing and drought might offset the effort of controlling woody encroachment by limiting grass fuel load which leads to less fire frequency and intensity. This may present hazardous issue for managers to maintain an open savanna in drought years, owing to the difficulties of reversing closed canopy in grass suppression and long fire free intervals (Hoffmann et al. 2012). The reversal of woody encroachment depends on rapid recovery of grass biomass and return of fire before trees grow to heights where they are no longer susceptible to fire top-kills (Bond & vanWilgen 1996; Bond & Midgley 2000).

Our findings are subject to some uncertainties associated with sampling errors in 2012. The number of small size classes may have been underestimated in 2012 due to difficulties in counting small trees in dense grass. In 2016, it was much easier to detect small trees in bare area or in less grass cover caused by drought. However, if the 2012 measurement was accurate, we suggest that severe drought might be an additional factor, besides carbon dioxide and temperature, that contributes to the increase in woody plants. Further investigations and more measurements at the end of the current growing season (2017) are clearly required in order to investigate the tree recruitment due to this recent severe drought, which we leave for future works.

4.3 The effect of the drought on grass demography

Monitoring of grass biomass and grass cover as response to recent severe drought revealed a rapid vigorous recovery by perennial grass. Our results are not consistent with O'Connor (2015) where he suggested that grass recovery from severe drought may take several decades under favourable condition of above-average rainfall, reduced grazing, and absence of disturbance.

There is widespread agreement that grass species in different areas respond differently to environmental drivers (Noble & Slatyer 1980; O'Connor 1994). Therefore, the response of grass community to environmental drivers and the recovery period of degenerated community is variable (Tainton 1999). However, it has been suggested that community recovery might depend on the timing of rainfall and drought events and the applied management strategies pre/post-drought such as grazing rate and burning (Bosch & Kellner 1991; O'Connor 1994).

Although grass cover and biomass showed a general decrease in response to drought, veld condition was not significantly degraded (from 91% to 87%) by drought. Veld condition may determine the extent to which severe drought can exert grass mortality (Hodgkinson 1995). For instance, Tacheba & Mphinyane (1993) showed subsequent increase in the abundance of annual grass and forbs (from 20% to over 50%) as a response to two year drought in Botswana under intensive stocking rate and only 28% increase at low stocking rate. It has been suggested that the greater the veld condition before a drought, the lower susceptibility to high mortality by droughts (Snyman & Fouché 1991; 1993). Also soil type plays a role in moderating grass response to rainfall variability driven by its capacity of holding water and soil fertility (Frost et al. 1986). Heavy textured soils are more susceptible to compositional change of perennial grass than are light textured soils (O'Connor 1985).

Severe drought shifted the species composition of grass communities. Classic rangeland theory predicts that drought acts like heavy grazing causing a successional shift to increaser 2 (pioneer) species (Westoby et al. 1989). There was some evidence to support this prediction since the decreaser species and the increaser IIb responded to drought by noticeable increase. In contrast, the increaser I species declined and the increaser IIc revealed a slight decrease as seen in figure 3.11. Also, drought favoured the palatable grass species over the unpalatable figure 3.12. We found that drought consistently and strongly decreased the biomass of unpalatable dominant perennial *Sporobolus pyramidalis* (only occurs in Hluhluwe) (see figure 3.13). The palatable grazing lawn grass *Urochloa mosambicensis* responded to drought by remarkable increase. Droughts triggered the recruitment of the pioneer grasses such as the annual *Tragus berteronianus* which is used as an indicator of disturbed fields and emerges as a result of long droughts or overgrazing (Tainton 1999). *Tragus berteronianus* was not recorded previously in 2012 in all our study sites, but currently exhibited marked increase exclusively in the sites in iMfolozi, whereas there is no single record for Tragus in Hluhluwe. It is possible that the steep decline of perennial grass cover in iMfolozi served to enhance the emergence of *Tragus berteronianus* from a seed bank, and possibly the grass cover in Hluhluwe is seldom reduced sufficiently for Tragus to occur.

In general, the succession model requires tuning of the stocking rate in order to keep the veld or range condition into an equilibrium between grazing pressure and successional tendency (Westoby et al. 1989). For instance, the grazing rate, in poor pioneer conditions (early successional heavy grazed), should be adjusted or reduced to favour grass transition towards climax condition (excellent condition ungrazed) (Westoby et al. 1989; Tainton 1999). In our case, adaptive management that is based on successional model, should mitigate the multiple effect of drought and grazing by reducing grazing pressure. This in turn maintains a long-term equilibrium between the multiple pressure of drought and grazing, and the successional tendency (Westoby et al. 1989). Despite the widespread use of the rangeland successional model in range management (Lewis 1969; Stoddart et al. 1975; Smith 1988; Westoby et al. 1989), other works (Paulsen & Ares 1962; Smith & Schmutz 1975; West et al. 1984) have disagreed with the succession model predictions particularly in the response of grass species to grazing. For instance, grazers removal from grasslands/shrub-lands did not reverse the direction toward the climax condition (Rice & Westoby 1978), or increased species without any compositional changes, contradicting the succession model predictions (Gardner 1950; Robertson 1971; Westoby et al. 1989). Climax state is basically worse for grazers as palatability declines in species that appear when rangeland is under-utilised. Hence, the most preferred grasses are the decreasers. These decreasers decrease in cover in over-grazing and under-grazing conditions, and consequently are replaced with Increaser II and Increaser I species during these conditions respectively.

Chapter 5

Conclusions

We have explored the impact of recent drought on plant dynamics in our open long term monitoring plots in the Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa. We have studied separately the drought impact on trees and perennial grass in terms of their dynamics and change in composition. We have performed tree-grass dieback survey and identified tree and grass species in 2016. Tree heights and grass aboveground biomass have also been measured. The survey data have been compared with the data from 2012. Our main findings are as follows:

- The recent 2016 drought is the most intense drought in Hluhluwe-iMfolozi Park history as compared with the drought of early 1980s. This recent drought is also intense according to the world- scale where Foleys index falls below -1.5 as shown in figure 3.2.

- Drought didn't contribute to tree mortality (see table 3.1). There is rather a substantial increase in tree population from 1585 trees in 2012 to 2825 trees in 2016, especially among the small size classes in the mesic (Hluhluwe) and semi arid (iMfolozi) savanna (see figure 3.4).

- The increase of small trees is not influenced by the disturbance (fire and herbivores) effect as seen in figure 3.5, 3.6, 3.7.

- Drought didn't cause substantial change in tree composition, as the abundance of most dominant tree species has increased as presented in figure 3.8.

- Grass biomass and grass cover responded to severe drought by a marked decline as shown in figure 3.9, 3.10. No significant mortality rate has been found and the grass biomass showed a rapid vigorous recovery.
- Drought impact on the veld condition is minimal.
- Drought has shifted grass composition by favouring the decreaser and increaser IIb species over the increaser I and increaser IIc species as figure 3.11 shows.
- The highly and moderately palatable grazing lawn species showed a slight increase, whereas the unpalatable grass exhibited a marked decline as displayed in figure 3.12.

Our findings reveal that this South African savanna ecosystem is resilient to this recent severe drought. These results are a complete contrast to Fensham et al. (2009) study where they concluded that a severe drought contributes to widespread tree mortality, which in turn favours an open savanna scenario. Our findings also contradict previous work by O'Connor (2015) where he suggested that grass sward may require many decades to recover from a severe drought. Nevertheless, we suspect that drought might facilitate woody encroachment by reducing the competitive effect of grass and fire fuel load. Further investigations and more measurements are clearly required to investigate the relative importance of drought on tree recruitment. This we leave for future work at the end of growing season in 2017.

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Appendix A

Classes definitions and categories

Ecological index classes definitions (Tainton 1999) of grass species according to their response to different conditions :

- Increaser Ia: increases in mild under-grazing condition.
- Increaser Ib: increases in moderate under-grazing condition.
- Increaser Ic: increases in severe under-grazing condition.
- Increaser IIa: increases under mild overgrazing
- Increaser IIb: increases under moderate overgrazing.
- Increaser IIc: increases under severe overgrazing.

Grass species	**WPCM**		**EIM**	
Name	Class	Weight	Class	Weight
Panicum coloratum	HP	3	decreaser	10
Digitaria longiflora	MP	2	-	-
Sporobolus nitens	MP	2	increaser IIc	1
Sporobolus pyramidalis	UP	1	increaser IIc	1
Panicum maximum	HP	3	decreaser	10
Themeda triandra	HP	3	decreaser	10
Bothriochloa insculpta	UP	1	increaser IIb	4
Urochloa mosambicensis	HP	3	increaser IIc	1
Eragrostis superba	MP	2	increaser IIa	7
Dactyloctenium australe	MP	2	decreaser	10
Chloris gayana	HP	3	increaser IIb	4
Aristida congesta	UP	1	increaser IIc	1
Heteropogon contortus	MP	2	decreaser	10
Eragrostis plana	UP	1	increaser IIc	1
Eragrostis curvula	MP	2	increaser IIb	4
Panicum deustum	HP	3	decreaser	10
Setaria sphacelata	HP	3	decreaser	10
Tragus berteronianus	MP	2	increaser IIc	1
Hyparrhenia filipendula	MP	2	increaser Ia	7
Chloris pycnothrix	UP	1	increaser IIc	1
Digitaria eriantha	HP	3	decreaser	10

TABLE A.1: Grass species with their corresponding palatability, ecological index classes, and weighting (Van Oudtshoorn 1992). UP represents unpalatable grass species. MP represents medium palatable grass species. HP represents highly palatable grass species.