Drought effects on the herbaceous community structure of transformed Mopaneveld

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“Great things are not done by one person. They’re done by a TEAM of people”
– Steve Jobs

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Abstract

Semi-arid Mopaneveld vegetation structure is driven by herbivory, fire, nutrients and rainfall variability. The floristically homogenous herbaceous layer is highly dynamic and dominated by forbs. Forb species contribute significantly to the herbaceous species diversity of Mopaneveld. The responses of Mopaneveld herbaceous layer to increasing stressors such as climate- and land-use change may be heightened by its dynamic nature. Species- and functional diversity may provide crucial information on the responses of Mopaneveld to disturbances and the effect thereof on ecosystem function and stability. Rainfall variability is a characteristic feature of savannas such as the Mopaneveld and consequently some species have developed adaptive traits to cope with unpredictable precipitation and drought. Mopaneveld was previously shown to absorb anthropogenic disturbance effects through functional trait redundancy. However, studies investigating the effect of drought on anthropogenically transformed semi-arid savannas remain limited. This study therefore, aimed to determine the response of herbaceous community composition, in terms of both species- and functional diversity, on mine dumps in the semi-arid Mopaneveld savanna to a severe drought.

The severe 2015-2016 drought period provided the opportunity to investigate the response of species- and functional attributes of herbaceous vegetation to a severe drought on the transformed Mopaneveld ecosystem at Palabora Copper Mine (PC) in Phalaborwa, Limpopo. Floristic- and environmental herbaceous vegetation surveys, following a random paired sampling design combined with the 1 m^2 quadrate method, were conducted at two mine dumps at PC (copper tailings dam – TD; and waste rock dump -RD), and benchmarked against an adjacent protected area Cleveland Game Reserve (CGR), before drought and during drought release (In this study, defined as a period whereby an area received increased, but not above average, rainfall compared to a preceding drought period.). Herbaceous species were identified to species level and plant functional traits conferring drought- and stress tolerance were attributed to each species. Species- and functional trait data were used to analyse herbaceous community composition and diversity. Functional trait data were further analysed and compiled into plant functional types (PFT's) to assess trait-based redundancy, and therefore resilience of the Mopaneveld herbaceous layer.

Community-level analyses revealed that forb species diversity declined significantly in the protected area and on the TD, but not on the RD (intermediate land-use type). Forb functional trait diversity declined significantly on both mine dumps, but was more stable in the protected area. This may be due to the variety of forb lineages and their adaptation to natural disturbance in the protected Mopaneveld over evolutionary time. On the other hand, grass species diversity declined significantly in the protected area and remained stable on the mine dumps, which could be attributed to careful selection of stress-tolerant species for mine dump restoration practices. Furthermore, grass functional trait diversity remained stable across all land-use types. Functional trait evenness increased on the TD for both life forms and grass trait evenness also increased in the protected area. Productivity decreased significantly in the protected area, and grass biomass was significantly higher than forbs on the mine dumps. Both life forms were site specific, although more so for forbs. Indicator species analyses revealed forbs as the dominant indicator species in the protected area.

Drought resulted in an increase in annual PFT’s across all land-use types. Forb PFT’s composed of allochorous dispersal modes and nitrogen fixing ability were particularly important during drought release, while grass PFT’s consisting of sun tolerant species with a low palatability and long-distance dispersal modes were favoured during drought release. Compared to mine dumps, the protected area was more associated with forb PFT’s made up of species with a specialized mode of dispersal and no nitrogen-fixing ability, and grass PFT’s consistent of species with shade tolerance, endozoochorous dispersal mode and high palatability. All PFT’s remained present during drought release, indicating that the Mopaneveld herbaceous layer retained its resilience, despite severe anthropogenic disturbance and drought.

In the face of increasing drought frequency and land-use change, this study stresses the importance of promoting functional diversity and maintaining functional redundancy, by conserving more species with diverging responses to disturbance.

Key words: *savanna; forb; grass; diversity; mining; plant functional traits; climate change*

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CHAPTER 1

Introduction

1.1.1 African Savannas

Semi-arid savanna vegetation dynamics are driven by herbivory, fire, nutrients and rainfall, that interact to maintain the coexistence between herbaceous and woody vegetation types (Frost *et al*., 1986; Scholes, 1990; Skarpe, 1992; Sankaran *et al*., 2004; Bond, 2005). Coexistence between different life forms, enabled by niche separation, competition and facilitation dynamics, results in a high plant species diversity (Scholes and Archer, 1997; Shackleton, 2000; Jacobs and Naiman, 2008; Pavlovic *et al*., 2011; World Tourism Organization, 2015). Several bioregions with different diversity patterns constitute the savanna biome (Mucina and Rutherford, 2006). Mopaneveld is the smallest savanna bioregion of South Africa (Rutherford *et al.*, 2012). Although floristically more homogenous compared to other savannas (Siebert, *et al.*, 2010), Mopaneveld is characterised by a highly dynamic herbaceous layer (Siebert, *et al.,* 2003a), typically dominated by either forb species or co-dominance between forbs and grasses (Jordaan *et al*., 2004; Siebert, *et al.*, 2010; Rutherford *et* al., 2012; O'Connor, 2015).

Mopaneveld diversity is under increasing threat and pressure related to various forms of natural and anthropogenic (direct and indirect) disturbances (Mouillot *et al.*, 2013; Sasaki *et al.*, 2015) and herbaceous vegetation responses to these disturbances may be heightened due to the dynamic nature of the Mopaneveld ecosystem. However, natural savanna disturbance regimes may have resulted in plants developing adaptive traits over time that unintentionally allow for more flexibility under an unanticipated, unnatural disturbance, such as mining (Crispo *et al*., 2010).

Successful conservation practices in Mopaneveld ecosystems are dependent upon the maintenance of interactive mechanisms involving bottom-up drivers (soil nutrient availability), and top-down controls (herbivory and fire) of savanna vegetation structure. In addition, the factors responsible for modification these drivers (climate change and rainfall variability) (Chidawanyika *et al.,* 2019) may also prove to be crucial in such practices.

1.1.2 Rainfall variability and climate change

Rainfall variability is a typical feature of savanna ecosystems (Fynn and O'Connor, 2000; Mucina and Rutherford, 2006), causing shifts in plant species composition between dry and wet periods (Skarpe, 1992; Gunderson, 2000; Siebert *et al.,* 2003a). After a disturbance event such as drought, the Mopaneveld herbaceous layer dies back and perennial species are typically depleted

(O'Connor, 1999; O'Connor, 2015). However, Mopaneveld herbaceous vegetation responds rapidly to rainfall after a dry period, since considerable increases in annual grass species and forbs typically occur (O'Connor, 1999; Siebert *et al.,* 2003a; Rutherford *et al*., 2012; Gibbes *et al*., 2014; O'Connor, 2015). These annual species temporarily increase species richness and diversity, and dominate the herbaceous layer (O'Connor, 1999). This increased species richness and diversity typically relates to a diverse range of plant functional traits (Laliberté *et al.,* 2010). High functional diversity among savanna species implies that at least some species are adapted to and are able to tolerate drought events through specific functional traits (Choat *et al*., 2012; Craine *et al*., 2011).

It is predicted that the frequency of extreme climatic events, such as drought, will increase due to a higher variance in climatic seasonality, as a consequence of gradual climate change (Jiguet *et al.,* 2011; Trenberth *et al.,* 2014; van Wilgen *et al*., 2016; Swemmer *et al*., 2018). Changes in inter-annual rainfall variability and mean annual rainfall as a result of global climate change (O'Connor and Kiker, 2004) are likely to lead to drastic changes in community structure and biodiversity on all trophic levels (Oliver *et al.,* 2013). Drastic changes to vegetation structure may include increases in C_3 plants (forbs and trees) and declines in C_4 plant (mostly grasses) in response to increasing CO_2 levels in the atmosphere (Cramer *et al*. 2001, Scheiter and Higgins 2009; Bond and Parr, 2010; Wang *et al.,* 2013; Siebert and Scogings, 2015; Smit and Prins, 2015). The consequences of the shift from C_4 to C_3 species remain largely unknown (Bond and Parr, 2010).

1.1.3 Anthropogenic disturbances

The five main global threats to biodiversity which are all associated with- or a result of anthropogenic disturbances, include habitat loss, climate change, overexploitation, alien plant invasion, and pollution (Dirzo and Raven, 2003; Davis *et al.,* 2014; Noonan-Mooney and Gibb, 2014). Habitat loss, as a result of land-use change, remains the most severe threat to biodiversity (Noonan-Mooney and Gibb, 2014). Severe disturbance may cause drastic declines in plant functional diversity and abundance (Botha *et al.,* 2017), and consequently, have adverse effects on ecosystem function and resilience.

Exploitation of natural resources for human benefit often depletes biodiversity (Ellis *et al*., 2013), where in some cases the safe limits for species loss (for the proposed Planetary Boundary) have been crossed (Mace *et al*., 2014; Steffen *et al*., 2015). This may cause ecosystems to shift into irreversible alternate states, and although new landscapes may be constructed by means of restoration practices, they may function differently to the original landscape (Van der Walt *et al.,* 2012; Mouillot *et al*., 2013; Sasaki *et al*., 2015).

Mining practices affect the functionality of soils, which negatively affects the vegetation growing on mine dump soils (Sheronan *et al.*, 2010), and is commonly associated with a reduction in herbaceous species richness (Van Staden, 2016). Mine dumps often have lower species richness compared to natural areas, as well as a higher percentage of invasive species (Van der Walt *et al.,* 2012, Lemke *et al.,* 2013, Zhao *et al*., 2016). However, previous studies have revealed no adverse effects of invasive species on native species diversity on mine dumps (Van Staden, 2016). Furthermore, it was postulated that Mopaneveld herbaceous vegetation is able to absorb the effects of mining through adaptive plant functional traits (Van Staden, 2016).

1.1.4 Combined effects of drought and mining

Disturbance can either function as a filter, or as a process which enhances the effects of other ecological filters (Myers and Harms, 2009). Thus, climate change may exacerbate the impact of environmental and anthropogenic filters on species in savanna ecosystems. The combined effects of anthropogenic disturbance and a prolonged, extensive drought on biodiversity are still largely unknown (Oliver and Morecroft, 2014). Increasing mean daily temperatures and decreasing precipitation may have stronger effects on semi-arid ecosystems compared to more temperate systems (Mantyka-Pringle *et al.,* 2012). High temperatures and low rainfall exacerbate the effects of habitat loss and fragmentation, since species with evolutionary adaptations to certain types of conditions may not be able to adapt to environmental changes fast enough (Mantyka-Pringle *et al.,* 2012). Localized land-use regimes may intensify the effects of increased drought frequency on biodiversity (Walther, 2010; Oliver and Morecroft, 2014). The effects of habitat loss caused by mining practices may mask the effects of drought (Pyke, 2018). For this reason, it was suggested that research focussing on the effect of a single driver of change may be inadequate (Oliver and Morecroft, 2014). Although the impact of complex interactions between global drivers of change on biodiversity may never be accurately predicted (Oliver and Morecroft, 2014), an increased understanding and knowledge related to these interactions may be invaluable for the appropriate and sustainable management of ecosystems in the face of future change (Tylianakis *et al.,* 2008; Mantyka-Pringle *et al.,* 2012; Oliver and Morecroft, 2014).

Future changes in savanna community structure are difficult to predict as various factors interact, resulting in a range of potential outcomes (Easterling *et al.,* 2000; Oliver and Morecroft, 2014). Global climate change could occur at an unmatched rate in combination with other drivers, such as land-use change (Oliver and Morecroft, 2014). Since biodiversity is a necessary driver of ecosystem stability, functionality and sustainability in the face of environmental changes (Loreau and de Mazancourt, 2013), it is important not to neglect the effect of interactions between multiple drivers on biodiversity (Oliver and Morecroft, 2014).

1.1.5 Resilience of African Savannas

Forbs, defined as non-graminoid herbaceous vascular plants (Siebert and Dreber, 2019) are an intrinsic part of the Mopaneveld herbaceous layer, and not merely a consequence a disturbance (Rutherford *et al.,* 2012). Ecological studies that consider forbs up to species level are relatively scarce and the role of forbs in savanna ecosystems remain largely unexplored (Scott-Shaw and Morris, 2015; Siebert and Dreber, 2019). Forb species contribute significantly to the herbaceous species diversity (Trollope *et al.*, 2014), and the subsequent functional diversity of Mopaneveld ecosystems. Therefore, forbs and grasses as individual herbaceous life forms could provide crucial information pertaining to Mopaneveld dynamics in the face of disturbance.

There is an increasing awareness of the use of plant functional trait diversity, as opposed to taxonomic richness and diversity, to better understand the effect of environmental disturbance on ecosystem function (Díaz and Cabido, 2001; Lososová *et al*., 2006; Lavorel *et al*., 2011; Siebert, 2011; Mori *et al.*, 2013; Hanke *et al.,* 2014; Balachowski and Volaire, 2018). A positive relationship exists between species- and functional diversity, which enhances functional redundancy as more species are available to perform similar functions and hence, lead to increased ecosystem resilience (Díaz and Cabido, 2001; Petchey *et al*., 2009; Laliberté *et al.,* 2010). Therefore, the overall ecosystem functioning may remain stable despite disturbance, as the loss of less tolerant species will not necessarily decrease the diversity of functional traits (Botha *et al.,* 2017).

1.2 Rationale

The severe 2015-2016 drought period experienced throughout the Lowveld (Swemmer, 2016) impacted both protected and disturbed Mopaneveld in the Phalaborwa area. The Mopaneveld savanna in the Phalaborwa region extends over multiple land-use types, ranging from communal lands, protected areas and mining sites. Although a large proportion of Mopaneveld savanna is conserved in protected areas, such as the KNP, many areas are exposed to severe anthropogenic activity. Developments along the boundary of the KNP pose a threat to the integrity of ecosystems within the Park, of which mining is the most significant. This is especially relevant for the Phalaborwa side of the KNP (De Villiers and Mkwelo, 2009).

Palabora Copper (PC), a copper mine and refinery in Phalaborwa, Limpopo, provides an ideal setting to investigate the impact of severe disturbances on ecosystem integrity and functioning. Despite environmental perturbations associated with mining activities, the PC mining area hosts a high diversity of fauna due to its close proximity to the Kruger National Park (KNP) and access into the mining area from the KNP. In addition, syenite koppies within the mining area and an adjacent game reserve support high plant diversity (Van Staden, 2016). PC is required to manage the ecosystem diversity according to a detailed management plan, indicating specific requirements for future mine closure (Palabora Mining Company, 2005; Van Dyk, 2018). The management plan stipulates the continuous rehabilitation actions and monitoring of the mine dumps, throughout the duration of the mine's operational time.

A previous study conducted at PC mining revealed that despite reduced species diversity, Mopaneveld herbaceous vegetation was resilient towards anthropogenic disturbances in terms of both functional trait and –group diversity (Van Staden, 2016). However, it was predicted that mine dump plant communities might be vulnerable to additional disturbances when loss of functional groups and traits are concerned. The prolonged drought in the area raised concerns on whether the ecosystem integrity of the mined areas could be maintained through herbaceous species- and functional diversity.

Pre-drought floristic and environmental data collected in 2014 provided a reference point to investigate changes in species- and functional diversity in response to an extreme drought event and whether drought effects were stronger in the transformed (i.e. mining) areas opposed to an untransformed benchmark site adjacent to the actively mined area.

1.3 Aims and objectives

This study aimed to compare pre-drought herbaceous communities to drought release communities and thereby determine the response of herbaceous community composition, in terms of both species- and functional diversity to severe drought, on mine dumps in the semi-arid Mopaneveld savanna.

In this study, drought release was defined as a period whereby an area received increased, but not above average, rainfall compared to a preceding drought period.

Specific objectives were to 1) assess and discuss changes in herbaceous community composition and diversity at i) species level (Chapter 5) and ii) functional trait level (Chapter 6); 2) relate observed patterns to changes in productivity (Chapter 5); 3) assess ecosystem resilience through analyzing trait-based redundancy across land-use types, and identifying plant functional groups that best express drought- and/or stress tolerance (Chapter 6) in a semi-arid Mopaneveld savanna.

1.4 Hypothesis

Chapter 5

Mine dumps are severely transformed systems with a characteristically depauperate flora (Mendez and Maier, 2008; Ekka and Behera, 2011; Mapaure *et al*., 2011; Shooner *et al*., 2015). Disturbance frequency together with additional environmental stressors in such transformed systems may become exacerbated by drought events (Mantyka-Pringle *et al*., 2012). From this, it is hypothesized that (i) a drought event will have a stronger negative effect on herbaceous species richness and diversity on mine dumps, compared to an adjacent protected Mopaneveld. This predicted decrease in species richness and diversity on mine dumps is typically accompanied by the persistence of species that are highly tolerant to both drought and anthropogenic disturbance (Copeland *et al*., 2016). It was therefore expected that (ii) species evenness will increase on mine dumps after a severe drought, as species that are not pre-adapted to harsh conditions (i.e. those that occur at low frequencies during normal years) would be filtered out.

Chapter 6

Drought tolerant species are able to persist during a drought due to a variety of pre-adapted traits (Balachowski *et al*., 2018). It is hypothesized that (iii) trait diversity will decrease on mine dumps due to lack of pre-adaptation to a severe drought, but will remain stable in protected Mopaneveld due to adaptation to natural drivers of vegetation structure over evolutionary time, with specific reference to rainfall variability in particular (Choat *et al*., 2012; Craine *et al*., 2011). Disturbance-sensitive species are known to be replaced by disturbance-tolerant species after a drought, due to drought-tolerant traits (Kotschy, 2013; Mouillot *et al*., 2013; Hoover *et al.,* 2014). It is therefore further hypothesized that (iv) sensitive species occurring during pre-drought conditions on mine dumps will be replaced by species assemblages with adaptive traits to better exploit the harsh conditions associated with drought. Species losses do not necessarily relate to loss of functional diversity, as some species may share functional traits that contribute to ecosystem function (Naeem, 1998; Mori *et al*., 2013; Pillar *et al*., 2013). Redundancy in functional traits promotes ecosystem resilience and stability (Naeem, 1998; Pillar *et al*., 2013). It is therefore expected that (v) the Mopaneveld will retain its resilience across land-use types through functional traits.

1.5 Structure of dissertation

This dissertation conforms to the guidelines set for a standard dissertation at the North-West University (See section 2.1 of the manual for Post Graduate Studies available at: www.nwu.ac.za/library/documents/manualpostgrad.pdf). It encompasses eight chapters. Cited literature is included as a single list of references at the end of the dissertation.

Chapter 2: Literature Review

This chapter contains a comprehensive outline of relevant literature pertaining to the effect of severe anthropogenic impact and drought on the herbaceous (forb and grass) vegetation of semi-arid savannas, with particular focus on an anthropogenically transformed section of Mopaneveld.

Chapter 3: Study area

Provides a detailed description of the sites surveyed in this study, which includes information on climate, vegetation, soil and geology.

Chapter 4: Methodology

This chapter provides a detailed description of experimental and sampling designs, followed by the methods applied to obtain floristic and environmental data used in this study, and a description of analyses conducted for species- and functional diversity.

Chapter 5: Results – taxonomic diversity and composition

This chapter presents results of analyses pertaining to species diversity and composition across land-use types included in this study, and in response to drought release.

Chapter 6: Results – functional diversity and composition

This chapter contains results relating to the functional diversity and composition of herbaceous vegetation across the land-use types included in this study, and in response to drought release.

Chapter 7: Discussion

This chapter provides a comprehensive discussion of the results presented in Chapters 5 and 6. Related studies are linked to the current study and findings are compared.

Chapter 8: Conclusions

This chapter integrates the findings discussed with concluding remarks and recommendations pertaining to the current study.

CHAPTER 2

Literature Review

2.1 Savanna vegetation dynamics

Savanna ecosystems have been under scientific observation for decades. More than half of the African continent is made up of the Savanna Biome and its associated ecosystem diversity (Osborne *et al.,* 2018). Savanna vegetation structure is driven by herbivory, fire, and rainfall (Smith *et al.,* 2013; Osborne *et al*., 2018), and is co-dominated by woody and herbaceous species (Hempson *et al.,* 2007; Mureithi *et al*., 2016; Osborne *et al.,* 2018). Herbaceous, as well as woody vegetation, is closely linked with the soil types and soil water availability at local and regional scales (O'Connor, 1992; O'Connor 1999; Belluau and Shipley, 2017). Valuable ecosystem services provided by savanna ecosystems include food, medicine, timber and biofuel, biocontrol agents and pollination (Naeem *et al.,* 2012; Osborne *et al*., 2018).

Southern African savannas can be divided into different bioregions namely, the Central Bushveld, Lowveld, Sub-Escarpment Savanna, Eastern Kalahari Bushveld, Kalahari Duneveld, and Mopane (Mucina and Rutherford, 2006). Compared to other bioregions in the savanna biome, the Mopane bioregion is the smallest (Mucina and Rutherford, 2006). Mopaneveld savannas are semi-arid ecosystems occurring throughout southern Africa (Mapaure, 1994). As the name suggests, the dominant woody species within this savanna system is the legume, *Colophospermum mopane. Colophospermum mopane* trees enhance herbaceous species in the Mopaneveld diversity by improving soil nutrient availability and enhancing productivity of sub-canopy habitats (Mlambo et al., 2005).

2.1.1 Biodiversity

Biodiversity loss in ecosystems has caused increasing concern over the last two decades (Van Ruijven and Berendse, 2010; Naeem *et al.,* 2012). As a result, more evidence supported the role of biodiversity in ensuring ecosystem function and stability (Duffy, 2009; Cardinale *et al*., 2012; Hooper *et al*., 2012; Mori *et al.,* 2013). By conserving ecosystem function, we maintain valuable ecosystem services (Díaz and Cabido, 2001; Elmqvist *et al*., 2003; Flynn *et al.,* 2009; Mori *et al.,* 2013). Convincing evidence surrounding the importance of biodiversity for human benefit led to the structuring of biodiversity policies (Naeem *et al*., 2012). Considering the predicted effects of global climate change, there is a need to conserve and maintain biodiversity and underlying ecological processes to ensure human well-being and food security for the future (Díaz *et al*., 2006; Loreau *et al*., 2006).

Due to anthropogenic exploitation of natural resources, human-induced climate change, introduction of exotic species, and landscape transformation, among other degenerative activities, biodiversity is increasingly succumbing, leading to a loss of ecosystem services (Naeem *et al*., 2012).

Plant diversity loss results in an “upward” cascading effect across trophic levels (Scherber *et al*., 2010). Therefore, knowing what ecosystem functioning looks like on a primary producer level should be indicative of what is happening beyond that. For the purpose of generalizing the findings surrounding biodiversity loss and ecosystem function, the inclusion of a more diverse range of taxa and ecosystems have gained increasing scientific interest. This is beneficial as some systems don’t have grass species, while others might only have microbes, and in such cases, other functional groups such as forbs could be included in ecological studies (Naeem *et al.,* 2012).

Furthermore, species that are dominant under certain environmental conditions may become rare when conditions change, or in different environments (Zerbo *et al*., 2016). There is a high percentage of rare herbaceous species in savanna ecosystems (Zerbo *et al*., 2016), which may point to the high heterogeneity of the herbaceous layer of savannas. However, it also points to the susceptibility of these rare species to environmental disturbances (Zerbo *et al*., 2016).

Savanna ecosystems are complex and heterogeneous, which adds to the rich biodiversity (Du Toit and Cumming, 1999; Okullo, 2012) although Mopaneveld savannas are less heterogeneous in terms of floristics, productivity and traits compared to other savanna ecosystems (Mucina and Rutherford, 2006). Biodiversity in African savannas is further enhanced by the unique vegetation structure, the coexistence of tree and herbaceous species, and with a continuous herbaceous vegetation layer and discontinuous woody layer (Frost *et al.,* 1986; Mucina and Rutherford, 2006). As a result of the dynamic response of the herbaceous layer to disturbance, herbaceous species drive diversity patterns in savanna ecosystems (Skarpe, 1992; Díaz and Cabido, 2001; Elmqvist *et al*., 2003; Hanke *et al*., 2014)

Savannas are particularly rich in biodiversity, although most of the naturally occuring ecosytem exists in small fragments in protected areas (Buitenwerf *et al.,* 2011). According to Osborne *et al.* (2018), the main threats to savanna ecosystems remain landscape alteration and transformation, unnatural fire, grazing and browsing regimes, climate change and increases in atmospheric CO_2. Land degradation, a process caused by land-uses that lead to a persistent loss of ecosystem productivity, is the greatest cause of biodiversity loss in southern African savannas (Scholes and Biggs, 2005; Naeem *et al.,* 2012; Osborne *et al.,* 2018). In this sense, mining plays a significant role in landscape alteration. In severely disturbed areas, such as a mine dumps, a low perennial species diversity, with high numbers of annual species as a result of early successional stages is expected and species with special adaptations to survive in disturbed environments are more likely to be found (Mapaure *et al*., 2011).

Biodiversity conservation is the main goal for the establishment of protected areas, although various protected areas are intensely managed for various, diverging sub-goals (Shackleton, 2000, Buitenwerf *et al.,* 2011). Siegfried (1989) indicated that although biodiversity preservation is one of the primary aims of protected areas, inadequate inventories of biodiversity in these areas are kept and thus there are no concrete means of keeping track of species losses and gains in these protected areas. Protected areas are fragmented and come with size concerns, edge effects, introduced species, and poaching that threaten biodiversity (Machlis and Tichnell, 1985). Fortunately, biodiversity is no longer only protected and conserved in these areas, but also extends to agricultural ecosystems, such as communal lands (Scoones *et al*., 1992; Halladay and Gilmour, 1995).

2.1.2 Functional diversity

Species richness is the most widely used diversity measure to quantify biodiversity loss and habitat degradation (Flynn, *et al*., 2009). However, it has been suggested that species diversity might not provide adequate information pertaining to vegetation structure and composition, and that more concrete evidence may be gathered from trait-based diversity measures instead (Hanke *et al.,* 2014). Therefore, scientific interest has recently shifted focus from species diversity to functional diversity (Lavorel, 2011; Mori *et al*., 2013; Skelton, 2015; Balachowski, 2018). Functional diversity focuses on aspects of diversity that affect the function of the ecosystem (Mori *et al*., 2013). The array and value of 'functional effect traits' are what is used to measure functional diversity (Díaz and Cabido, 2001; Hooper *et al*., 2005). Functional diversity provides a trait-based means of understanding and investigating ecosystem dynamics in savannas (Lavorel and Garnier, 2002; Standish *et al*., 2015). Loss of functional diversity reduces the stability of the system, which may result in the loss of ecosystem functions (Mori *et al.,* 2013).

Although the loss of a species is of high concern to conservationists, the loss of a species as an entity that performs a specific function in the ecosystem might not be as much of a concern when other species are available to fulfill and take over that function (Naeem, 1998; Díaz and Cabido, 2001). This concept is termed 'functional redundancy' (Naeem, 1998). Functional redundancy does not justify continuous ecosystem change, for in the face of climate change and increasing global population numbers and anthropogenic activity, the reality is that species loss is inevitable. Therefore, it is of utmost importance that species are not lost as this may compromise sustainable ecosystem services.

Understanding functional diversity and trait-based redundancy, and applying this knowledge, could potentially provide answers for prolonged sustainability (Naeem, 1998; Elmqvist *et al*., 2003). Some studies have also shown that functional groups with low functional diversity, could be more stable in the face of perturbation (e.g. Elmqvist *et al.,* 2003; Laliberté *et al*., 2010). Functional and spatio-temporal complementarity adds to the system's ability to recover after disturbance (Mori *et al.,* 2013). It is important to consider spatial and temporal variations with functional redundancy, especially in savanna ecosystems which are one of the biomes with the greatest spatio-temporal variability (Hüttich *et al*., 2011).

High functional redundancy results in ecosystem resilience (Díaz and Cabido, 2001). Ecological resilience is the ability of an ecosystem to maintain its structure and functioning after disturbance (Holling, 1973). When a system can no longer maintain its original functioning, it may shift into an alternative stable state (Gunderson, 2000; Beisner, 2012; Sundstrom *et al.*, 2012). A greater range of functional responses among species towards disturbances increases resilience (Elmqvist *et al.*, 2003, Chillo *et al.,* 2011). This allows for ecological functioning to remain even if some species are lost from the system. However, it is not as beneficial for rare species with rare functions (Sundstrom *et al*., 2012). Extinctions of species may also allow for a higher average resilience for the remaining species as their competitors have been reduced (Ives and Cardinale, 2004; Van Coller and Siebert, 2015). Increased losses of species may, however, allow for increased colonization by alien species (Sundstrom *et al.*, 2012).

According to the insurance hypothesis (Yachi and Loreau, 1999), ecosystem resistance and resilience should increase as diversity increases. The insurance hypothesis assumes that species have different responses to changes in the environment. It can, therefore, be expected that as the number of species increases, so does the array of response traits they possess. This should ensure that more species are able to resist disturbance or environmental change. As a consequence, the ecosystem does not lose functionality when disturbed and remains resilient to perturbation (Van Ruijven and Berendse, 2010). Response diversity (Elmqvist *et al.,* 2003) describes the different ways in which species respond to environmental alteration or perturbation and may indicate the ecosystem's resilience after these events. Increasing anthropogenic resource extraction activities, such as mining, can reduce response diversity globally, and therefore result in ecosystems becoming increasingly susceptible to disturbances and environmental change (Laliberte *et al*., 2010). A variety of different plant responses to environmental change and disturbance will allow ecosystems to cope with unexpected perturbations more successfully (Elmqvist *et al*., 2003). As more functional contexts are taken into account, more species are included to enhance ecosystem functioning (Isbell *et al.,* 2011; Maestre *et al.,* 2012). In the Mopaneveld, forb species dominate and increase ecosystem diversity

(Jordaan *et al*., 2004). The greater the variety of functional traits they possess (Laliberte *et al.,* 2010), the greater the redundancy, the greater the resilience of an ecosystem to disturbance (Díaz and Cabido, 2001).

2.1.3 Functional traits in savannas

Reich *et al.* (2003) define plant functional traits as "any attribute that has a potentially significant influence on establishment, survival, and fitness, and traits related to the ability to acquire, use, and conserve resources". Plant traits and their relationship with the environment are determined by climatic conditions, disturbance and biotic interactions (Díaz *et al.,* 1998).

In savanna ecosystems plants generally have traits that confer resistance and tolerance to herbivory and fire, as well as physiological traits for tolerance to drought and drought avoidance strategies (Díaz *et al.,* 1998; Rosenthal *et al.,* 2010; Copeland *et al.,* 2016; Linder *et al.,* 2018; Osborne *et al.,* 2018). Species in environments with low productivity, such as semi-arid savannas, usually have traits that enforce resistance to drought (Van Ruijven and Berendse, 2010, Zhenqi *et al.,* 2012). When drought is accompanied by extreme temperatures, species that have traits to utilize water more efficiently may become dominant (De Boeck *et al.*, 2006).

Critical traits also include those for dispersal, establishment, and persistence (Ilunga wa Ilunga *et al.,* 2015; Zirbel *et al.,* 2017; Linder *et al.,* 2018). Traits for dispersal include dispersal mode (animals/insects and their mobility, wind), vegetative height, pollination mode, specific leaf area, diaspore size, shape and mass, as well as the amount thereof (Díaz *et al.,* 1998; Weiher *et al*., 1999; Díaz and Cabido, 2001; Ilunga wa Ilunga *et al.,* 2015; Linder *et al.,* 2018). For establishment, plants need traits relating to generation time and embryo structure, growth and shoot phenology, polyploidy and apomixes, and hygroscopic awns (Díaz *et al.,* 1998; Ilunga wa Ilunga *et al.,* 2015; Linder *et al.,* 2018). For persistence, plants need to have traits relating to the life cycle, lateral spreading capacity (vegetative spread/clonality), bud bank and root depth (Díaz *et al.,* 1998; Ilunga wa Ilunga *et al.,* 2015; Osborne *et al.*, 2018).

Other important general traits include shade tolerance, growth form, life span, life form, nitrogen-fixing ability, mycorrhizal status, carbon storage and investment into support tissue (Díaz *et al.,* 1998; Van Staden, 2016; Osborne *et al.,* 2018).

Traits desired for unfavourable environmental conditions include those for environmental flexibility, such as photosynthetic pathway (CAM, C_4 or C_3), flexible growth form, competitive resource extraction (Díaz *et al.,* 1998; Linder *et al.,* 2018) and for drought stress, traits relating to stomata and rooting systems (Díaz *et al.,* 1998; Chirino *et al.,* 2017), drought avoidance traits such as having taproots and succulent stems (Díaz *et al.,* 1998), and responsiveness of stomata to increased CO_2 (Osborne *et al.,* 2018).

2.2 Climate variability in savannas

The importance of species- and functional responses to natural disturbances, such as drought, becomes increasingly important as climate change strongly affects ecosystem stability (Van Ruijven and Berendse, 2010). Drought events are increasing in frequency and intensity in arid regions, and is predicted to become more apparent as a result of climate change (Williams *et al.,* 2015, Copeland *et al.,* 2016; Standish *et al.,* 2015). Heatwaves are expected to increase across Africa (Battisti and Naylor, 2009), and so is the frequency of occurrence and duration of drought for the southern parts of Africa (Field *et al.,* 2012). This could have implications such as species losses (Tilman and El Haddi, 1992; McDowell and Allen, 2015) across different vegetation types and functional groups.

Climatic variability affects and shapes plant communities. Previous findings concluded that diversity-driven resilience is dependent upon the ecosystem performance before disturbance, although recovery of the system post-disturbance accelerated with diversity, irrespective of performance (Van Ruijven and Berendse, 2010). Wang, Yu and Wang (2007) determined that plant biomass before drought affects resistance, rather than diversity, however, in their study diversity and biomass were not related. A decrease in resistance with increased diversity is largely the result of pre-drought performance (Wang, Yu and Wang, 2007). This was supported by the findings of Van Ruijven and Berendse (2010) and others (De Boeck *et al*., 2008).

Vegetation composition in semi-arid savannas changes in response to rainfall (Fynn and O'Connor, 2000). This is especially true when communities are made up of short-lived perennial or annual herbaceous species (Fynn and O'Connor, 2000). Savannas are resilient to climate variability, as long-lived perennial grasses are temporarily replaced by short-lived perennials and annuals so that the system can recover faster after seasonal drought (Fynn and O'Connor, 2000). High inter-annual rainfall variability is common in savannas, and acts as a driver for annual vegetation states, structure and productivity changes (Rutherford, 1980; Illius and O'Connor, 1999; Swemmer *et al.,* 2007; Buitenwerf *et al.,* 2011).

Drought may lead to tree mortalities or woody encroachment (McDowell and Allen, 2015; Osborne *et al.,* 2018), loss of primary production (Zhao and Running, 2010, Knapp *et al.*, 2015), herbaceous species loss and loss of rare (Tilman and El Haddi, 1992) and less adapted species (Harte *et al*., 2006), which lead to conservation concerns. Although drought may result in the altered structure of the savanna landscape and woody-herbaceous interactions through reduced cover, biomass, and species richness, little change is expected in functional diversity of the herbaceous community (Copeland *et al.,* 2016). Plant functional traits associated with drought-adaptations have therefore developed over a long period in savannas (Mucina and Rutherford, 2006; Osborne *et al.* 2018). These adaptations include attributes such as deeper root systems and deciduousness (Mucina and Rutherford, 2006; Fan *et al*., 2017). Drought changes herbaceous species composition radically, as this component is more vulnerable to drought conditions compared to woody species (Scholes, 1985). Herbaceous species richness is commonly expected to decline as precipitation declines in savanna ecosystems (Zerbo *et al*., 2016).

In a Mopaneveld ecosystem, drought resulted in a reduction of perennial grasses (O'Connor, 1999). Buitenwerf *et al.,* (2011) reported increases in perennial grass abundance with increasing rainfall. Susceptibility to drought conditions varies across different perennial grass species. In the Mopaneveld savanna, it has been found that *Bothriochloa radicans, Cenchrus ciliaris, Digitaria eriantha, Eragrostis rigidior, Panicum maximum, Schmidtia pappophoroides, Stipagrostis uniplumis,* and *Urochloa mosambicensis* recede under drought conditions, and return when conditions improve (Dye and Spear, 1982; O'Connor, 1999). Reduction in palatable grass abundances will result in increased grazing pressure on remaining grasses, further exacerbating the initial effects of drought (O'Connor, 1999). However, according to Osborne *et al.* (2018), even under dry conditions, savanna grasses remain more tolerant towards grazing compared to other biomes. It has been shown that grasses with dense tufts such as *Themeda triandra* decline as a result of drought events, while *Aristida congesta* and *Tragus berteronianus* with sparse tufts have a positive response after a severe drought (O'Connor, 1995; Moyo *et al.,* 1995).

2.2.1 Drought related functional traits

Plant adaptations to arid environments prone to drought stress include traits such as elongated leaves with a low nutrient concentration, low photosynthetic rate, higher root to shoot ratios (Ackerly, 2004) and physiological adaptations (such as cavitation avoidance by xylem tissues which lead to having a tolerance towards water stress). Plant root depth influences drought tolerance abilities (Lamoureux *et al.,* 2016). Individuals with a shallow root system are less adapted to drought and could be lost from the system (Copeland *et al.,* 2016). Soil moisture has a filtering effect on the types of herbaceous plant community assemblages. The combinations of functional traits will determine whether their adaptations tolerate either moist or drier soil (Belluau and Shipley, 2017). However, predicting the impact of extreme drought on various life species- and functional types is still a great challenge, due to the variable nature of plant communities driven by multidimensional climatic inconsistencies and top-down drivers (Copeland *et al.,* 2016).

2.3 Mining

Despite human dependence upon ecological services provided, anthropogenic activities for resource extraction is often destructive to ecosystems. Savannas and tropical grasslands are considered to be the biomes experiencing the most conversion from natural to anthropogenic land-use systems (Boakes *et al*., 2010, Ellis, 2011).

Copper is in high demand due to its valuable uses in, among others, construction, electricity, and consumer products (Northey *et al.,* 2014). Based on extensive modeling and scenarios, copper production is expected to continue successfully at least for the next 20 to 25 years (Northey *et al.,* 2014). Copper ore grades are declining, and this, along with environmental and economic impacts, may impose some obstructions to the future production of copper. Mines will typically be built around high-grade copper ores in order to achieve the greatest financial benefit. There is a clear correlation between copper ore decline and the impact on the environment, as more copper ores become depleted and natural habitat gets displaced to make way for additional mining (Mudd and Weng, 2012). Increased prices of copper allow for re-investment into the mine, therefore increasing the mine lifetime, resulting in a lower rate of exploitation of copper resources situated elsewhere (West, 2011).

2.3.1 Mining effects on savannas

Mining causes extensive damage to the landscape, by creating, among others, open pits, rock dumps and tailings dams (Mudrák *et al.,* 2010; Zhenqi *et al.,* 2012; Kapusta and Sobczyk, 2015). This requires the removal of soil and rock debris, thereby intensely disturbing soil structure (Ekka and Behera, 2011) and changes the natural topography and drainage system of the area (Chaulya *et al*., 2000). The mining process may deposit waste material containing pollutants such as heavy metals and organic pollutants that contaminate soil and water sources and have serious effects on ecosystems (Dary *et al.,* 2010; Mapaure *et al*., 2011). The alteration of soil structure and chemistry results in widespread impacts on the environment, such as biodiversity loss, altered vegetation structure, and prevention of natural succession from taking place on mine dumps (Singh *et al*., 1996; Morgenthal *et al*., 2003; Mapaure *et al*., 2011; Zhenqi *et al.,* 2012; Kapusta and Sobczyk, 2015; Wang *et al.,* 2017). Declines in biomass and species richness and diversity have also been reported in response to mining activity (Jadia and Fulekar, 2009; Mapaure *et al*., 2011).

The ecological features of mine sites vary from one another, although they all have low water availability in soils, low nutrient content and very low organic material (Nurtjahya and Franklin, 2017). Soil erosion and compaction prevents successful colonization by herbaceous species, although in some cases, with the help of fertilization and the careful selection of species, soils on mine dumps may be colonized (Siebert *et al.,* 2003b; Lamoureux *et al.,* 2016; Nurtjahya and Franklin, 2017; Wang *et al.,* 2017). Altered soil chemistry will also favour species that are tolerant to the soil conditions brought on by mines, such as high salt and heavy metal concentrations along with nutrient deficiencies (Siebert *et al.,* 2003b; Nurtjahya and Franklin, 2017). Mining soils are shallow and lack sufficient moisture, which also impedes colonization and alters community structure (Siebert *et al.,* 2003b; Evanylo *et al.,* 2005; Nurtjahya and Franklin, 2017).

Soil is paramount for the functioning of ecosystems and ecosystem processes (Kapusta and Sobczyk, 2015). Unfortunately, mining is destructive and results in severely degraded soil, which is extremely challenging to restore (DeJong *et al*., 2011). Soil structure differs considerably between mine dumps and natural areas. Mining changes fertile, non-toxic soil into toxic soil. Natural heavy metal soils host more native and endemic plant species (Copeland *et al*., 2016), however, in mine-disturbed soils, this is not the case.

Where drought was the only disturbance, species composition may vary between wet and dry periods, remaining stable, however, with continuous severe disturbance such as that caused by mining activities, the system does not return to its original stable state (Westoby *et al.,* 1989; Rapport and Whitford, 1999; Siebert *et al.,* 2003b). Woody cover is also removed during the mining process, which changes the dynamics and structure known to savanna ecosystems. Trees are important to provide protection to seedlings, aiding in their establishment (Thrash, 1998).

2.3.2 Rehabilitation and restoration

Mines are required to restore biodiversity once mining activity has been terminated (Goh *et al.,* 1998; Fitton, 2007; Fadda *et al.,* 2010; Mapaure *et al.,* 2011). The restoration process largely involves the re-seeding of mine dumps and thereby restoring vegetation (Evanylo *et al.*, 2005). This has many advantages, such as the stabilization of soils, and preventing pollution of wind and water caused by mining (Evanylo *et al.*, 2005; Nurtjahya and Franklin, 2017; Wang *et al.,* 2017).

Promoting vegetation cover through rehabilitation acts as a valuable technique to improve the microclimate of the disturbed landscape (Zhao *et al.,* 2015). Zhao *et al.* (2015) reported significantly lower soil and air temperatures but increased relative air humidity after the re-establishment of vegetation in an open-pit coal mine. Mining leads to more favourable microclimates in arid and semi-arid ecosystems, improving ecosystem function, ecological processes and landscape configuration (Mendez and Maier, 2008; Zhao *et al.,* 2015).

Being highly susceptible to wind and water erosion, mine tailings pose a threat in the sense of contamination of nearby water bodies and environmentally sensitive areas and surrounding communities (Mendez and Maier, 2008; Liu *et al.,* 2017). The stabilization of these soils with suitable vegetation does not only allow for the restoration of the mining area itself but also prevents the contamination and pollution of surrounding areas. Due to the general acidity (Johnson and Bradshaw, 1977, Krzaklewski and Pietrzykowski, 2002), toxicity and metal concentrations in mine tailings, and the lack of organic material and nutrients, natural vegetation establishment is hampered (Mendez and Maier, 2008). Kapusta and Sobczyk (2015) suggested that rehabilitation and establishment of vegetation will be increasingly difficult closer to a smelter on the mine premises, as smelters are a source of severe air pollution and heat.

The structure of overburden waste dumps consists of a base that takes the form of the natural, possibly undulating landscape, after which more waste material is deposited on top with specific lift heights (Ortiz, 2017). Optimizing mine design has become of paramount importance as a means to minimize costs. Not only do they need to consider transport costs of waste material, but also the cost to adhere to environmental demands, such as those relating to long term stability (Ortiz, 2017). Further, methods that aid restoration include preventing wind and water erosion include physical- (capping on mine tailings), chemical- (use of chemical agents), and phytostabilization (revegetation). Phytostabilization provides a potential long term solution to the stabilization of mine dumps. Vegetation on mine dumps promotes more diverse, heterotrophic microbial communities, which further enhances plant growth and metal stabilization (Mendez *et al*., 2007; Chaulya *et al.*, 1999; Ortiz *et al.,* 2018). Revegetation with grasses, in particular, aids in waste dump stabilization as they have significant soil binding properties that prevent erosion (Chaulya *et al.,* 1999).

Plants commonly used for phytoremediation include metal hyperaccumulators and biomass producers (Moreno *et al.,* 2004). Plants that accumulate heavy metals have a slow growth rate and low biomass (Wang *et al*., 2017), which makes them less favoured when the aim is rapidly colonized mine dumps and tailings. Hyperaccumulation of metals is beneficial as it removes bioavailability and mobility of harmful contaminants from the environment and human food-chain (Cooke and Johnson, 2002; Wang *et al.,* 2017). The ultimate goal in mine dump rehabilitation and phytoremediation is to ensure self-sustenance of the plant community on the mine dumps. Over time, certain species might dominate the system as a result of their adaptation to the environmental conditions, although the presence of other less dominant species is still important to ensure the successful functioning of the community (Tilman *et al.,* 2001; Mendez and Maier, 2008). Typically, competitive exclusion and colonization from surrounding species pools determine species richness and species diversity in savannas (Savadogo, *et al.,* 2009).

Species with pre-adapted traits are typically selected for establishment on mine dumps (Lamoureux *et al.,* 2016; Nurtjahya and Franklin, 2017; Wang *et al.,* 2017). Such selections affect the species pool, making it quite dissimilar from that of nearby protected areas. It is critical to consider the functional traits of plant species used for the rehabilitation of mine landscapes to ensure long-term success (Evanylo *et al.,* 2005). Due to the unfavorable conditions of these areas, such as shallow and low nutrient soils, the plants need to have special traits in order to establish and persist in these circumstances (Evanylo *et al.,* 2005; Nurtjahya and Franklin, 2017). Often, seeds arriving from nearby species pools may not be able to colonise a mine dump, which is why seeding is essential to ensure faster reclamation and eventual recovery of the ecosystem (Nurtjahya and Franklin, 2017).

2.3.3 Impact of drought on mine dump rehabilitation

The challenge of rehabilitation and restoration of mine dumps increases in arid environments (Lamoureux *et al.,* 2016) due to the lack of sufficient water availability for plant establishment and growth (Lamoureux *et al.,* 2016). Additionally, mine tailings facilities in semi-arid to arid environments are especially exposed to wind and water erosion (Mendez and Maier, 2008). Water limitations combined with unfavourable soil chemistry and structure on mine dumps are expected to hamper establishment success. Plant survival under drought-stressed conditions requires the ability of xylem to tolerate these stressed conditions and still allow moisture uptake from dryer soils (Bhaskar and Ackerly, 2006). Soil metal content and toxicity (Evanylo *et al.,* 2005; Zhan and Sun, 2012; Kapusta and Sobczyk, 2015), topsoil depth, moisture-holding capacity (Sheoran *et al.,* 2010), soil texture, among other properties, are all factors that plants on mine dumps are exposed to and therefore need to show some tolerance to these conditions to establish and grow (Lamoureux *et al.,* 2016).

Plant traits that allow for more successful establishment on mine dump soils include being native (being adapted to the natural environmental conditions of the area) and having a tolerance to drought, salt, and high metal concentrations, and accumulate as little as possible metal within shoots (Munshower, 1994; Mendez and Maier, 2008). Extensive lateral root systems allow for better water uptake from near dry soils, and therefore plants growing on mine dumps in arid or semi-arid savanna systems might benefit from investing into lateral root growth (Lamoureux *et al*., 2016).

A study done by Zerbo *et al.* (2018) assessed the effects of climate change and land-use on West African savanna ecosystems. They stated that as a result of anthropogenic impact and climate change, plant species cover and composition in these savannas are experiencing drastic changes. Although Zerbo *et al.* (2016) determined that the combined effect of land-use and climate is what determines the distribution of herbaceous species, they focused on human activities such as grazing, agriculture, and harvesting that might not have the same effect as mining. In a study conducted at the Impala Platinum mining area in Rustenburg, South Africa, Van Der Walt *et al.* (2012) reported greater functionality in the rehabilitated mine dumps compared to the natural thornveld savanna areas, which was suggested to be a result of fertilization and slope design. Although alien species are generally unfavourable, alien species add to the functionality of rehabilitated mine dump systems (Van Der Walt *et al.,* 2012).

There is a gap in the savanna literature focusing on assessing and understanding the interaction effects of mining in combination with prolonged drought events. This highlights the need to fill the gap and determine what the interaction effects between drought and mining are.

2.3.4 Land-use effects on herbaceous communities at Palabora Copper

Two studies were conducted at the PC mining site before the prolonged drought event that followed (Smith, 2016; Van Staden, 2016). These studies were aimed at assessing land-use effects on the herbaceous vegetation in a Mopaneveld savanna. Van Staden (2016) and Smith (2016) identified the disturbance-tolerant species in the larger PC mining areas, which included the grasses *Aristida adscensionis, Cenchrus ciliaris, Digitaria eriantha, Enneapogon cenchroides, Schmidtia pappophoroides, Stipagrostis hirtigluma,* and *Urochloa mosambicensis*. These studies also suggested that the forbs *Kyphocarpa angustifolia, Ocimum americanum, Phyllanthus incurvus,* and *Tephrosia purpurea* are adapted to transformed habitats, such as communal lands and mine dumps. Characteristic forb species found on the mine dumps before the drought included *Indigastrum costatum, Tephrosia purpurea, Tephrosia rhodesica,* and *Sesbania bispinosa.*

Compared to protected areas, the mine dump species composition was very unique in terms of species assemblages (Van Staden, 2016), which can be attributed to the artificial seeding (Surmon, 2018b) and the complete transformation of natural vegetation (Sheoran *et al.,* 2010; Domingo & David, 2014). Species richness on mine dumps was low as a result of mining practices (Van Staden, 2016). High percentages of bare soil and plant density were also found on mine dumps (Van Staden, 2016). High plant density on the dumps was a result of restoration practices aimed at preventing erosion and soil stabilization (Van Staden, 2016). Low levels of evenness on mine dumps are attributed to seed selection aimed at rapid colonization (Van Staden, 2016).

The protected area in the study hosted the highest plant species diversity (Van Staden, 2016). Protected areas had higher levels of biomass and more perennial, non-weedy herbaceous vegetation. A larger number of alien species were associated with more anthropogenically disturbed areas, specifically the mine dumps. This might be beneficial as alien and weedy species may function as pioneer species, stabilizing the soils for colonization of other herbaceous species (Van Staden, 2016).

Life form is adequate in predicting the effects of different land-uses in the Mopaneveld savanna system. Therophytes are more readily found in disturbed soils, compared to other life forms (Van Staden, 2016). Species dispersed by wind and those with nitrogen-fixing abilities are also more associated with mine dumps (Smith, 2016; Van Staden, 2016). Less annual, weedy species were found in the protected area as a result of less anthropogenic activity. However, annual species are expected to prevail after drought events (Skarpe, 1992; Buitenwerf *et al*., 2011; Rutherford *et al*., 2012; Van Staden, 2016).

The study of Smith (2016) was particularly focused on the effect of different structural attributes of the mine dumps, which included a rock dump and a tailings dam. A greater herbaceous species diversity and richness, and better soil quality was found on the older levels of the eastern aspect of both the tailings dam and rock dump. However, for the rock dump, this was more evident on the slopes, and for the tailings dam, it was more evident on the terraces (Smith, 2016).

2.4 Summary

Mining and drought, both, have clear implications for biodiversity, which in turn affects ecosystem services. Ecosystem services are crucial for the effective management of disturbed mining sites. Therefore, drought exacerbates the effect of land degradation and transformation that follows a major disturbance. It is vital to understand the impact of anthropogenic disturbance on the environment to develop mitigation measures to counter the stressors that hamper vegetation establishment and recovery. This review highlights the importance to also study environmental factors, such as severe droughts, and the associated effects on savanna dynamics. Investigating the impact of natural and anthropogenic disturbance on vegetation, as primary producers, may indicate “bottom-up” cascading effects and lead the way in managing and maintaining biodiversity for the well-being of the ecosystem and future human generations.

CHAPTER 3

Study area

3.1 Locality

The study was undertaken in the Ba-Phalaborwa Municipality (23.9424° S, 31.1409° E) in the Limpopo Province of South Africa. Phalaborwa is situated approximately 500 km northeast of Johannesburg and is located on the border of the Kruger National Park (KNP) (23.9884° S, 31.5547° E) (Fig. 3.1). The specific study site in which plant surveys were conducted, was at the Palabora Copper (PC) mining site and the adjacent Cleveland Game Reserve (CGR), a privately-owned protected area that is managed by PC (Fig. 3.2).

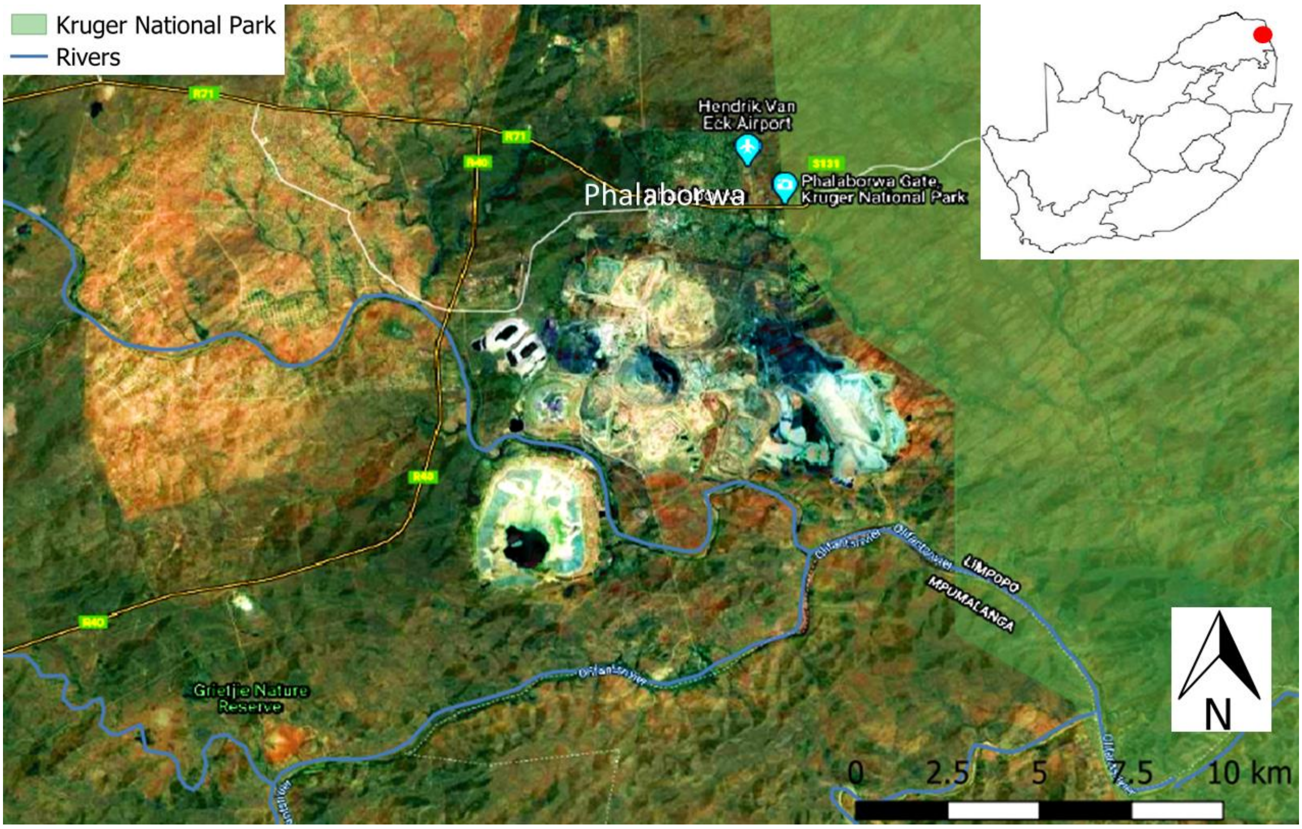

Figure 3.1: Location of major towns, river systems and the Kruger National Park relative to the study area, as well as an inset map of South Africa indicating the position of Phalaborwa. (Base map obtained from GoogleEarth, 19 February 2020; http://earth.google.com)

Figure 3.2: Aerial view of Palabora Copper indicating the three areas where herbaceous vegetation surveys were conducted (GoogleEarth, 19 February 2020; http://earth.google.com).

PC is situated less than 10 km from the confluence of the Ga-Selati and Olifants Rivers, with the Ga-Selati River flowing through the Phalaborwa area forming the southern boundary of PC. The mine is centred on the original site of Loolekop (the original copper ore outcrop) and is situated in close proximity to the KNP (4 km from Phalaborwa Gate).

PC owns a copper mine which was established in 1956 (Lennox, 2018). By 1964, PC was operating as a large-scale, open-pit mine, and is presently operating block-cave mining underground (Southwood and Cairncross, 2017). Smelting and refining of copper are also done on-site (De Villiers and Mkwelo, 2009). PC formed part of the Rio Tinto global mining group, before being sold to a corporate association that includes the South African Industrial Development Corporation and the Chinese Hesteel Group (Southwood and Cairncross, 2017). PC is the largest copper mine, and the only refined copper producer in South Africa (Moukodi, 2008; Lennox, 2018). By-products such as magnetite, vermiculite, nickel sulphate, sulphuric acid, and anode slimes produced during the mining process (Lennox, 2018) are dumped on various mine dumps at PC.

PC lies within the Phalaborwa-Timbavati Mopaneveld vegetation unit (SVmp 7) (Mucina and Rutherford, 2006). Mopaneveld is protected in multiple nature- and game reserves such as CGR and KNP. CGR is situated between PC and KNP and functions as a buffer zone between the two contrasting land-use types.

The land-use types in this study were defined according to the land-use classes outlined by Scholes and Biggs (2005). Scholes and Biggs (2005) used a Biodiversity Intactness Index (BII), which is a sensitive and realistic measure of biodiversity decline that takes a wide range of species and entire landscapes, as well as the causes of biodiversity decline, into account. BII therefore indicates the overall condition of biological diversity in a specified area.

CGR is considered a protected area since it is a private nature reserve exposed to minimal direct human impact, as opposed to PC which is classified as an urban land-use class in which ecological processes are severely disrupted through complete transformation (Scholes and Biggs, 2005). Protected areas and transformed landscapes constitute 8 % and 2 % of the southern African region respectively (Scholes and Biggs, 2005).

3.2 Climate

3.2.1 Rainfall

Mopaneveld savanna falls under a summer rainfall regime and receives the bulk of their rainfall in the summer months, particularly in January (midsummer). The Mopaneveld is associated with clear seasonal rainfall varying between wet summers and dry, frost-free winters (Mucina and Rutherford, 2006). The mean annual rainfall for Mopaneveld savanna systems ranges from 400 – 600 mm (Mucina and Rutherford, 2006) (Fig. 3.3).

Mopaneveld savannas are associated with and adapted to highly variable inter-annual rainfall, which is one of the main drivers of the dynamic herbaceous vegetation structure and composition (Rutherford, 1980; Gibson and Hulbert, 1987; Lauenroth and Sala, 1992; Illius and O'Connor, 1999; Swemmer *et al*., 2007; Buitenwerf *et al*., 2011). Historical rainfall data for Phalaborwa obtained from the South African Weather Services (SAWS; 1990-2007) and from a manual rain gauge at the SAEON Ndlovu Node (2008 - 2018) in the KNP reflect this inter-annual variability in rainfall cycles for the Mopaneveld ecosystem (Fig. 3.3).

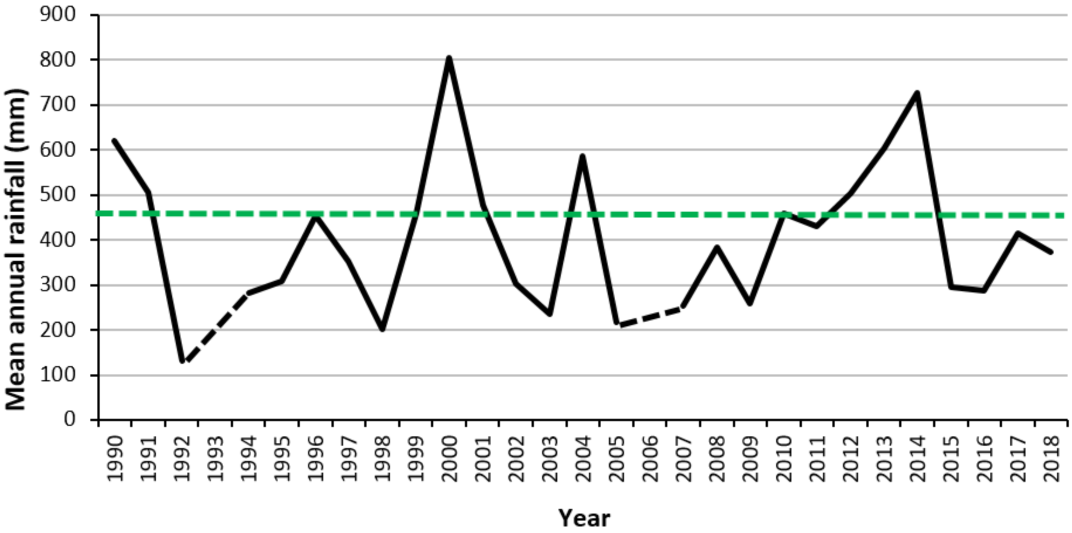

Figure 3.3: Annual rainfall for Phalaborwa including the most recent drought period from 2015-2016 (two-year average: 292 mm). Long-term mean annual rainfall for Phalaborwa is ~ 460 mm and indicated with the green dotted line. No data were obtained for 1993 and 2006.

The mean annual rainfall recorded in Phalaborwa during the year prior to pre-drought sampling (i.e. in 2012), was above average at 502 mm (Fig. 3.3). Mean annual rainfall for the following years (i.e. 2013 and 2014) was 603 mm and 728 mm for the area respectively. A below-average rainfall of 296 mm was recorded in 2015, whilst the rainfall for 2016 was 288 mm and therefore also well below the long-term average for the area. Botha (1998) suggested that the “below-normal” rainfall decile range 3 would indicate drought, and “very well below normal” rainfall decile range 1 would indicate severe drought. Average rainfall during the drought years 2015-2016 fell in the 2nd decile, which indicates drought to severe drought (Botha, 1998). Preceding rainfall years fell in the “normal” to “well above normal” rainfall decile ranges 7-10. Annual rainfall increased to 416 mm for 2017, which is closer to the long-term average rainfall for Phalaborwa (460 mm), and therefore considered the drought release year for the purpose of this study. Rainfall for 2017 fell in the “normal” decile range 5 (Botha, 1998). Vegetation surveys for this study were done in March 2018, after the drought release year.

3.2.2 Temperature

In 2015 and 2016 record high global temperatures were recorded. This was the result of a strong El Niño effect in combination with anthropogenically-induced global warming and increased atmospheric CO_2 levels (WMO, 2016). Adding to the severe effects of high temperatures was the extremely dry conditions (WMO, 2015), with annual rainfall recorded as the lowest in 112 years

(De Jager, 2016). Although the El Niño phase ended in May of 2016, subsequent effects thereof such as ongoing droughts remained evident (WMO, 2016).

During average climate conditions in Phalaborwa the mean minimum and maximum temperatures range between 5.7 °C and 38.4 °C (Mucina and Rutherford, 2006). These temperatures were exceeded during surveys done in 2014. For 2018 mean maximum temperatures reached 30 °C and mean minimum temperatures 20 °C. However, during the study period (i.e. March 2018) the mean maximum temperatures reached 31 °C, whilst minimum temperatures were considered very high, at 21 °C (World Weather Online, 2019).

3.3 Vegetation

3.3.1 Natural vegetation

The prevalent vegetation type of the study area is the Phalaborwa-Timbavati Mopaneveld (SVmp7) (Mucina and Rutherford, 2006) (Fig. 3.4). *Colophospermum mopane* trees dominate the naturally undulating plains of this Mopaneveld Savanna Bioregion, along with other tree and shrub species such as *Combretum apiculatum, Commiphora africana, Dichrostachys cinerea, Grewia bicolor, Grewia flavescens,* and *Terminalia sericea* (Siebert *et al*., 2003a; Mucina and Rutherford, 2006). In savanna systems, broad-leaved trees dominate on crests and microphyllous trees in the bottomlands, but although most broad-leaved trees, such as *C. apiculatum* and *T. sericea* become fewer lower down the catena, *C. mopane* (also broad-leaved) remains dominant throughout Mopaneveld, and could even increase towards the bottomlands (Mucina and Rutherford, 2006).

The dynamic herbaceous layer of Mopaneveld consists of common grasses such as *Andropogon gayanus, Aristida congesta, Brachiaria nigropedata, Digitaria eriantha, Eragrostis rigidior, Melinis repens, Panicum maximum, Perotis patens, Pogonarthria squarrosa, Schmidtia pappophoroides*, *Themeda triandra,* and *Tragus berteronianus (*Mucina and Rutherford, 2006). Common forbs include *Evolvulus alsinoides, Heliotropium steudneri, Ipomoea magnusiana, Kohautia virgata,* and *Syncolostemon elliottii* (Skarpe, 1992; Mucina and Rutherford, 2006). Other significant herbaceous species in Mopaneveld include grasses like *Eragrostis superba* and *Urochloa mosambicensis* and forbs like *Commelina benghalensis* (Siebert *et al*., 2003a). Forbs constitute an important part of the Mopaneveld herbaceous layer as they substantially contribute to the dynamic and diverse nature of the plant communities (Rutherford *et al*., 2012; Trollope *et al*., 2014). A complete list of herbaceous species sampled in this study, along with acronyms used for analyses is, presented in Appendix B, Table B1.

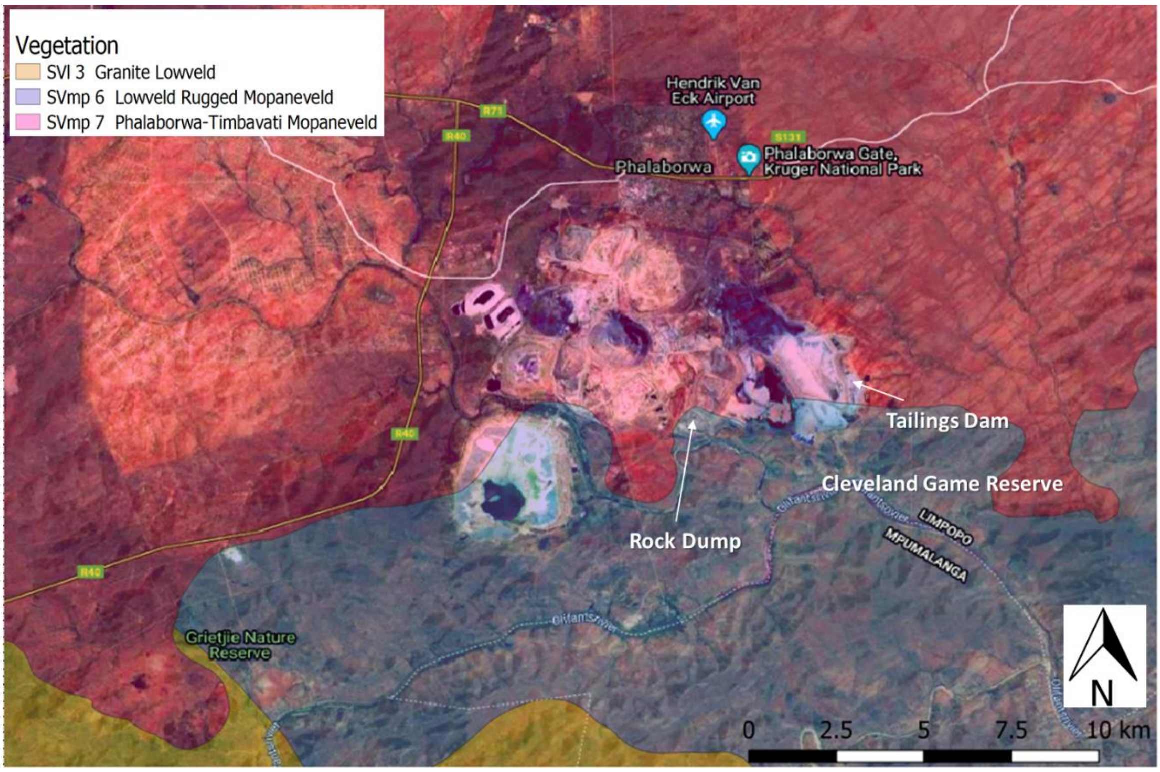

Figure 3.4: Vegetation types surrounding Phalaborwa, Limpopo. (Base map obtained from GoogleEarth, 19 February 2020; http://earth.google.com)

3.3.2 Revegetation

Rehabilitation of mined sites at PC is in accordance with the requirements of the ISO 14001 environmental management system (Palabora Mining Company, 2005). Physical, chemical and structural properties of mine dumps are unfavourable for natural colonization by plants and hinder or even prevent the germination of seeds (Yang *et al*., 1997). Despite these adverse conditions, rehabilitation efforts at PC reveal high success rates due to soil amelioration practices (Surmon, 2018b; Van Staden, 2016). This success rate is supported by parameters such as species composition, number of species, vigour, and basal cover (Surmon, 2018b). As a main advantage increased vegetation cover on mine dumps ensures decreased wind and water erosion, which allows for a self-sustaining and stable environment (Surmon, 2018b; Zhenqi *et al.,* 2012). It furthermore improves the aesthetics of the mine in light of eventual closure (Surmon, 2018b).

To improve vegetation establishment and productivity, waste dumps were capped with a 250 – 300 mm deep mixture of soil and vermiculite (fine waste produced at a nearby vermiculite production plant). This mixture is then fertilized and grass seed mixes containing *Anthephora pubescens*, *Cenchris cilliaris*, *Cynodon dactylon*, *Digitaria eriantha* and *Panicum maximum* were added (Surmon, 2018b). Additional historic records of seed mixtures and fertilizers used on the waste dumps at Palabora were poorly documented (Surmon, 2018b; Lennox, 2018). After germination grasses were monitored to document the success of self-sustaining cover on mine dump soil (Surmon, 2018b).

3.4 Geology

PC is underlain with the unique geology of the Phalaborwa Igneous Complex (PIC) (Fig.3.5), the only alkaline complex that is mined extensively for its ore minerals (Frick, 1986). Igneous rocks form when magma or lava from volcanic eruptions cool and solidify. These rocks are rich in minerals and elements with over 100 recorded up to date which include copper, phosphate, zirconium, iron, titanium and uranium (Frick, 1986; Southwood and Cairncross, 2017).

Loolekop hill was gradually removed during the mining process for copper and phosphate. Loolekop comprised of an outcrop of the inner and younger zone of the PIC, which is elongated from east to west and encompassed 1.4 km by 0.8 km (Southwood and Cairncross, 2017). Baddeleyite, a rare zirconium mineral of commercial importance, had also been uncovered during mining of Loolekop.

The PIC is a concentrically formed alkaline intrusion (Southwood and Cairncross, 2017). The surface dimensions of the PIC are roughly 6.5 km x 2.5 km (Southwood and Cairncross, 2017). It comprises of outer ultramafic rock, with banded and transgressive carbonatite rock at the very core of the PIC. Carbonatite and foskorite rocks host low-grade resources which are mined by PC. Copper is mined from the banded carbonatite intrusion. From the center outward, the cabonatite rocks are followed by foskorite and then pyroxene pegmatoids. The pegmatoids are an important source of vermiculite, which makes up one of the main mining operations at PC. The largest component of the PIC comprises of micaceous pyroxenite which is then surrounded by a sporadic occurrence of feldspathic pyroxenite, fenite, and syenite. The syenite is composed of fairly resistant feldspar minerals which are not easily weathered, giving rise to koppies protruding from the surrounding landscape (Frick, 1986). The entire PIC is surrounded by granite and gneiss gabbroic/doleritic intrusions. Multiple gabbro/doletrite dykes occur throughout the PIC (Gertenbach, 1983; Southwood and Cairncross, 2017).

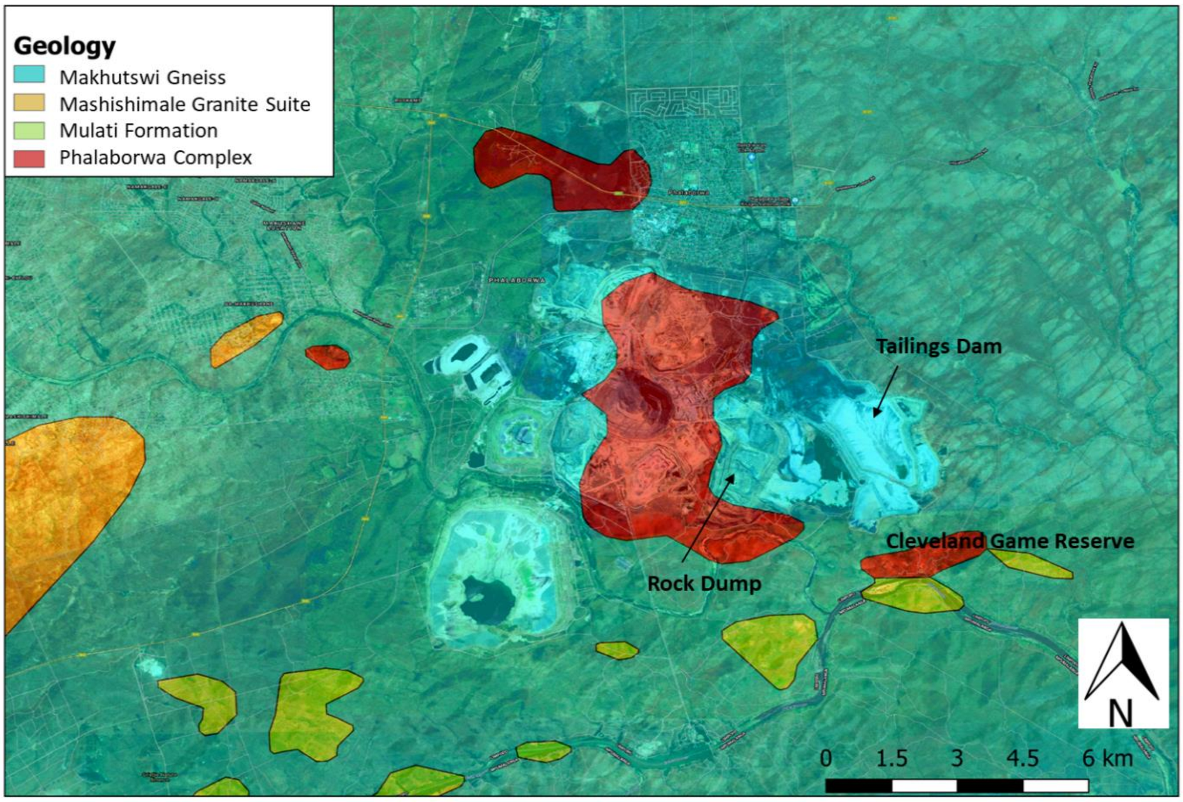

Figure 3.5: Underlying geology of Palabora Copper, Cleveland Game Reserve, and surrounding areas. (Base map obtained from GoogleEarth, 19 February 2020; http://earth.google.com)

3.5 Soil

The soils of the Phalaborwa-Timbavati Mopaneveld are underlain by quartz-feldspar rocks of Makhutswi Gneiss, with intrusions of Lekkersmaak Granite parent material (Fig. 3.5). Feldspar is a source of potassium (K) in the granite parent material, whilst phosphorus (P) is sourced from the mineral, apatite, abundant in both carbonatite and granite, enhancing P and K content of the soil at PC (Manning, 2010).

The hilltops are generally characterized by sandy soils, whilst soils toward the bottomlands generally contain high levels of dispersed clay (Mucina and Rutherford, 2006). The uplands of the Phalaborwa-Timbavati Mopaneveld typically consist of sandy soils such as Clovelly (Mucina and Rutherford, 2006). Clovelly consists of an orthic A horizon, yellow-brown apedal B horizon and lithic C horizon (Soil Classification Working Group, 2018). Soil with high clay content like Valsrivier and Sterkspruit occur in the bottomlands (Mucina and Rutherford, 2006) and is made up of an orthic A horizon and thick pedocutanic and prismacutanic B horizon respectively (Soil Classification Working Group, 2018).

The soil of PC is shallow and eutrophic, yet reasonably fertile with an acceptable amount of nutrients (Kendall, 2012). Sandy soils dominate both mine dumps at PC (Smith, 2016), and are alkaline with a pH of ~8 (Moukodi, 2008; Smith, 2016) due to the high concentrations of bicarbonate (HCO_3) (Merry, 2004). Macro-elements such as Ca, Mg, K and Na are the most important alkali metals for plant nutrition (Jakovljevic *et al*., 2003; Singh and Agrawal, 2008), and are abundant on the mine dumps due to the rock mineralogy (Smith, 2016). High concentrations of Mg result from the vermiculite capping, as vermiculite consists of a hydrous silicate of Mg (20-25%) (Schoeman, 1989; Malandrino *et al*., 2006). Vermiculite aids in stabilisation of mine dumps by retaining heavy metals and reduces their uptake by plants (Malandrino *et al*., 2006). Elevated concentrations of Cu and sulphides exist on the PC mine dumps, which is a direct result of copper extraction (Smith, 2016).

3.6 Land-use types

Rock dumps and mine tailings are two of the main waste categories at mines after the extraction of ores (Eriksson and Destouni, 1997). At PC, these waste dumps consist of terraces with multiple levels each of approximately 5 m in height. After the completion of a new level, the terraces are capped with topsoil and vermiculite waste material which promotes the establishment of vegetation, and reduces soil erosion and the spread of harmful mine waste products into the surrounding environment (Malandrino, 2011).

Despite capping of tailings with topsoil and artificial fertilization, waste disposal heaps are generally species-poor as re-establishment of natural vegetation is impeded by unfavourable conditions, especially in the soil (Yang *et al*., 1997; Mendez *et al.,* 2007). These conditions include high salinity, high metal concentrations, poor nutrient content and low water availability, lack of organic matter, and harsh microclimatic conditions (Wong *et al.,* 1998; Mendez *et al.,* 2007; Mendez and Maier, 2008; Zhenqi *et al.,* 2012; Shooner *et al*., 2015). Establishment of vegetation is further impeded by other mine-related factors such as pollution (Mapaure *et al.,* 2011; Zhao *et al.,* 2015).

In the Mopaneveld savanna, mining-related factors that impede vegetation establishment and growth is additionally exacerbated by extreme temperatures and reduced water availability that is consistent with semi-arid systems (Mendez and Maier, 2008). Soil conditions on mine dumps therefore require the careful selection of tolerant and adaptable plants for re-vegetation (Mendez and Maier, 2008).

3.6.1 Tailings dam

The tailings dam (TD) at PC is situated roughly 5.5 km east from the open pit and covers approximately 395 ha (Smith, 2016). Tailings are fine waste material (<0.1 mm), produced and removed when the copper ore is processed (Eriksson and Destouni, 1997; Cooke and Johnson, 2002; Rashed, 2010; Hansen *et al.,* 2013). The fine gangue is mixed with water forming a slurry (Khorasanipour *et al.,* 2011) which is then discarded on top of the TD.

The TD consists of multiple levels of which four levels were surveyed for the purpose of this study. Level 1 is the oldest level (35 years), followed by level 2 (33 years), level 3 (27 years) and level 4 (23 years). Chemical and physical properties of the soil at the TD differ across these levels. High concentrations of micro-elements (Fe, Mn, Cu, Zn, and B), organic carbon, increased alkalinity, and low clay contents are found on the oldest level of the TD, largely as a result of leaching (Smith, 2016). However, the highest concentration of nutrients on the TD is found on the youngest level, likely due to chemical enrichments on the newest tailings (Smith, 2016).

Tailings typically lack vegetation cover and soil structure before being rehabilitated (Krzaklewski and Pietrzykowski, 2002). They are unstable and susceptible to wind and water erosion, which leads to pollution and contamination of surrounding environments (González and González-Chávez, 2006; Mendez and Maier, 2008; De Villiers and Mkwelo, 2009).

3.6.2 Rock dump

The rock dump (RD) at PC is situated ~3 km east from the open pit. It covers an area of approximately 290 ha with a height of 148 – 163 m (Smith, 2016). It consists of heterogeneous waste rock material that was removed to expose the copper ore body. It also contains vermiculite and magnetite waste particles and other discarded materials such as rubber from old tyres (Van Dyk, 2018). Waste rock particles can range from fine sand to large rocks (Eriksson and Destouni, 1997). These particles are generally low-grade ores and were disposed of (Khorasanipour *et al.,* 2011).

Similar to the TD, the RD comprises of levels representing different ages. Three of the four ages were included in the study, namely level 1, the oldest, (~45 years old) followed by level 2 and 3 (established 35 and 31 years ago respectively). The highest level (i.e. the most recently added level) is radio-active and was not included in the study. Chemical and physical attributes of the RD soils also varied across post-rehabilitation age levels. The highest concentrations of all attributes occurred on the oldest levels of the RD (Smith, 2016). However, the highest concentration of nutrients was not found on the youngest level, as was the case on the TD, but rather also on the oldest post-rehabilitation level (Smith, 2016).

3.6.3 Cleveland Game Reserve

CGR is a protected Mopaneveld area bordering the Kruger National Park (KNP), PC and Hans Merensky Golf Estate. The landscape is naturally undulating with numerous koppies. CGR has a typical homogenous Mopaneveld vegetation structure which is dominated by *C. mopane (*Siebert *et al*., 2003a; Mucina and Rutherford, 2006) and is comparatively undisturbed by anthropogenic activity in terms of soil, vegetation and mammal diversity (Davis *et al.,* 2014). The main disturbances include those with which the Mopaneveld evolved, such as herbivory, fire, nutrient availability and rainfall variability (Frost *et al*., 1986; Scholes, 1990; Skarpe, 1992; Sankaran *et al*., 2004; Bond, 2005).

Due to previously ineffective barriers between the KNP and CGR, and the absence of barriers between CGR and PC, wildlife can roam freely between these areas (Davis *et al.,* 2014). Large game observations made at CGR and on mine dumps during the current study, as well as previous studies (Smith, 2016; Van Staden, 2016; Surmon, 2018b), included Cape buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*), greater kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus*), hippopotamus (*Hippopotamus amphibious*), plains zebra (*Equus quagga*), and giraffe (*Giraffa camelopardalis*). Other sightings include impala (*Aepyceros melampus*) and warthog (*Phacochoerus africanus*), as well as predators/scavengers such as lion (*Panthera leo*), hyena (*Crocuta crocuta*), caracals (*Caracal caracal*), African wild dog (*Lycaon pictus*) and black-backed jackal (*Canis mesomelas*) (Smith, 2016; Van Staden, 2016; Surmon, 2018a).

CHAPTER 4

Methodology

4.1 General

Extensive floristic and environmental field surveys were conducted in accordance with previous studies on the same site (Smith, 2016; Van Staden, 2016)., which followed the guidelines provided by the Ndlovu Node of the South African Environmental Observation Network (SAEON).

4.2 Experimental- and sampling design

Previous surveys at PC and CGR were conducted in 2014. The herbaceous community was resampled in March 2018 after the drought release. Drought release surveys were conducted on two mine dumps at PC (tailings dam = TD, rock dump = RD), and at CGR, a protected area functioning as a buffer zone between PC and KNP (from here on TD, RD and CGR will be collectively termed as “land-use types”). Due to minimal disturbance of Mopaneveld vegetation dynamics, CGR represents the benchmark site for this study.

A random, paired sampling design was followed for the placement of plots at all land-use types (Fig. 4.1). The pairs were placed so that one plot was on a slope and the other on a terrace for each of the different levels of waste material on mine dumps. This ensured that topography and post-rehabilitation ages could be taken into account. Since the 2014 studies, additional dumping covered sites on the southern slope of TD, thus limiting sampling to the eastern and western aspects of the mine dumps. CGR sites were placed at least 100 m away from the mine dumps and roads, and paired plots were located 50 m apart. Due to the slightly undulating topography of natural Mopaneveld (Mucina and Rutherford, 2006), CGR was not stratified using slope, topography and aspect.

The 1 x 1m quadrat method was used to sample herbaceous vegetation of land-use types. Plot positions were recorded with a Geographical Positioning System (GPS) during previous studies (Smith, 2016). These plot locations were revisited and drought-release sampling was done at the previously sampled sites. Plots were not sampled at the exact locations of the original plots, as the original plots were not permanently marked, and because biomass was harvested from them, which may have led to skewed results.

Plots were located on slopes and terraces (i.e. 10 on each), covering eastern and western aspects for each mining site respectively (i.e. RD and TD). The plots were placed on levels in such a way as to have three or more plots covering at least three rehabilitation ages. Four levels were sampled on TD and three on RD. Therefore, each new level consisted of a younger suit of planted vegetation (a younger rehabilitation age) (Fig. 4.1). A more detailed description of rehabilitation ages can be found in section 3.6 in chapter 3.

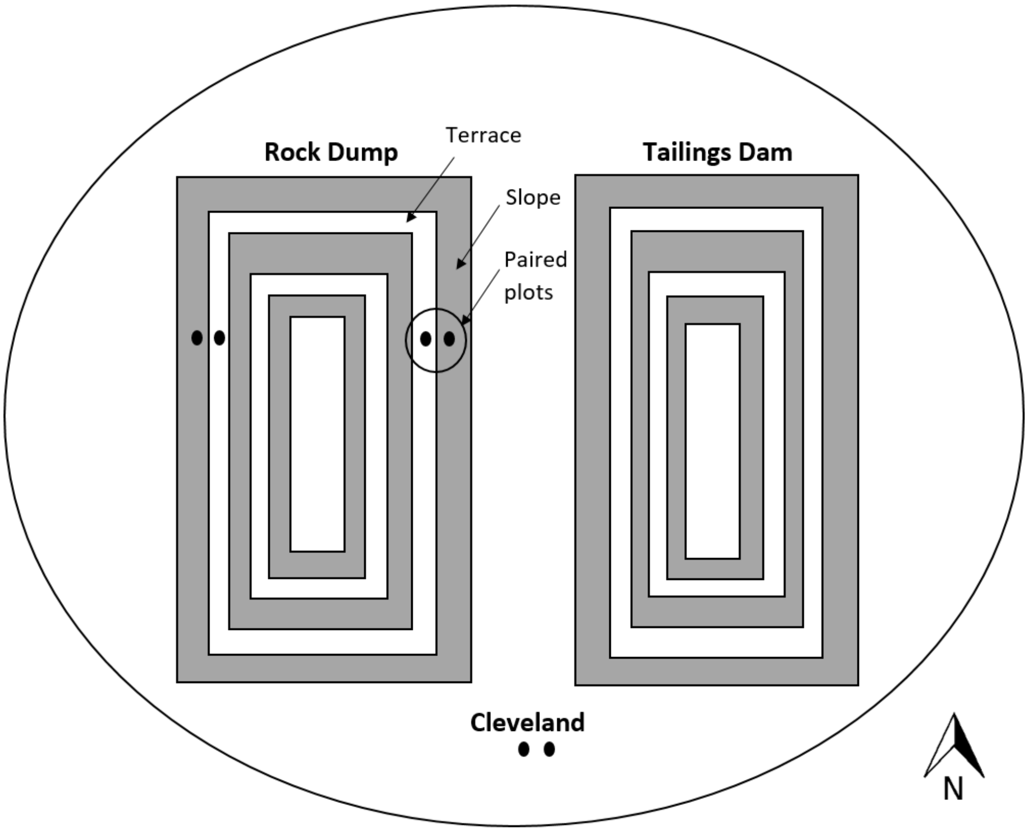

Figure 4.1: Placement of plots in 2014 and repeated in 2018 on terraces and slopes of levels at each of the sites (Rock Dump, Tailings Dam, and Cleveland Game Reserve).

The following data were recorded at each plot:

- Forbs and grasses rooted inside each 1 m^2 plot were identified up to species level;
- All individuals per species were counted. Counts were separated for dead individuals and seedlings;
- Cover estimates: percentage of grass, forbs, debris, bare soil and woodies were estimated;
- Measurements: (i) grass tufts (> 1 cm) and (ii) tallest (cm) individual within the plot;
- Disturbance and animal activity within a plot or its direct surroundings were noted;
- Dry weight, above ground phytomass sampling: A 50 cm x 50 cm quadrat was placed in the centre of the 1 x 1 m plot and all live and rooted individuals were cut with secateurs and placed into brown paper bags. These were oven dried at 40 °C for three days. Contents of the paper bag were sorted into forbs and grasses and weighed separately. Weights were converted to kg/ha.

(Refer to Appendix C, Table C1 for an example datasheet)

4.3 Plant identification

Herbaceous specimens that could not be identified in the field, were tagged using jewellery tags and placed in a plant press. Jewellery tags contained the date of collection, a temporary specimen name, transect and plot numbers. These details were also recorded on the field data sheets (Appendix C, Table C1) corresponding with the plot under observation. Voucher specimens are housed at the AP Goossens herbarium (PUC) of the North-West University, Potchefstroom Campus and additional field guides (Van Wyk and Malan, 1998; Van Wyk, 2000; Henderson, 2001; Smith and Crouch, 2009; Bromilow, 2010; Kirby, 2013; Van Oudtshoorn, 2015) were used to identify unknown specimens collected from the study area.

4.4 Functional traits

Functional traits related to drought- and stress tolerance were assigned to plant species using field guides (Van Wyk and Malan, 1998; Van Wyk, 2000; Henderson, 2001; Smith and Crouch, 2009; Bromilow, 2010; Kirby, 2013; Van Oudtshoorn, 2015), floras (Germishuizen and Meyer, 2003, JSTOR, 2018; KEW Royal Botanical Gardens, 2018), and reputable websites (Kyffhäuser, 2018; Biodiversity Explorer, 2018; SANBI, 2018). Motivation for trait selection in this study are summarised in Table 4.1.

Table 4.1: Functional traits included in this study.

Trait	Category and numerical score	Motivation for inclusion	Data sources and references
Life form	1 = Forb 2 = Grass	Forbs and grasses do not respond equally to stressed conditions, such as drought. Forb species typically increase in dominance in response to drought.	Lavorel *et al*. (1997); O'Connor (1999); Germishuizen and Meyer (2003); Rutherford *et al* (2012); O'Connor (2015); Van Coller *et al*. (2018)
Growth form	1 = Tussock 2 = Prostrate 3 = Climber 4 = Erect 5 = Rosette	Depicts path and extent of growth from main shoot. Associated with plant strategies, photosynthetic adaptations, climate change, drought, land-use, and herbivory (height and foliage position). Low-growing prostrate or rosette forb growth forms are favoured in disturbed environments. Tussock grasses are less effective at colonising bare soils caused by disturbance, compared to stoloniferous grasses.	O'Connor (1995); Debussche *et al.* (1996); Lavorel *et al.* (1997); Cornelissen *et al.* (2003); Germishuizen and Meyer (2003); De Bello *et al.* (2005); Peco *et al.* (2005); Castro *et al*. (2010); Pérez-Harguindeguy *et al*. (2013); Van Oudtshoorn (2015)
Leaf area (mm^2)	1 = 1-100	Response to climatic variation, geology, drought, nutrient deficiency, and disturbance.	Skarpe (1996); Fonseca *et al*. (2000); Ackerly (2003, 2004); Vogel

	2 = 101-1000 3 = 1001+	Determines energy efficiency and water balance within leaves. Small leaves have a direct hydraulic benefit and transfer heat more effectively. Therefore, small leaves are more abundant in arid, exposed habitats.	(2009); Yates *et al.,* (2010); Chillo *et al.* (2011); Scoffoni *et al*. (2011); Pérez-Harguindeguy *et al*. (2013)
Life span	1 = Annual 2 = Perennial	Strongly associated with land-use and climate variability. Also associated with temperature, nutrient availability and disturbance. Annual grasses (and forbs) dominate following a disturbance event such as drought, as they have drought-adapted traits and function as pioneer species in early successional stages.	Lavorel *et al*. (1997); Wilcox (1998); Stanton *et al*. (2000); Cornelissen *et al*. (2003); Heschel and Riginos (2005); Sherrard and Maherali (2006); Kotschy (2013); Pérez-Harguindeguy *et al*. (2013); O’Connor (2015)
Palatability	1 = Low 2 = Moderate 3 = High	Herbivore preference. Unpalatable grasses and forbs increase in abundance following drought.	Van Wyk and Malan (1998); Walker *et al.* (1999); Van Wyk (2000); Manning (2009); Van der Walt (2009); Kirby (2013); Pérez-Harguindeguy *et al*. (2013); Siebert

			and Scogings (2015); Van Coller *et al.* (2015); Van Oudtshoorn (2015);
Spinescence	1 = Present 2 = Absent	Anti-herbivore defence; also sometimes involved in reducing drought and heat stress. In African savannas, spines mainly evolved as an anti-herbivore defence strategy.	Alves-Silva and Del-Claro (2016); Cornelissen *et al*. (2003); Milton (1991); Pérez-Harguindeguy *et al*. (2013); Scholes *et al*. (2003); Chillo *et al.* (2011)
Vegetative growth	1 = Absent 2 = Above-ground 3 = Below-ground 4 = Above- and below-ground	Resprouting ability and clonal growth. Tolerance to- and recovery from disturbance. Growth of new vegetative parts from remaining above- or below-ground propagules (bud banks, storage organs or ramets - clonal). Below-ground storage organs are important for resprouting in herbaceous vegetation. Lateral spread (clonality) aids in dispersal under poor conditions, especially important in grasses.	Hutchings and Mogie (1990); Weiher *et al*. (1999); Bellingham and Sparrow (2000); Bond and Midgley (2001); Vesk and Westoby (2004); Klimesova and Klimes (2007); Clark *et al*. (2012); Kotschy (2013); Pérez-Harguindeguy *et al*. (2013); Zeppel *et al*. (2015); Sankaran (2019)
Nitrogen-fixing	1 = Present 2 = Absent	Symbiosis with nitrogen fixing microbes for efficient nitrogen (N_2) uptake. Nutrient cycling, and plant growth. Semi-arid systems	Cornelissen *et al*. (2003); Naisbitt *et al*. (1992); Sprent *et al*. (2013); Van Oudtshoorn (2015); Chillo *et al.*

		and mine dumps have low soil moisture, which favours N_2-fixing species and allows them to outcompete other plant species.	(2011); Monks *et al*., (2012); Pérez-Harguindeguy *et al*. (2013); Botha *et al*. (2017)
Dispersal mode	1 = Allochory 2 = Anemochory 3 = Autochory 4 = Ballochory 5 = Hydrochory 6 = Endozoochory 7 = Ectozoochory	Plant range size, and colonization ability. Recolonisation of disturbed areas depend on the dispersal ability of species in the surrounding source populations. Long-distance dispersal mechanisms are typically favoured in disturbed areas. Limited dispersal affects species diversity and resilience of ecosystems.	Bakker *et al*. (1996); Chillo *et al.* (2011); Cornelissen *et al*. (2003); Pérez-Harguindeguy *et al*. (2013); Ilunga wa Ilunga *et al*. (2015)
Shade tolerance	1 = Sun (Shade intolerant) 2 = Shade (Shade tolerant)	Affects niche partitioning, competitiveness and growth rate. Shade tolerance is associated with efficient carbon gain under low light and other stresses that come with shaded environments. Plant species that are adapted to high sun exposure are more resistant to limited shade in exposed area such as mine dumps	Baker (1967); Valladares and Niinemets, 2008; Pons and Poorter, 2014

Additional information pertaining to functional trait selection

According to Cornelissen *et al.* (2003), 23 categories exist for growth form, of which 15 of these categories apply to herbaceous vegetation. However, this study only focussed on the growth forms applicable to the study area (Table 4.1). Where multiple growth forms exist for a single species in the literature, the most common growth form associated with the species in the study area were considered to assign a single growth per species.

Leaf area (mm^2) is commonly used as a proxy for leaf size (Pérez-Harguindeguy *et al*., 2013). Therefore, leaf areas were measured and averaged for each species, where after each species was placed in one of three categories.

Three categories exist for life span, namely annual, biennial and perennial (Pérez-Harguindeguy *et al*., 2013). Annual species die after producing seeds during the first growth season; biennial species grow vegetatively during the first growth season, produce flowers and fruit during the second growth season, and die thereafter; perennial species survive for three or more growth seasons (Pérez-Harguindeguy *et al*., 2013).

The presence of spines and thorns were recorded, although species with spines exclusively on fruit/flower bracts were not considered as 'spinescent' in this study, largely because of the short fruiting/flowering period during which these species will bear spines.

Above-ground and below-ground vegetative growth by means of resprouting and clonality (Marshall, 1990*;* Kotschy, 2013) was considered in this study. Above-ground and below-ground resprouting species is considered the most fundamental trait conferring disturbance tolerance (Noble and Slatyer 1980). Clonal species, as opposed to resprouters, form new ramets by means of stolons or rhizomes (Cornelissen *et al.,* 2003). Above-ground resprouting/clonal species included those with stolons or bulbils. Below-ground resprouting/clonal species included rhizomes, tubers, bulbs, corms, among others (Cornelissen *et al.,* 2003). Bulbs and tubers are also important plant organs for storage of nutrients and water (Cornelissen *et al.,* 2003), that may provide the plant with essential nutrients that are lacking during unfavourable environmental conditions. Clonality and resprouting ability provides competitive vigour and efficient resource acquisition, and bud-bank formation (Pérez-Harguindeguy *et al*., 2013), which is especially useful under drought conditions.

Some plant species have symbiotic relationships with nitrogen-fixing bacteria or mycorrhizal fungi (Pérez-Harguindeguy *et al*., 2013). These nitrogen-fixing species typically have nodules on stems (*Sesbania* spp.) and roots (Cornelissen *et al.,* 2003). Nitrogen availability affects plant productivity and plant community assemblages (Tan *et al*., 2003). In addition to fertilizer, nitrogen-fixing plant species are also important for nitrogen input on mine dumps under restoration (Zhan and Sun, 2012).

Dispersal mode (Table 4.2) depicts the distance and route that propagules can travel. Some species may, however, be dispersed accidentally via a dispersal mode they are not specifically adapted for (Pérez-Harguindeguy *et al*., 2013).

Table 4.2: Descriptions of dispersal modes pertaining to this study.

Dispersal mode	Description	References
Allochory	Includes multiple dispersal modes (excluding autochory)	
Autochory	Self-dispersal; no specialized dispersal structures	Frank and Klotz, 1990; Zerbo *et al.*, 2017.
Anemochory	Wind dispersal; “flat or elongated appendages”	Frank and Klotz, 1990; Zerbo *et al.*, 2017.
Ballochory	Explosion of the fruit expels the seeds (ballistic dispersal)	Vittoz and Engler, 2007.
Hydrochory	Water dispersal	Frank and Klotz, 1990.
Endozoochory	“Dispersal via an animal’s digestive system”; Accidental ingestion	Frank and Klotz, 1990; Castro *et al*., 2010.
Ectozoochory	External dispersal by animals; Adhesive structures; Elongated appendages	Frank and Klotz, 1990; Castro *et al.,* 2010; Zerbo *et al*., 2017.

4.5 Data analyses

4.5.1 Species composition analyses

The data analysis approach discussed here is of relevance to Chapter 5.

Species occurrence data were compiled into species abundance per plot matrices (species abundance-plot). Forb and grass species were split into two different matrices and analysed to assess response differences between the two life forms. The composition of herbaceous species across land-use types (i.e. beta diversity; Kent, 2012) during pre-drought and drought release sampling, were investigated using Non-Metric Multi-Dimensional Scaling (NMDS) analyses in PRIMER 6 Software (Clarke and Gorley, 2006). For NMDS analyses, species abundance data were fourth root transformed to reduce significant differences in the total abundances of species as well as to balance the contribution of highly abundant and rare species (Kent, 2012).

NMDS results presents two-dimensional plots, whereby similar species or sites are clustered closer together and dissimilar species or sites further apart (Rabinowitz, 1975). Stress values indicate the fidelity of the plot. A stress value of (i) < 0.05 is considered an excellent ordination with zero chance of being misinterpreted, (ii) < 0.1 is considered a good ordination with a low chance of misinterpretation, (iii) < 0.2 is considered a good two-dimensional illustration, and finally (iv) > 0.2 indicated a poor depiction and should be interpreted with care (Clarke, 1993; Clarke and Warwick, 2001).

Bray-Curtis similarity distance measure was applied followed by Permutational Multivariate Analysis of Variance (PERMANOVA; permutation = 999; type III sums of squares) (Buitenwerf *et al*., 2011; Scogings *et al*., 2012; Hanke *et al.,* 2014; Campos *et al.,* 2018). PERMANOVA is an adequate tool to test for significant variation in floristic data, used in cases where data do not conform to assumptions of normality, which is common in plant community analyses (Buitenwerf *et al*., 2011; Scogings *et al*., 2012; Hanke *et al.,* 2014; Campos *et al.,* 2018). To test whether significant differences occurred between areas, pair-wise tests were conducted, along with Monte Carlo tests to determine the likelihood that stress values for NMDS ordinations were a result of chance (Kent, 2012).

The final analysis applied to species-abundance data was Similarity Percentage Analysis (SIMPER). SIMPER was used to determine which species were explaining the similarities observed in community assemblages across the protected and transformed sites for pre-drought and drought release communities (Clarke and Gorley, 2006). SIMPER analyses were conducted in PAST (Hammer *et al*., 2001).

Indicator Value (IndVal) analyses (Dufrêne and Legendre, 1997) were applied to the floristic data set and analysed in R version 3.5.1 (R Development Core Team, 2018). Indicator species were identified for each of the groupings obtained from ordinations. The robustness of associations between species at the different sites as well as in the two different years were also revealed. IndVal combines a degree of specificity and fidelity for site groups (Dufrêne and Legendre 1997; De Cáceres *et al.,* 2016). IndVal presents indicator values in percentage (%) for each species. This was performed using R package ‘indicspecies’ that corrects for groups of different sizes (De Cáceres and Jansen 2016) and the ‘multipatt’ function.

4.5.2 Species diversity analyses

The data analysis approach discussed here is of relevance to Chapter 5.

A species-plot matrix was compiled to create species accumulation curves for each land-use type before drought and during drought release, using R version 3.5.1 (R Development Core Team, 2018). Species accumulation curves indicate sufficient sampling effort, as the number of species increases with increasing sampling, to the point where no additional species are recorded and the curve reaches a plateau. The rarefaction method estimates the number of species that occur in a random sample of individuals (Sanders, 1968). If the species accumulation curve reaches a plateau, rarefaction allows for the extrapolation of the curve to determine complete species richness (Krebs, 2014). Although 40 1 m^2 plots were sampled at all land-use types during the drought release, only 20 plots were recorded before the drought. Therefore, the rarefaction analysis only illustrates 20 plots across all land-use types and rainfall years. Visual assessments could subsequently be made regarding species richness differences at each land-use type cross rainfall years.

Species abundance-plot matrices, with separate matrices for forbs and grasses were used to analyse diversity indices (Table 4.3) in PRIMER 6 software (Clarke and Gorley, 2006). Histograms, Q-Q plots and Kolmogorov-Smirnov and Shapiro-Wilk normality tests were used to test for normality of the datasets. Data that were not normal were log-transformed ($\log_{10}$ (x+1); retains zero values in the data). This was done for species richness and abundance data plotted for protected and transformed areas as well as pre-drought and drought release years.

Two-way ANOVA type Hierarchical Linear Modelling (HLM) was applied to richness, abundance and diversity index data to determine investigate interaction effects on rainfall year (pre-drought and drought release) and land-use type (protected and transformed areas) using R version 3.5.1 (R Development Core Team, 2018). Significance was determined at the standard level of $p < 0.05$ (Manderscheid, 1965). Bonferroni *post-hoc* tests were applied for each pairwise comparison of diversity indices to reveal the significance of differences between land-use types and rainfall years, for both life forms.

Table 4.3: Diversity indices applied in this study.

Index	Definition and purpose	Calculation
Total species (S)	Indicates total species richness.	Mean number of species per plot (m^2).
Margalef's species richness (d)	Indicates species richness. Sensitive to sample size (Gamito, 2010; Magurran, 2004).	$$d = \frac{S-1}{\ln N}$$ S represents the number of species, N is the total number of individuals in the sample and ln = log base$_n$.
Shannon-Wiener diversity (H')	Indicates species diversity. Assumes random sampling from infinitely large population and the samples include all species present in that community (Kent, 2012). Widely used in biological sciences (Kent, 2012).	$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$ S represents the number of species, p_i is the abundance of the i^{th} species and ln = log base$_{n.}$
Pielou's evenness (J')	Indicates distribution of individuals over species (Crowder *et al*., 2012). Depends on sample size and inclusion/exclusion of rare species (Crowder *et al*., 2012).	$$J' = \frac{H'}{\ln(S)}$$ S represents the number of species in the sample, *H'* represents the Shannon-Wiener diversity index.
	Indicates species evenness. Best when common species are more emphasized than rare species (Krebs, 2014). Best overall evenness	

Smith and Wilson's evenness (E_{var})	index for most datasets (Krebs, 2014). Calculates variance in abundance over species (Smith and Wilson, 1996). Independent of species richness, and sensitive to abundance of rare species (Von Csefalvay, 2015). $E_{var} = 1 - 2/\pi \arctan \left\{ \sum_{s=1}^{S} \left(\ln(x_s) - \sum_{t=1}^{S} \ln(x_t)/S \right)^2 \Big/ S \right\}$ S represents the number of species in the sample, x_s is the abundance of the s^{th} species and ln = log base$_{n}$.

4.5.3 Functional trait composition analyses

The data analyses approach discussed here is of relevance to Chapter 6.

Data were compiled into matrices of functional trait abundance per plot (trait-plot) with the MMult function in Microsoft Excel (2013). A functional trait-plot matrix resulted from multiplying a presence/absence trait-species matrix with a species-abundance matrix. The functional-trait-plot matrix was then used for NMDS ordinations to present trait assemblages. Similar to species composition analyses, the forb and grass species were split into two different matrices and analysed accordingly. The composition of plant functional traits across land-use types and pre-drought and drought release years, were investigated using NMDS analyses in PRIMER 6 Software (Clarke and Gorley, 2006). Functional trait data were fourth root transformed prior to NMDS analyses to reduce significant differences in the total abundances of functional traits as well as to balance the contribution of highly abundant and rare traits (Kent, 2012).

Bray-Curtis similarity distance measure was applied followed by PERMANOVA (permutation = 999; type III sums of squares) to test for significant variation in plant functional trait data (Buitenwerf *et al*., 2011; Scogings *et al*., 2012; Hanke *et al.,* 2014; Campos *et al.,* 2018). Stress values were also attributed to the plant functional trait ordinations (see section 4.4.1). To test between which areas significant differences occurred, pair-wise tests were conducted, along with Monte Carlo tests to determine the likelihood that stress values for NMDS ordinations were resulting from chance (Kent, 2012).

4.5.4 Plant functional type (PFT) identification

The data analyses approach discussed here is of relevance to Chapter 6.

The trait dataset was separated into forbs and grasses for analyses to compare differences between the two life forms across sites as well as pre-drought and drought release years. This was done as life form has been shown to have a strong influence on plant functional trait separation (Lavorel *et al*., 1997). Thereafter, a matrix was compiled with species as rows and traits as columns for each life form. Each trait was given a numerical score (Table 2). The dataset was further separated into the four main plant groups (annual grasses, perennial grasses, annual forbs, and perennial forbs), allowing for detailed analyses within these groups.

Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clusters were then created using hierarchical agglomerative clustering analyses and the Modified Gower distance measure in PRIMER 6 software (Clarke and Gorley, 2006; Kent, 2012). UPGMA analyses group species according to the allocated numerical scores (Botha, 2017). Gower's modified similarity coefficient is suitable for binary and categorical mixed data, therefore appropriate for this study. Traits that did not present significance in grouping of species were left out in the following repetitions of the UPGMA cluster analyses (McIntyre *et al.,* 1999; Klem, 2018). This allowed strong clustering results for the final UPGMA cluster diagrams. UPGMA clusters delivered 16 PFT's in total. Each PFT consisted of between 2 and 19 species. Frequencies of PFT's were then obtained to construct circle diagrams for visual representation of percentage contribution of PFT's to the respective rainfall years at each land-use type.

PFT's obtained from UPGMA analyses were used to construct a functional type-plot matrix using the MMult function in Microsoft Excel as was done to construct a trait-plot matrix. A treatment-plot matrix was also created using the three land-uses (RD, TD, and CGR) as treatments. This was done for pre-drought data, as well as data obtained after drought release. Associations between PFT's and land-use types, and community shifts before the drought and after drought release were then explored using Canoco for Windows version 5 (Ter Braak and Šmilauer, 2002). This was done using Principal Component Analyses (PCA) to provide a breakdown of community variation (Ter Braak and Šmilauer, 2002) in associations between PFT's and rainfall years and land-use types. Eigenvalues were obtained with PCA's and are directly related to the strength of contribution that a component adds to the total variation in the data (Kent and Coker, 1994).

CHAPTER 5

Drought responses of herbaceous communities

5.1 Introduction

Transformation and exploitation of ecosystems leads to severe reductions in biodiversity (Butchart *et al*., 2010; Noonan-Mooney and Gibb, 2014). Biodiversity loss due to the mining industry sets off a cyclic cascade whereby the health of ecosystems is affected, which in turn, influences the ecosystem services that they provide (Hooper *et al*., 2005; Butchart *et al*., 2010; Zhao *et al.,* 2016).

The detrimental consequences of mining on the environment have resulted in the implementation of restoration and rehabilitation practices as specified in detailed management and closure plans (Parotta *et al*., 1997; Sánchez and Neri, 2014). One of the primary objectives for restoration practices involves the re-establishment of vegetation on mining areas that are no longer in use (Parotta *et al*., 1997). Such vegetation types would ideally include species that are tolerant to nutrient-poor and dry soil conditions in unpredictable environments (Evanylo *et al*., 2005; Zhan and Sun, 2014; Nurtjahya and Franklin, 2017). Therefore, determining which species are tolerant to the effects of mining may promote better understanding of ecosystem function, and the maintenance thereof, in transformed areas.

The herbaceous vegetation layer of the Mopaneveld savanna is exposed, not only to mining practices occurring at Palabora Copper (PC), but also potential exacerbation of the mining impact through rainfall variability. The Mopaneveld in the Limpopo area recently suffered severe, prolonged drought (Swemmer, 2016). Drought in the Mopaneveld typically results in the loss of perennial grasses and post-drought dominance of in forbs and annual grasses (Jordaan, 2004; O’Connor, 2015).

The dynamic nature of the Mopaneveld herbaceous layer relates to interactions between various plant groups within the system and their response to disturbance events. Annual grasses and forbs contribute the most to the herbaceous layer during drought (Jordaan *et al*., 2004). Perennial grasses are slow to establish after disturbance and have to compete with better adapted annual grasses, forbs and trees for limited soil moisture and nutrients (O’Connor, 1999; Jordaan *et al*., 2004; Buitenwerf *et al*., 2011).

Various observational and simulation (modelling) studies have indicated a marked increase in tree mortality in response to drought (Fensham and Holman, 1999; Choat *et al.,* 2012, McDowell and Allen, 2015). Although grasses decline in response to drought, the recovery time is contradicted in multiple studies (O’Connor, 2015; Danckwerts and Stuart-Hill, 1988). Perennial grasses, for instance, have been shown to only recover after multiple decades (O’Connor, 2015), whereas another study reported rapid recovery within a year, after a two-year severe drought (Abbas *et al.,* 2019). Recovery of grass species is dependent upon various factors including rainfall variability and veld management (Bosch and Kellner, 1991; O'Connor, 1994). Forb species responses to drought are less well-known. However, forb recovery could be more vigorous than that of grasses as a result of the removal of competitive species (Van Coller and Siebert, 2015). Forbs have different responses to rainfall variability, and exhibit diverse recovery rates depending on moisture availability and life-history traits (Fynn and O’Connor, 2000).

Along with novel investigations into interactions between forbs and grasses as separate entities, the shift in dominance between forb and grass species after disturbance events have also become widely acknowledged (Illius and O'Connor, 1999; Koerner and Collins, 2014; Van Coller *et al*., 2018). The shift in dominant life-forms result from the differences in how they respond to disturbance events. The dynamics of the forb community in response to disturbance and general drivers of savanna ecosystems is less well-known compared to that of grasses (Lettow *et al*., 2014; Scott-Shaw and Morris, 2015; Siebert and Dreber, 2019), making the response of forb species a potentially valuable attribute in investigating Mopaneveld resilience under pressure from anthropogenic disturbance and drought events.

Understanding the dynamics of forb-grass interactions within an anthropogenically transformed and drought-stressed semi-arid savanna will improve management of such ecosystems. Advanced restoration practices may result from additional insight into plant species tolerance towards anthropogenic impact and drought events. Selecting tolerant pioneer grass-, as well as forb species may further improve the success of mine restoration. Finally, successful management and restoration, may ensure the sustainability of ecosystem services, vital for human well-being.

The aim of this chapter was to gain insight into how the forb and grass community responded to drought across both disturbed and protected areas in a Mopaneveld savanna. It was expected that a lower herbaceous diversity will be observed on the mine dumps after drought and that the species dominating on the mine dumps would be hardy species with a tolerance to nutrient-poor and dry soil conditions. Sensitive species were expected to be filtered out on mine dumps, leading to an increase in evenness. A shift in dominance between life span and life form was expected in response to drought due to differences in stress tolerance and competitive ability. Changes were assessed in terms of species composition, richness and diversity before drought and after the drought release in a protected area, Cleveland Game reserve (CGR), and two rehabilitated mine dumps: a rock dump (RD) and tailings dam (TD). The herbaceous species responsible for compositional changes within the anthropogenically transformed and drought-stressed Mopaneveld were identified and discussed.

5.2 Methods

For information on the methodology for this chapter, please refer to Chapter 4 section 4.2 and 4.3 for experimental- and sampling design, and sections 4.5.1 and 4.5.2 for data analyses.

5.3 Results

5.3.1 Herbaceous community responses and species composition

5.3.1.1 Anthropogenic disturbance

Significant clustering between land-use types was evident for both the forb- and grass communities before drought and during drought release (Fig. 5.1). The forb community revealed a greater community-level divergence between land-use types before the drought, whereas the grass community revealed a greater divergence during drought release (See *F*-values, Table 5.1). Separation was more apparent between the protected area (CGR) and the mine dumps (RD and TD), than between the RD and TD, for both life forms (Fig. 5.1). Pair-wise tests revealed significant differences in community composition of both life forms between all land-use areas irrespective of rainfall variability (Table 5.1).

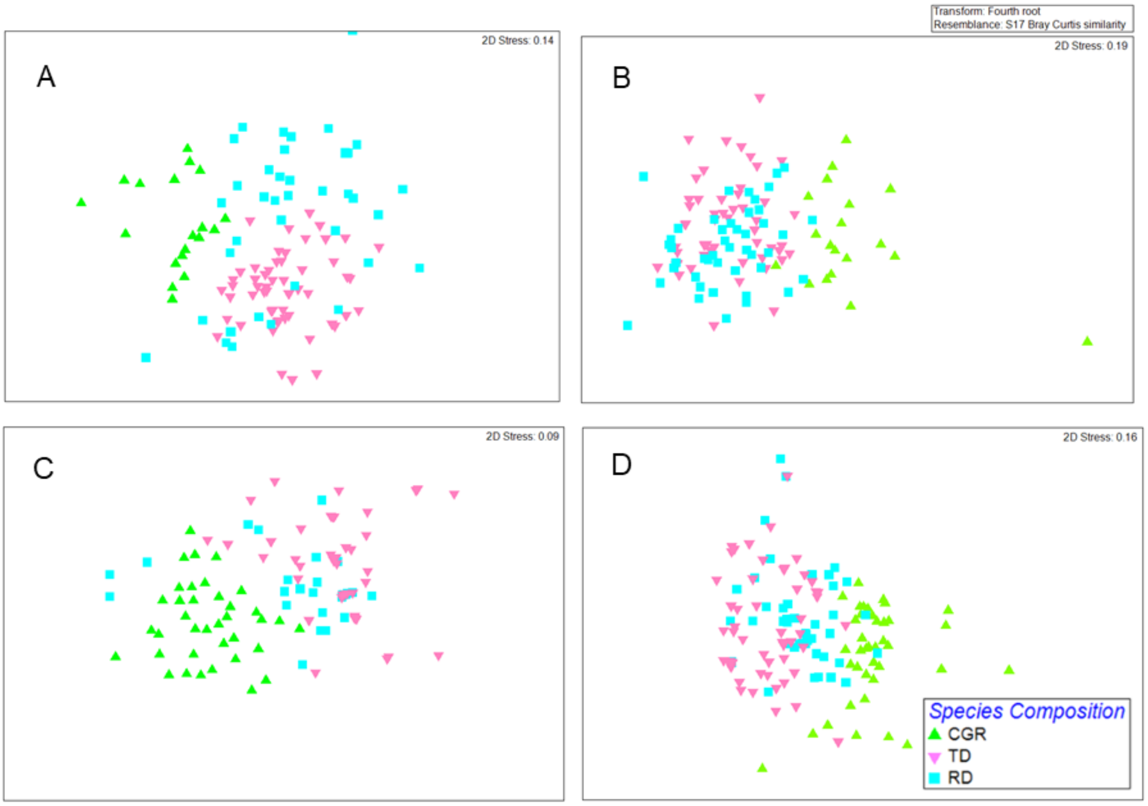

Figure 5.1: Non-metric multi-dimensional scaling (NMDS) ordinations indicating species composition differences across transformed (RD and TD) and protected (CGR) areas before drought (A – forbs, B – grasses), and during drought release (C – forbs, D – grasses).

Table 5.1: PERMANOVA and pair-wise comparisons indicating significance of variation between land-use types for forb and grass communities respectively, in response to rainfall variability.

	***F*-value**	***t*-value**	***p*-value**
Pre-drought			
Forbs	12.75		0.001*
Cleveland Game Reserve and Rock Dump		2.97	0.001*
Cleveland Game Reserve and Tailings Dam		4.12	0.001*
Rock Dump and Tailings Dam		3.59	0.001*
Grasses	11.30		0.001*
Cleveland Game Reserve and Rock Dump		3.77	0.001*
Cleveland Game Reserve and Tailings Dam		4.21	0.001*
Rock Dump and Tailings Dam		2.03	0.001*
Drought release			
Forbs	14.16		0.001*
Cleveland Game Reserve and Rock Dump		4.32	0.001*
Cleveland Game Reserve and Tailings Dam		4.41	0.001*
Rock Dump and Tailings Dam		2.03	0.002*
Grasses	16.32		0.001*
Cleveland Game Reserve and Rock Dump		3.98	0.001*
Cleveland Game Reserve and Tailings Dam		5.19	0.001*
Rock Dump and Tailings Dam		2.54	0.001*

* Denotes significant variation at $p \leq 0.05$; *F* and *t*: measure of effect size relative to variation in the data.

5.3.1.2 Drought effects

Non-Metric Multidimensional Scaling (NMDS) combining all three land-use types revealed a distinct shift in forb and grass communities in response to drought (Fig. 5.2). A larger community shift was observed for forbs (Fig. 5.2A).

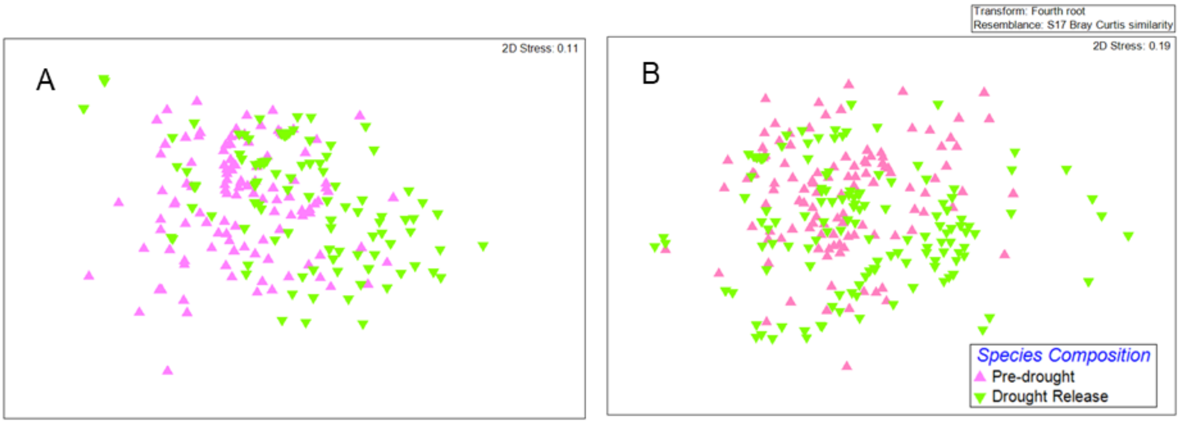

Figure 5.2: Non-metric multi-dimensional scaling (NMDS) indicating herbaceous community shifts in response to drought release for forb (A) and grass (B) communities respectively, irrespective of land-use type.

Analyses of drought effects on herbaceous communities for individual land-use types revealed significant shifts in community composition across land-use types and life forms (Fig. 5.3, Table 5.2). Mine dumps revealed a stronger clustering of forb communities and weaker clustering of grass communities in response to rainfall variability (Fig. 5.3A-D, Table 5.2). The herbaceous communities in the protected area responded inversely (Fig. 5.3E, F) since the forb community presented weaker clustering than the grass community (Fig. 5.3E, F; Table 5.2).

SIMPER analyses revealed that the reduced abundance of *Indigastrum costatum, Sesbania bispinosa*, and *Tephrosia purpurea* on the TD drove the divergence of forb community assemblages, while reduced abundances of *Cenchrus ciliaris*, *Enneapogon cenchroides*, and *Stipagrostis hirtigluma* led to the divergence of grass community assemblages. Decreasing abundances of *Acalypha indica*, *Rhynchosia minima, Tridax procumbens* and *Tephrosia rhodesica*, and the slight increase of *T. purpurea* drove divergence in forb community assemblages on the RD. Grass species responsible for community shifts on the RD included *Aristida adscensionis, Aristida congesta,* and *C. ciliaris*, which all decreased in abundance, while *E. cenchroides* and *S. hirtigluma* increased. Increases in *Mollugo nudicaulis, Ocimum americanum, and Tribulus terrestris* and reductions in *Bulbostylis burchellii* and *Waltheria indica* drove forb assemblage shifts in CGR. Decreases in grass species such as *A.*

adscensionis, Digitaria eriantha, E. cenchroides, Eragrostis superba and *Urochloa mosambicensis* were responsible for shifts in grass communities in CGR in response to drought.

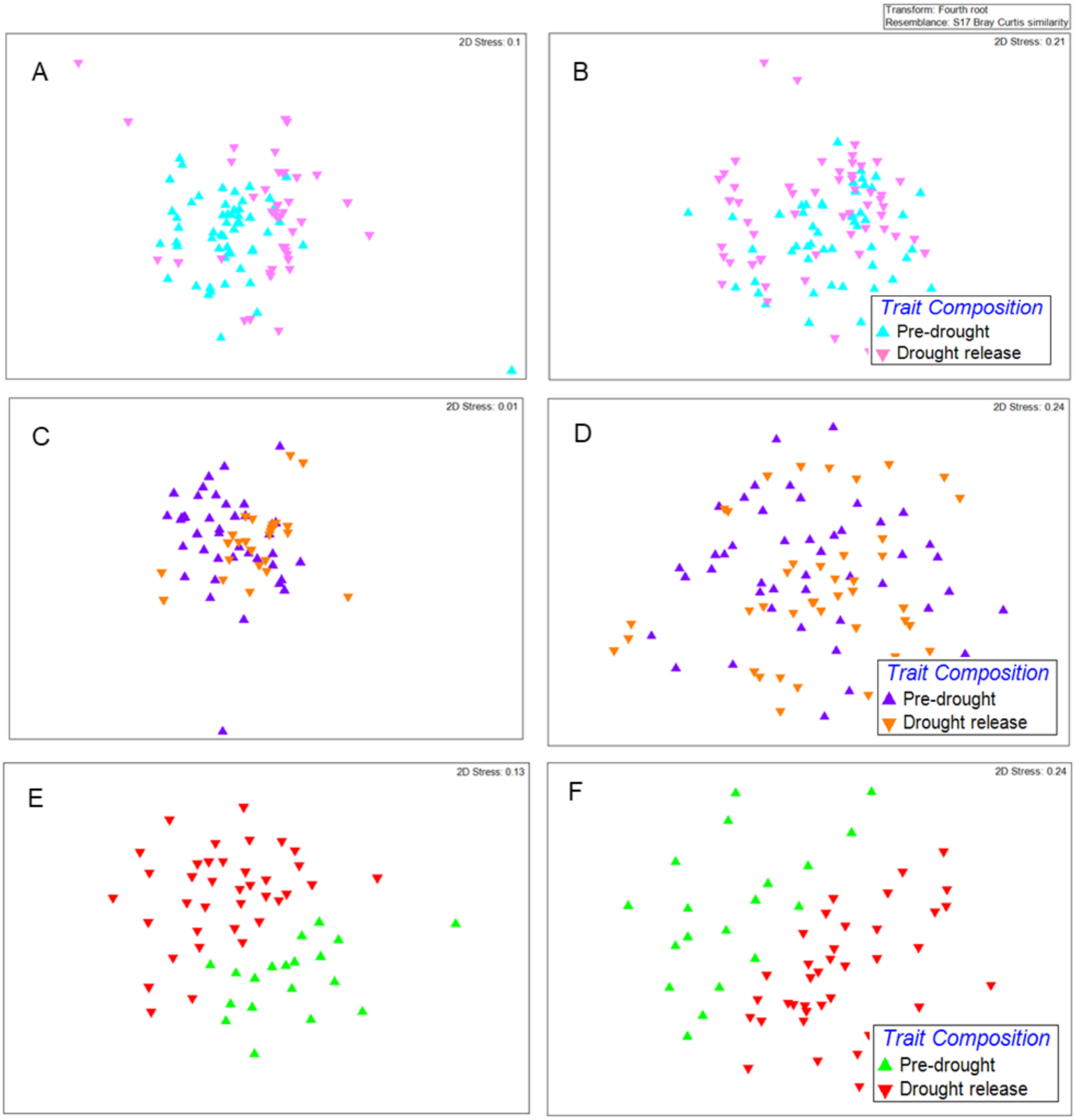

Figure 5.3: Non-metric multi-dimensional scaling (NMDS) ordinations indicating herbaceous community shifts in response to drought for forb and grass life forms at each land-use type, tailings dam (TD), rock dump (RD) and Cleveland Game Reserve (CGR). (TD - forbs (A), grass (B); RD - forbs (C), grass (D); CGR - forbs (E), grass (F).

Table 5.2: PERMANOVA results indicating significant variation between pre-drought and drought release herbaceous communities for forb and grass species respectively.

* Indicates significant variation at $p \leq 0.05$.

	Forbs		**Grasses**	
	***F*-value**	***p*-value**	***F*-value**	***p*-value**
Combined land-use types	9.68	0.001*	7.50	0.001*
Tailings dam	9.87	0.001*	6.64	0.001*
Rock dump	9.10	0.005*	3.29	0.005*
Cleveland Game Reserve	6.12	0.001*	9.53	0.001*

* Denotes significant variation at $p \leq 0.05$

5.3.2 Species frequency, density and diversity

The mean number of individuals per 1 m^2 plot decreased from 66 (SD ± 44.82) before the drought to 39 (SD ± 56.11) after the drought. Plots were dominated by grass individuals regardless of rainfall (Fig. 5.4). The frequencies of life form groups were much more balanced before the drought compared to the drought release (Fig. 5.4). However, a shift in annual and perennial grass individuals, as well as forbs occurred, which resulted in equal and increased dominance by individuals of annual life forms during the drought release, and visible decline in perennials (Fig. 4).

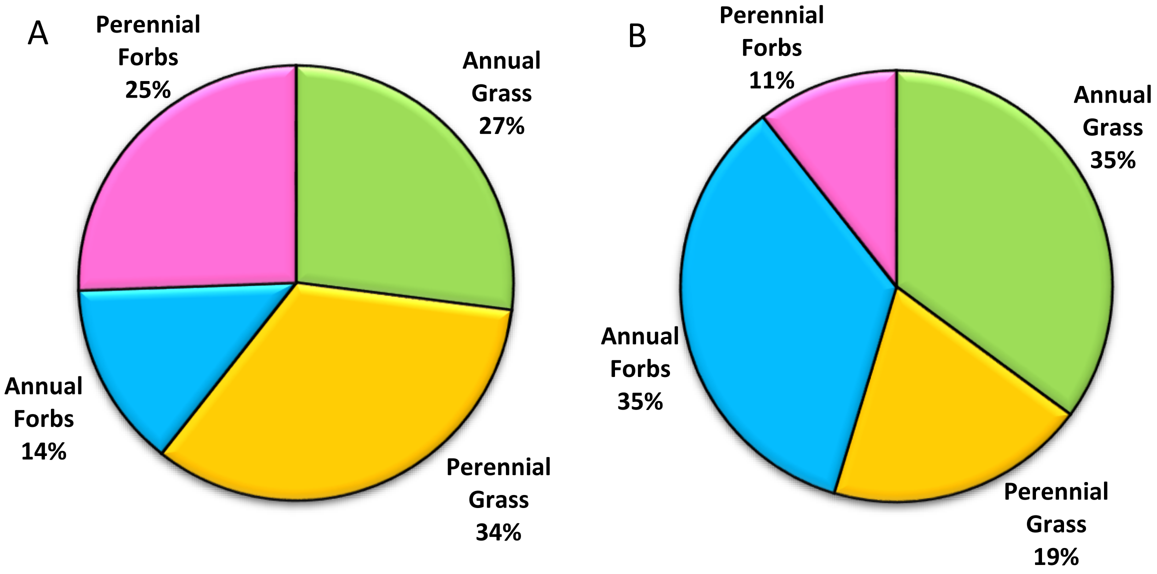

Figure 5.4: Frequency of individuals per herbaceous life form in the pre-drought (A) and drought release (B) communities.

The drought induced a decrease in total species richness from nine (SD ± 5.69) to six (SD ± 3.56). Forb richness dominated in pre-drought and drought release plots (Fig. 5.5A). Annual and perennial forb richness were relatively equal regardless of rainfall variability, and collectively, even increased their proportion within the total community during drought release (Fig. 5.5B). Perennial grass species remained dominant over annual grass species (Fig. 5.5).

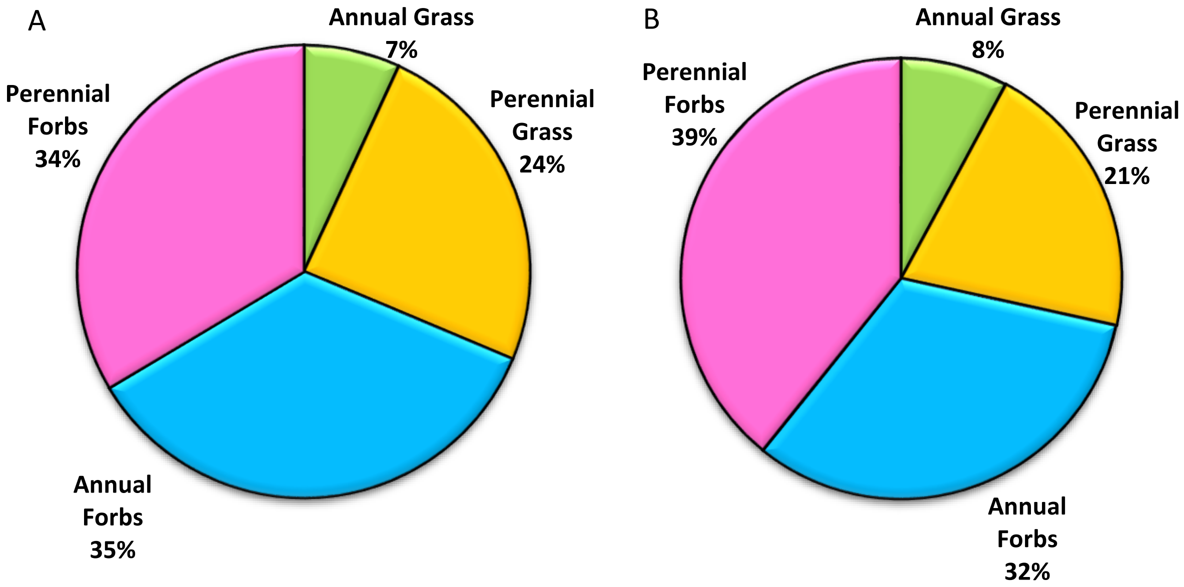

Figure 5.5: Frequency of species representing different herbaceous plant groups before drought (A) and after drought release (B)

Rarefaction curves (Fig. 5.6) illustrated species richness of plots and sampling effort across land-use types. Highest species richness was observed for CGR before the drought and the lowest for the RD during drought release. Species richness at CGR for both rainfall years, was higher than both pre-drought and drought release species richness on mine dumps. All land-use types exhibit lower species richness during drought release compared to before the drought. All curves reached a plateau or were close to a plateau indicating that adequate sampling was done.

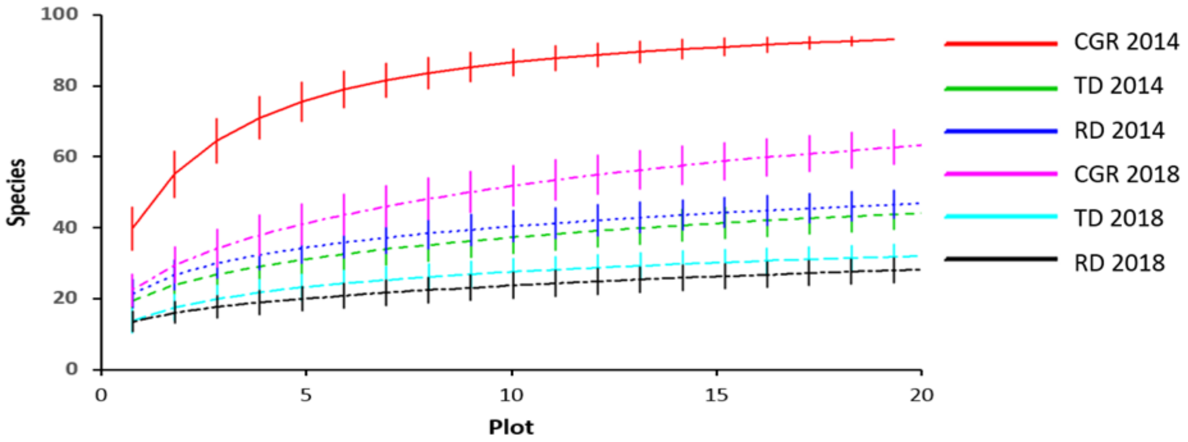

Figure 5.6: Species richness before the drought (2014) and during drought release (2018) for transformed (RD, TD) and protected (CGR) areas.

Results from the two-level hierarchical linear model (HLM) revealed a significant interaction effect between rainfall year and land-use type for total forb species, forb species richness and –diversity, but not for evenness (Table 3). Rainfall year and land-use type interacted to significantly affect total grass species (Table 3). Forb evenness was more sensitive to land-use type than rainfall, whilst grass evenness revealed to be more sensitive to rainfall variability than land-use type (Table 3).

Table 5.3: Two-way ANOVA type Hierarchical Linear Modelling (HLM) results for differences in herbaceous species diversity index values across land-use types in response to drought.

Fixed effects:	**Forbs**		**Grasses**	
Rainfall year*Land-use				
	F_{df}	P	F_{df}	P
Total species				
Rainfall year	20.76_1	< 0.001*	26.41_1	< 0.001*
Land-use	166.44_2	< 0.001*	13.20_2	< 0.001*
Rainfall year : Land-use	6.05_2	0.003*	6.60_2	0.002*
Margalef's species richness				
Rainfall year	8.94_1	0.003*	5.27_1	0.023*
Land-use	85.42_2	< 0.001*	12.69_2	< 0.001*
Rainfall year : Land-use	6.24_2	0.002*	2.46_2	0.087
Shannon diversity				
Rainfall year	9.44_1	0.002*	6.26_1	0.013*
Land-use	78.12_2	< 0.001*	10.25_2	< 0.001*
Rainfall year : Land-use	3.58_2	0.030*	1.88_2	0.155
E_{var} evenness				
Rainfall year	0.04_1	0.842	5.06_1	0.025*
Land-use	5.21_2	0.006*	2.51_2	0.083
Rainfall year : Land-use	0.32_2	0.727	0.33_2	0.717

* Denotes significance at $p \leq 0.05$; df: degrees of freedom

Post hoc significance tests on diversity indices revealed that forb species had significantly higher total species, Margalef richness and Shannon diversity index values in the protected area and on the TD during the pre-drought sample when compared to drought release (Fig. 5.7A, C, E; Bonferroni, $p < 0.05$; Appendix D, Table D1). Pre-drought grass species revealed significantly higher values for these same indices, although only in the protected area, before and after drought (Fig. 5.7B, D, and F; Bonferroni, $p < 0.05$; Appendix D, Table D1).

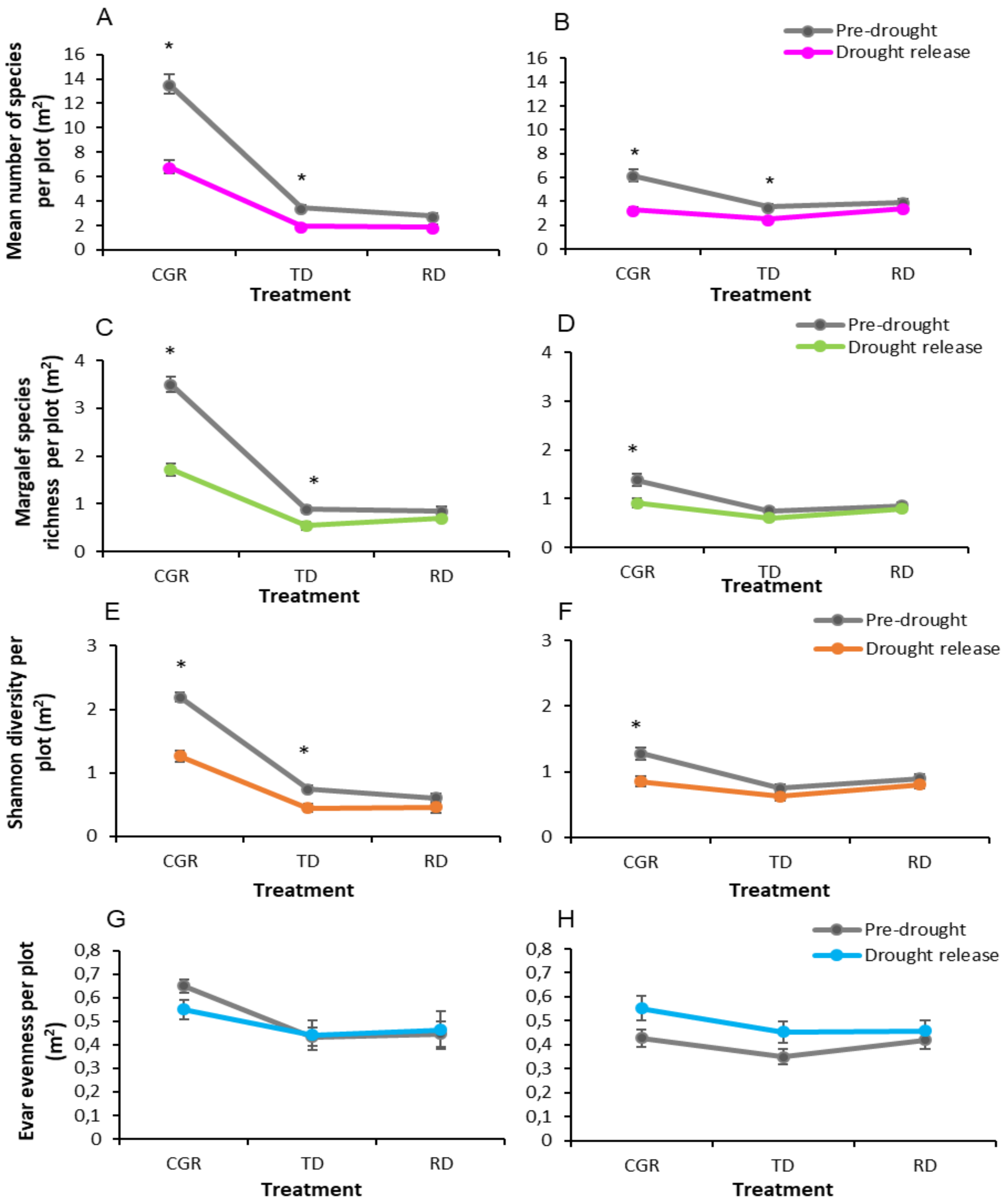

Figure 5.7: Diversity indices for herbaceous species before drought and during drought release across land-use types (Mean number of species: forbs (A), grasses (B); Margalef's richness: forbs (C), grasses (D); Shannon diversity: forbs (E), grasses (F); E_{var} evenness: forbs (G), grasses (H)). * Indicates significant differences at $p \leq 0.05$, following Bonferroni *post-hoc* tests (Appendix D, Table D1).

5.3.3 Biomass and Cover

5.3.3.1 Biomass

The interaction effects of rainfall year and land-use on mean herbaceous biomass was significant (Table 5.4). The drought resulted in a significant decline in biomass in the protected area, but biomass remained stable on the mine dumps (Fig. 5.8; Bonferroni, $p < 0.05$; Appendix D, Table D2). Before the drought, the protected area had the highest mean biomass. However, during drought release, the protected area had the lowest mean biomass, and the RD the highest (Fig. 5.8; Bonferroni, $p < 0.05$; Appendix D, Table D2).

Table 5.4: Two-way ANOVA type Hierarchical Linear Modelling (HLM) for pre-drought and drought release mean herbaceous biomass across land-use types

Fixed effects: Rainfall year*Land-use	F_{df}	P	
Biomass			
Rainfall year	21.30_1	< 0.001	*
Land-use	3.89_2	0.022	*
Rainfall year : Land-use	6.08_2	0.003	*

* Denotes significance at p ≤ 0.05; df: degrees of freedom

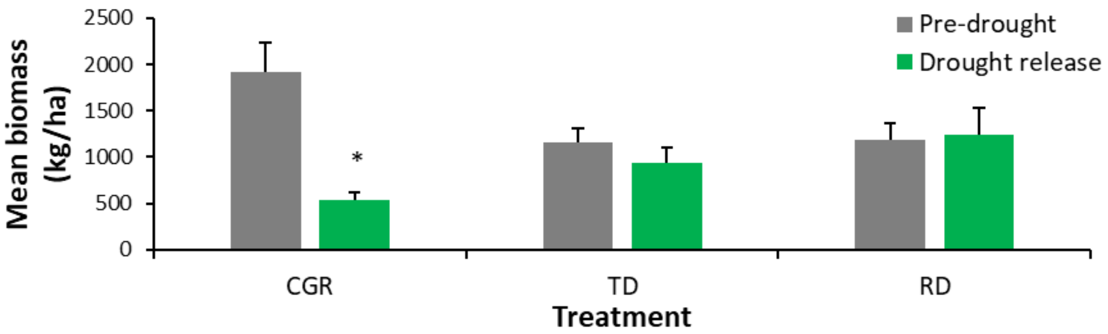

Figure 5.8: Changes in mean biomass at protected (CGR) and transformed (TD, RD) areas in response to drought. *Denotes significant differences at $p \leq 0.05$, following Bonferroni *post-hoc* tests (Appendix D, Table D2).

Life form and land-use type had a significant interaction effect during the drought release year (Table 5.5). Grass biomass was significantly higher than forb biomass on the mine dumps during drought release (Fig. 5.9; Bonferroni, $p < 0.05$; Appendix D, Table D3). Post-hoc tests revealed that mean grass biomass was significantly higher at the TD and RD compared to the protected area (Fig. 5.9; Bonferroni, $p < 0.05$; Appendix D, Table D3). Mean forb biomass was significantly higher in the protected area than on mine dumps (Fig. 5.9; Bonferroni, $p < 0.05$; Appendix D, Table D3).

Table 5.5: Two-way ANOVA type Hierarchical Linear Modelling (HLM) tests for differences in biomass per life form across land-use types during the drought release year.

Fixed effects: Life form*Land-use

	F_{df}	P
Biomass		
Life form	93.00_1	< 0.001*
Land-use	0.04_2	0.963
Life form : Land-use	40.17_2	< 0.001*

* Denotes significance at $p \leq 0.05$; df: degrees of freedom

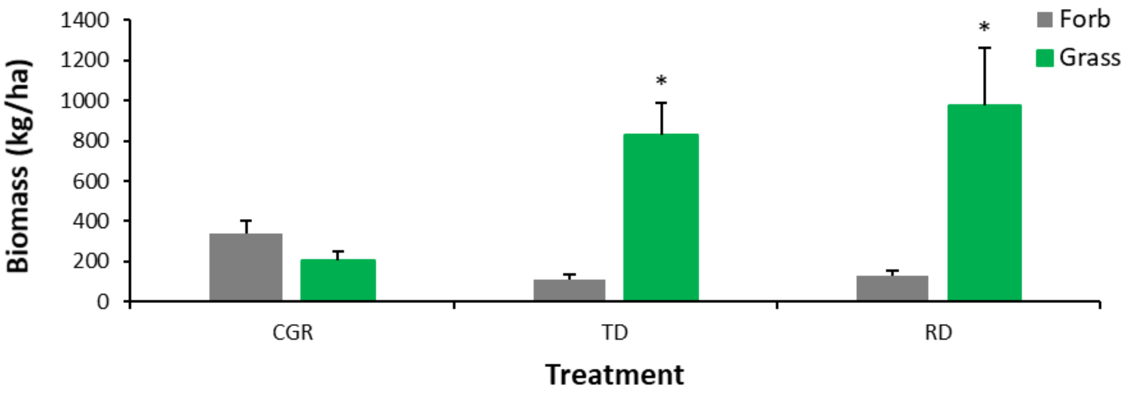

Figure 5.9: Comparisons between mean forb and grass biomass during drought release in protected (CGR) and transformed (TD, RD) areas. * Denotes significant differences between life forms at $p \leq 0.05$, following Bonferroni *post-hoc* tests (Appendix D, Table D3).

5.3.3.2 Cover

Significant interaction effects between rainfall year and land-use type were revealed for grass and bare soil, while the effect of land-use outweighed that of rainfall variability for forb and debris cover (Table 5.6).

Table 5.6: Two-way ANOVA type Hierarchical Linear Modelling (HLM) tests for differences in cover percentages across land-use types in response to drought.

Fixed effects: Rainfall year*Land-use	F_{df}	***P***
Forbs		
Rainfall year	0.03_1	0.855
Land-use	38.54_2	< 0.001*
Rainfall year : Land-use	1.23_2	0.294
Grass		
Rainfall year	9.71_1	0.002*
Land-use	9.23_2	< 0.001*
Rainfall year : Land-use	32.07_2	< 0.001*
Bare soil		
Rainfall year	10.01_1	0.002*

Land-use	2.70_2	0.069
Rainfall year : Land-use	6.14_2	0.002*
Debris		
Rainfall year	0.19_1	0.666
Land-use	5.81_2	0.003*
Rainfall year : Land-use	4.10_2	0.385
Herbaceous cover		
Rainfall year	90.48_1	< 0.001*
Land-use	19.57_2	< 0.001*
Rainfall year : Land-use	55.68_2	< 0.001*

* Denotes significance at $p \leq 0.05$; df: degrees of freedom

A significant decline in grass cover and significant increase in bare soil was observed at the protected area (Fig. 5.10; Bonferroni, $p < 0.05$; Appendix D, Table D4). Differences in cover remained stable at the mine dumps (Fig. 5.10).

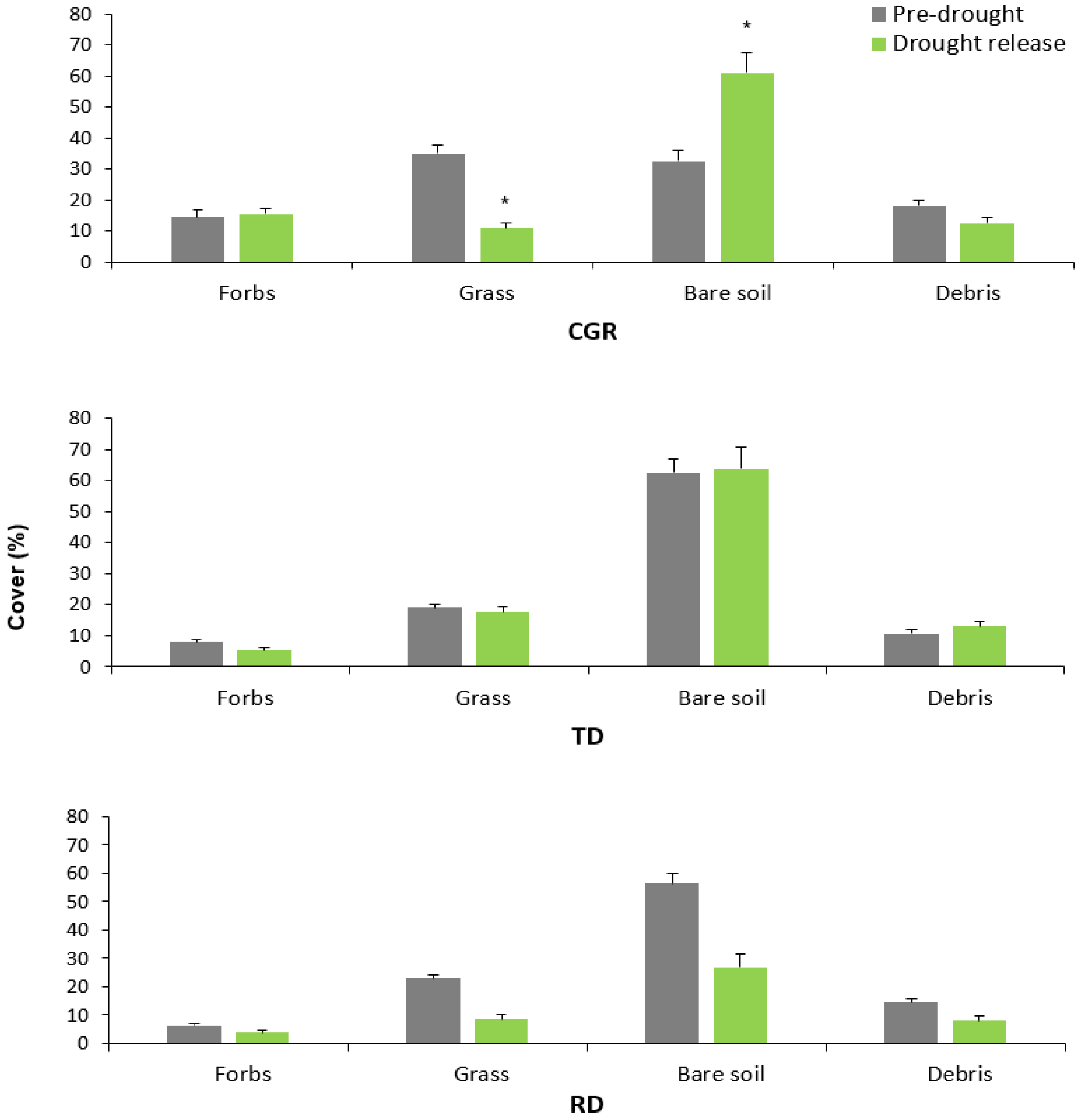

Figure 5.10: Mean percentage of herbaceous plant cover, bare soil and debris per plot at protected (CGR) and transformed (TD, RD) areas in response to drought. * Denotes significant differences at $p \leq 0.05$, following Bonferroni *post-hoc* tests (Appendix D, Table D4).

There was a significant interaction effect between rainfall year and land-use type for overall herbaceous cover at the protected area and TD (Table 5.6). *Post hoc* Bonferroni tests revealed that total herbaceous cover decreased significantly at the protected area and on the TD (Fig. 5.11; Bonferroni, $p < 0.05$; Appendix D, Table D4).

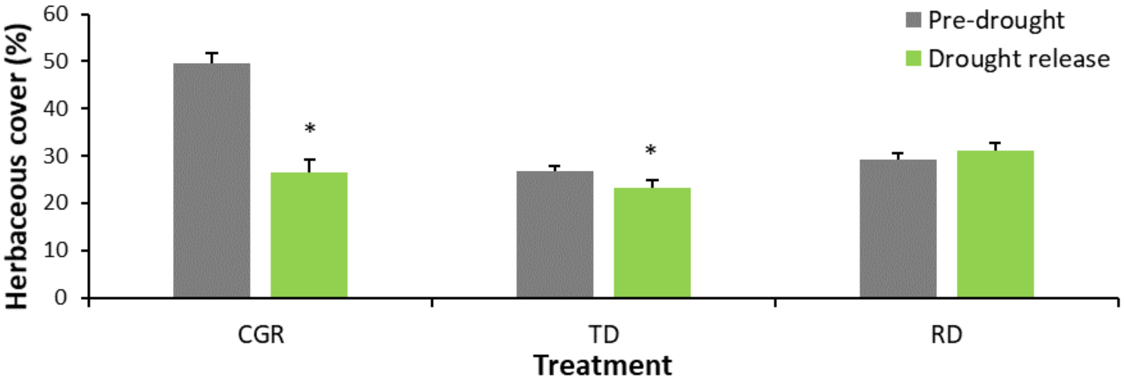

Figure 5.11: Mean herbaceous plant cover at protected (CGR) and transformed (TD, RD) areas before the drought and during drought release. * Denotes significant differences at $p \leq 0.05$, following Bonferroni *post-hoc* tests (Appendix D, Table D4).

5.3.4 Individual species responses and tolerance to drought in anthropogenically transformed areas

5.3.4.1 Relative abundance of species

Forb species *A. indica, I. costatum, R. minima,* and *T. purpurea* remained among the 10 most abundant species on both mine dumps before drought and during drought release. *B. burchellii* and *O. americanum* remained abundant in CGR and *Polygala serpentaria* remained among the 10 most abundant forb species on the TD. Although *A. indica* and *T. purpurea* did not fall among the 10 most abundant species in CGR, these two species still occurred before drought as well as during drought release.

The most abundant grass species surveyed before the drought largely remained abundant during drought release. Among the ten most abundant grass species per land-use type, the grass species that existed throughout all three areas before drought and during drought release included *A. adscensionis, E. cenchroides,* and *U. mosambicensis*. Species that remained abundant on both mine dumps were *C. ciliaris, S. hirtigluma,* and *Sporobolus ioclados*. Grass species that remained among the ten most abundant species in the protected area were *D. eriantha* and *Schmidtia pappophoroides*. On the TD, species most abundant before and after were *Heteropogon contortus* and *S. pappophoroides*, and on the RD they were *A. congesta* and *Pennisetum setaceum*.

Mapaure *et al*. (2011) described species as 'sensitive' when only occurring in protected areas (control site), 'resistant' when occurring at both protected areas and mine dumps (polluted sites), and 'tolerant' when occurring only on mine dumps. In this study, sensitive forbs were more abundant than sensitive grass species across both rainfall years, although the abundance of sensitive grasses increased after drought (Table 5.7). Resistant grasses had the highest abundance of all grass classes (Table 5.7).

Sensitive forbs species made up 11 times that of sensitive grasses before the drought, and four times during drought release. Life forms contained relatively equal abundances of resistant species regardless of rainfall variability, although less forbs were present among the most dominant sensitive forb species compared to grasses. At least double as many tolerant forb species existed on the mine dumps compared to grasses before drought and during drought release. The most abundant sensitive forbs largely consisted of annual species during drought release, whilst all drought release sensitive grass species were perennial. (Table 5.7).

Table 5.7: Species tolerance classes as denoted by Mapaure *et al*. (2011). Species shown in this table are those present among the 10 most abundant species shared between land-use types and across rainfall year. The total number of species among these classes are also indicated.

	Pre-drought	Drought release
Sensitive forbs	*Bulbostylis burchellii*	*Bulbostylis burchellii*
	Corchorus asplenifolius	*Commelina benghalensis*[a]
	Kyllinga alba	*Corchorus asplenifolius*
	Syncolostemon canescens	*Cyperus obtusiflorus*.
	(Total n = 55)	*Gisekia africana*[a]
		Hermannia boraginiflora
		Mollugo nudicaulis[a]
		Ocimum americanum[a]
		(Total n = 41)
Sensitive grass	*Brachiaria deflexa*[a]	*Bothriochloa radicans*
	Chloris virgata[a]	*Digitaria eriantha*

	Eragrostis lehmanniana	*Eragrostis trichophora*
	Pogonarthria squarrosa	*Eragrostis rigidior*
	Sporobolus fimbriatus	*Eragrostis superba*
	Themeda triandra	*Microchloa caffra*
	(Total n = 6)	*Panicum maximum*
		Sporobolus fimbriatus
		Tricholaena monachne
		(Total n = 9)
Resistant forbs	*Indigofera heterotricha*	*Acalypha indica*[a]
	Tephrosia purpurea	(Total n = 17)
	(Total n = 22)	
Resistant grass	*Aristida adscensionis*[a]	*Aristida adscensionis*[a]
	Enneapogon cenchroides[a]	*Aristida congesta*[a]
	Heteropogon contortus	*Enneapogon cenchroides*[a]
	Sporobolus ioclados	*Urochloa mosambicensis*
	Urochloa mosambicensis	(Total n = 12)
	(Total n = 18)	
Tolerant forbs	*Indigastrum costatum*[a]	*Indigastrum costatum*[a]
	Rhynchosia minima	*Rhynchosia minima*
	Tephrosia rhodesica	(Total n = 17)
	(Total n = 29)	
Tolerant grass	*Stipagrostis hirtigluma*[a]	*Cenchrus ciliaris*

(Total n = 11)	(Total n = 6)

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[a] denotes annual species.

5.3.4.2 Indicator species

Indicator species analyses (ISA) revealed that 48 % of the total number of species recorded before the drought were indicator species for CGR (Table 5.8). Indicator species comprised of 4 % and 2 % for the TD and RD respectively (Table 5.8). Indicator species for CGR during drought release made up 28 % of all species recorded and 4 % for both the TD and RD (Table 5.9). Before the drought, 67 species were revealed as indicator species for CGR (Table 5.8), which decreased to 29 during drought release (Table 5.9). Six indicator species existed for the TD before the drought (Table 5.8), and four indicator species during drought release (Table 5.9). The RD had three indicator species before the drought (Table 5.8) and four during drought release (Table 5.9). Indicator species in CGR that could not maintain their indicator values after the drought amounted to 38 (Table 5.8, 5.9). Out of the three indicator species for the RD, two were lost, *T. procumbens* and *T. rhodesica*. No indicator species were lost from the TD after the drought.

The highest indicator values across all sites before the drought were revealed for *K. angustifolia* in the protected area (0.57), and *S. bispinosa* on the RD (0.64). *C. asplenifolius* had the highest drought release indicator value (0.58) (Table 5.8, 5.9). *Bulbostylis burchellii, Brachiaria deflexa, D. eriantha, Kyphocarpa angustifolia* and *O. americanum* remained among the indicator species with the highest indicator values for CGR during drought release (Table 5.9). *C. ciliaris, I. costatum* and *S. hirtigluma* remained indicator species for the TD during drought release (Table 5.9). However, *Polygala erioptera* replaced *P. serpentaria* on the TD. These differences might, however, have been due to identification discrepancies between the respective years as these species easily be confused. On the TD, only *P. setaceum* remained one of the indicator species for the RD (Table 5.9). Forb species made up the majority of indicator species across all land-use types irrespective of rainfall variability, except for the RD during the drought release year where grasses made up all indicator species (Table 5.8, 5.9). The majority of the drought release indicator species across all land-use types were annuals.

Table 5.8: Indicator species analyses (IndVal) revealing significant indicator species for land-use types before the drought.

Species	Site	Indicator Value	*p*-Value	Frequency
Kyphocarpa angustifolia[a]	CGR	0.57	0.001	12
Bulbostylis burchellii	CGR	0.53	0.001	10
Ocimum americanum[a]	CGR	0.45	0.001	12
Schmidtia pappophoroides	CGR	0.43	0.001	17
Corchorus confusus	CGR	0.42	0.001	8
Indigofera vicioides	CGR	0.33	0.001	8
Brachiaria deflexa[a]	CGR	0.32	0.001	6
Melhania acuminata	CGR	0.32	0.001	6
Pupalia lappacea[a]	CGR	0.32	0.001	6
Digitaria eriantha	CGR	0.31	0.001	7
Waltheria indica[a]	CGR	0.31	0.001	8
Aristida adscensionis[a]	CGR	0.27	0.014	31
Commelina africana	CGR	0.26	0.001	5
Commelina benghalensis[a]	CGR	0.26	0.001	5
Hibiscus sidiformis[a]	CGR	0.26	0.001	5
Hypoestes forskaolii	CGR	0.26	0.001	5
Kyllinga alba	CGR	0.26	0.001	5
Zornia glochidiata[a]	CGR	0.26	0.001	5
Eragrostis superba	CGR	0.25	0.001	6
Hibiscus micranthus	CGR	0.21	0.007	11
Blepharis integrifolia	CGR	0.21	0.002	4
Clerodendrum ternatum	CGR	0.21	0.001	4
Corbichonia decumbens[a]	CGR	0.21	0.002	4
Evolvulus alsinoides[a]	CGR	0.21	0.001	4
Justicia flava	CGR	0.21	0.002	4
Leucas sexdentata[a]	CGR	0.21	0.002	4
Phyllanthus incurvus	CGR	0.21	0.002	4
Pogonarthria squarrosa	CGR	0.21	0.002	4
Seddera suffruticosa	CGR	0.21	0.001	4
Sporobolus fimbriatus	CGR	0.21	0.001	4
Syncolostemon canescens	CGR	0.21	0.002	4
Phyllanthus parvulus	CGR	0.21	0.002	11

Bothriochloa radicans	CGR	0.20	0.004	9
Hermannia glanduligera	CGR	0.18	0.005	6
Tragus berteronianus[a]	CGR	0.18	0.002	6
Panicum maximum	CGR	0.17	0.005	8
Achyranthes aspera	CGR	0.16	0.005	3
Becium filamentosum	CGR	0.16	0.004	3
Bidens bipinnata[a]	CGR	0.16	0.005	3
Calostephane divaricata[a]	CGR	0.16	0.003	3
Chamaecrista absus[a]	CGR	0.16	0.004	3
Chloris roxburghiana	CGR	0.16	0.006	3
Commelina erecta	CGR	0.16	0.003	3
Crabbea velutina	CGR	0.16	0.002	3
Dicoma tomentosa[a]	CGR	0.16	0.003	3
Euphorbia neopolycnemoides[a]	CGR	0.16	0.005	3
Gisekia africana[a]	CGR	0.16	0.004	3
Ipomoea sinensis[a]	CGR	0.16	0.001	3
Leucas glabrata	CGR	0.16	0.005	3
Melhania forbesii	CGR	0.16	0.004	3
Microcharis galpinii[a]	CGR	0.16	0.004	3
Monechma debile[a]	CGR	0.16	0.002	3
Talinum arnotii	CGR	0.16	0.007	3
Eragrostis rigidior	CGR	0.16	0.005	4
Ipomoea magnusiana	CGR	0.14	0.015	5
Corchorus asplenifolius	CGR	0.14	0.006	5
Brachiaria xantholeuca[a]	CGR	0.14	0.01	4
Eragrostis lehmanniana	CGR	0.11	0.019	2
Justicia protracta	CGR	0.11	0.021	2
Ledebouria revoluta	CGR	0.11	0.021	2
Melhania prostrata	CGR	0.11	0.021	2
Mollugo nudicaulis[a]	CGR	0.11	0.023	2
Rhinacanthus xerophilus	CGR	0.11	0.029	2
Ruellia cordata	CGR	0.11	0.033	2
Sida cordifolia[a]	CGR	0.11	0.022	2
Tragia rupestris[a]	CGR	0.11	0.022	2
Gnidia rubescens	CGR	0.09	0.037	3
	TD		0.001	41

Sesbania bispinosa		0.64		
Tephrosia purpurea	TD	0.48	0.004	56
Cenchrus ciliaris	TD	0.47	0.001	86
Polygala serpentaria	TD	0.38	0.001	25
Indigastrum costatum[a]	TD	0.33	0.004	27
Stipagrostis hirtigluma[a]	TD	0.31	0.025	39
Pennisetum setaceum	RD	0.35	0.001	26
Tephrosia rhodesica	RD	0.29	0.014	28
Tridax procumbens[a]	RD	0.20	0.005	9

Table 5.9: Indicator species analyses (IndVal) revealing significant indicator species for land-use types during drought release.

Species	Site	Indicator Value	*p*-Value	Frequency
Corchorus asplenifolius	CGR	0.58	0.001	23
Brachiaria deflexa[a]	CGR	0.48	0.001	26
Tribulus terrestris[a]	CGR	0.42	0.001	23
Ocimum americanum[a]	CGR	0.37	0.001	16
Digitaria eriantha Steud.	CGR	0.35	0.001	14
Kyphocarpa angustifolia[a]	CGR	0.35	0.001	14
Bulbostylis burchellii	CGR	0.33	0.001	13
Sida cordifolia[a]	CGR	0.33	0.001	13
Tragus berteronianus[a]	CGR	0.31	0.002	31
Mollugo nudicaulis[a]	CGR	0.30	0.001	12
Hermannia boraginiflora	CGR	0.28	0.001	11
Phyllanthus maderaspatensis[a]	CGR	0.28	0.001	11
Gisekia africana[a]	CGR	0.23	0.001	9
Acalypha indica[a]	CGR	0.22	0.002	18
Corbichonia decumbens[a]	CGR	0.17	0.001	8
Cyperus obtusiflorus	CGR	0.13	0.001	5
Hibiscus micranthus	CGR	0.12	0.007	8
Commelina benghalensis[a]	CGR	0.12	0.004	6
Clerodendrum ternatum	CGR	0.10	0.005	4
Phyllanthus incurvus	CGR	0.10	0.009	4
Portulaca oleracea[a]	CGR	0.09	0.017	5

Hermbstaedtia odorata	CGR	0.08	0.032	5
Abutilon grandiflorum[a]	CGR	0.08	0.028	3
Dicoma tomentosa[a]	CGR	0.08	0.035	3
Limeum viscosum[a]	CGR	0.08	0.021	3
Ornithogalum tenuifolium	CGR	0.08	0.019	3
Spermacoce sinensis[a]	CGR	0.08	0.026	3
Syncolostemon canescens	CGR	0.08	0.024	3
Talinum arnotii	CGR	0.08	0.024	3
Cenchrus ciliaris	TD	0.33	0.002	62
Indigastrum costatum[a]	TD	0.33	0.001	22
Stipagrostis hirtigluma[a]	TD	0.23	0.035	37
Polygala erioptera[a]	TD	0.14	0.004	8
Enneapogon cenchroides[a]	RD	0.40	0.001	74
Aristida congesta[a]	RD	0.28	0.005	33
Pennisetum setaceum	RD	0.16	0.004	13
Stipagrostis uniplumis	RD	0.16	0.022	18

CHAPTER 6 Herbaceous functional trait assemblage and diversity shifts in response to drought

6.1 Introduction

Plant functional trait-based approaches to assess ecosystem function has become increasingly popular (Lavorel and Garnier, 2002; Petchey *et al.,* 2004; Pakeman, 2011; Díaz *et al.,* 2013; Kotschy, 2013). This is likely a result of growing evidence that ecosystem function and the effect of disturbance on plant communities is more related to the functional diversity of species within the community compared to taxonomic diversity (Díaz and Cabido, 2001; Lavorel and Garnier, 2002; Lososová *et al.,* 2006). Specific traits enable tolerance or resistance to environmental- and anthropogenic perturbation, which promotes persistence in unfavourable environments and facilitates ecosystem function (Laliberté *et al.,* 2010).

Variation in species response under different management regimes, and subsequent generalizations thereof, can be adequately explained by means of plant functional trait analyses rather than taxonomy (Clark *et al.,* 2012). The role of plant functional traits is therefore valuable to predict plant community responses to natural and anthropogenic disturbance associated with mining and drought (Castro *et al*., 2010; Mabry and Fraterrigo, 2009). Functional traits may also provide insight into possible resilience of the ecosystem in response to such disturbances (Clark *et al*., 2012; Sterk *et al.*, 2013; Zirbel *et al.,* 2017), as ecosystem function and stability is increased with an increase in functional trait diversity (Petchey and Gaston, 2006; Flynn *et al.*, 2009).

6.1.1 Plant functional trait assemblages

Ruderal species colonising bare mine dump soil are typically hardy pioneer species from a surrounding species pool along with species that were artificially introduced for restoration purposes (Zhenqi *et al.,* 2012; Ilunga wa Ilunga *et al*., 2015). Introduced species are carefully selected according to desired functional traits that would allow successful establishment in unfavourable conditions that accompany mining operations (Ilunga wa Ilunga *et al.,* 2015; Lamoureux *et al.,* 2016). Known conditions, such as limited water availability on mine dumps and increasing frequencies of drought events, necessitates the selection of species adapted to drought prone ecosystems for restoration purposes. This increases the likelihood of species persistence on mine dumps (Balachowski and Volaire, 2018).

Herbaceous species that successfully colonise habitats in harsh environmental conditions, typically bear traits such as efficient (typically long-distance) dispersal mechanisms, such as anemo- and ectozoochorous species, low shade tolerance (i.e. ability to tolerate high UV radiance and temperatures), vegetative reproduction (i.e. clonal species or species with the ability to resprout from below or at the soil surface), and nitrogen-fixing abilities in association with mycorrhiza (Bakker *et al*., 1996; Tainton, 1999; Funk *et al.,* 2008; Rosenthal *et al.,* 2010; Hermanutz *et al.,* 1989; Cripps and Eddington 2005). Therefore, it was expected that herbaceous plant species with the abilities to persist on mine dumps would possess a suit of functional traits that aid survival in harsh environmental conditions (Ilunga wa Ilunga *et al*., 2015). Forbs possess a variety of drought tolerant traits resulting in sound recovery after drought events (Siebert and Dreber, 2019). Under stressed environmental conditions, it was suggested that forb abundances remain relatively stable, and changes observed in forb abundances were more correlated with grass abundances (Uys *et al*., 2004; Koerner and Collins, 2014). However, this has not yet been observed for transformed systems such as the herbaceous communities on mine dumps. On the other hand, grass species often possess traits such as long-distance dispersal, C_4 photosynthesis (pre-dominant in savannas), short generation time and effective establishment mechanisms that ensures persistence under drought conditions (Linder *et al*., 2018).

Traits that enable persistence in unstable and harsh environments likely evolved through adaptation to natural disturbance (Shooner *et al.,* 2015). Although novel disturbances, such as agriculture and mining may threaten natural ecosystems, regional species may possess adaptive traits for natural disturbances that allow them to persist under these novel disturbances as well (Moreno García *et al.,* 2014; Osborne *et al.*, 2018). For example, tree species in savanna ecosystems are adapted to fire and herbivory that result in defoliation, which brought on rapid recovery traits such as resprouting ability and clonality (Osborne *et al*., 2018). These traits aid persistence of species under agricultural disturbance, and could potentially drive persistence in mining areas.

Environmental changes, such as those brought on by mining and drought, could filter out specific species that do not harbour traits to withstand these environmental pressures (Shooner *et al*., 2015). In turn, the original suit of traits that would be present in the natural community are replaced by alternative trait assemblages, mainly traits associated with ruderal species. Such alternate states affect community and ecosystem function (Díaz *et al.,* 2013), and may not be able to return to its original stable state (Castro *et al.,* 2010; McNeall *et al*., 2011; Westoby *et al*., 1989).

6.1.2 Functional redundancy

All species occurring within an ecosystem contribute to ecosystem function. Loss of some species may be more detrimental to ecosystem function than others. This is because some functional traits are carried by multiple species, whereas other functional traits may only be carried by one or two species (Díaz and Cabido, 2001). When all species responsible for a specific trait or function are lost, ecosystem function is reduced. However, when functionally similar species persist after disturbance, these species continue to perform the function of the lost species, ensuring stability in ecosystem function (Díaz and Cabido, 2001; Petchey *et al*., 2009; Oliver *et al.,* 2015). More functionally similar species, with a range of varied responses ("response diversity" – Elmqvist *et al*., 2003) to disturbance will increase the ecosystem stability and preserve ecosystem function (Díaz and Cabido, 2001, Elmqvist *et al.,* 2003; Mouillot *et al.,* 2013, Mori *et al.,* 2013; Oliver *et al.,* 2015). Therefore, higher functional trait diversity and abundance of species with the ability to compensate for lost species through similar traits, will ensure functional redundancy and hence, resilience of the ecosystem (Díaz and Cabido, 2001; Laliberté *et al.,* 2010).

Disturbance related filters and environmental factors typically select for specific species traits and groups, or functional types (McIntyre *et al*., 1995; Lavorel *et al*., 1997). The grouping of herbaceous plant species according to similar functional traits and responses to disturbance into plant functional types (PFT's) have been used successfully as a substitute for taxonomic species (Lavorel *et al.,* 1997, Lavorel and Garnier, 2002). Using multiple trait analyses provides greater explanatory power and successful generalization when predicting species responses (Küster *et al.,* 2008; Roberts *et al.,* 2010). Investigations into functional types under major functional groups (i.e. annual and perennial forbs or grasses) may therefore reveal trends in functional stability despite taxonomic species loss in response to perturbation (Fuhlendorf *et al*., 2001; Liira *et al*., 2008; Rutherford *et al*., 2012). The loss of taxonomic diversity is therefore not necessarily linked to functional trait diversity loss (Botha *et al.,* 2017). Functional type richness is the most well-known measure for determining functional trait diversity in a community (Cadotte *et al*., 2011; Pakeman, 2011).

Improved understanding of plant functional trait variation among plant species may allow for more accurate interpretation and predictions of plant abundance and distribution patterns within communities and ecosystems in response to disturbance (Weiher *et al*., 1999; McGill *et al*. 2006; Kraft *et al*., 2008; Zirbel *et al*., 2017). Understanding the trait assemblages and functional types present within an ecosystem could contribute to the conservation of species that uniquely contribute to ecosystem function. Managing ecological restoration according to ecosystem function as predicted by plant functional traits could possibly ensure increased success in restoration efforts despite the known unpredictable outcomes of ecological restoration (Suding, 2011; Zirbel *et al*., 2017).

This chapter aimed to investigate the responses forb- and grass trait assemblages to drought across land-use types within the Mopaneveld. It was expected that regional species that persist on mine dumps will present pre-adapted traits that confer stress-tolerance. Forbs were expected to remain stable in abundance or increase in dominance compared to grass species due to a variety of functional traits prompting sound recovery. Differences between functional traits were assessed in terms of pre-drought- and drought release trait composition and diversity in a protected area, Cleveland Game reserve (CGR), and two rehabilitated mine dumps: a rock dump (RD) and tailings dam (TD). This study also anticipated that the Mopaneveld may maintain its resilience to anthropogenic disturbance (Van Staden, 2016) despite the recent drought, through diverse functional traits. Herbaceous functional traits and –groups that confer drought tolerance in transformed Mopaneveld were explored.

6.2 Methods

For experimental- and sampling design, please refer to sections 4.2 and 4.3. Detailed descriptions of plant functional traits considered in this study, are presented under section 4.4. Refer to sections 4.5.1 to 4.5.4 for methodology on data analyses related to hypothesis testing in this chapter.

6.3 Results

Results presented here considered the effects of drought (during the 2015-2016 rainfall season) on herbaceous vegetation (i.e. forbs and grasses) as measured during drought release (i.e. after substantial rain in March 2018). This chapter reports on shifts in plant functional trait assemblages and plant functional type shifts across land-use types at PC in response to the drought.

6.3.1 Plant functional trait composition

6.3.1.1 Anthropogenic impact on trait assemblages

Significant trait assemblage variation was revealed across all land-use types, except between the TD and RD for pre-drought grass communities (Table 6.1). Distinctive forb and grass trait assemblages were revealed for each land-use irrespective of rainfall variability (Fig. 6.1). The differences observed were significant for both life forms, although forbs presented stronger clustering compared to grasses, especially during drought release (Table 6.1). Forb trait assemblages revealed a clear separation between mining and protected areas, which was not as clear for grass trait assemblages (Fig.6.1A, C). Grass trait assemblages in the protected area became even less clustered during drought release (Fig.6.1B, D).

Table 6.1: PERMANOVA and pair-wise comparisons indicating significance of differences between land-use types for forb and grass functional traits respectively, in response to rainfall variability.

	***F*-value**	***t*-value**	***p*-value**
Pre-drought			
Forbs	16.21		0.001*
Cleveland Game Reserve and Rock Dump		4.68	0.001*
Cleveland Game Reserve and Tailings Dam		4.37	0.001*
Rock Dump and Tailings Dam		3.38	0.001*
Grasses	6.13		0.001*
Cleveland Game Reserve and Rock Dump		2.98	0.001*
Cleveland Game Reserve and Tailings Dam		3.41	0.001*
Rock Dump and Tailings Dam		0.89	0.494
Drought release			
Forbs	17.87		0.001*
Cleveland Game Reserve and Rock Dump		5.57	0.001*
Cleveland Game Reserve and Tailings Dam		4.71	0.001*
Rock Dump and Tailings Dam		1.67	0.032*
Grasses	8.08		0.001*
Cleveland Game Reserve and Rock Dump		2.47	0.002*
Cleveland Game Reserve and Tailings Dam		3.22	0.001*
Rock Dump and Tailings Dam		2.68	0.001*

* Denotes significant variation at $p \leq 0.05$; *F* and *t*: measure of effect size relative to variation in the data.

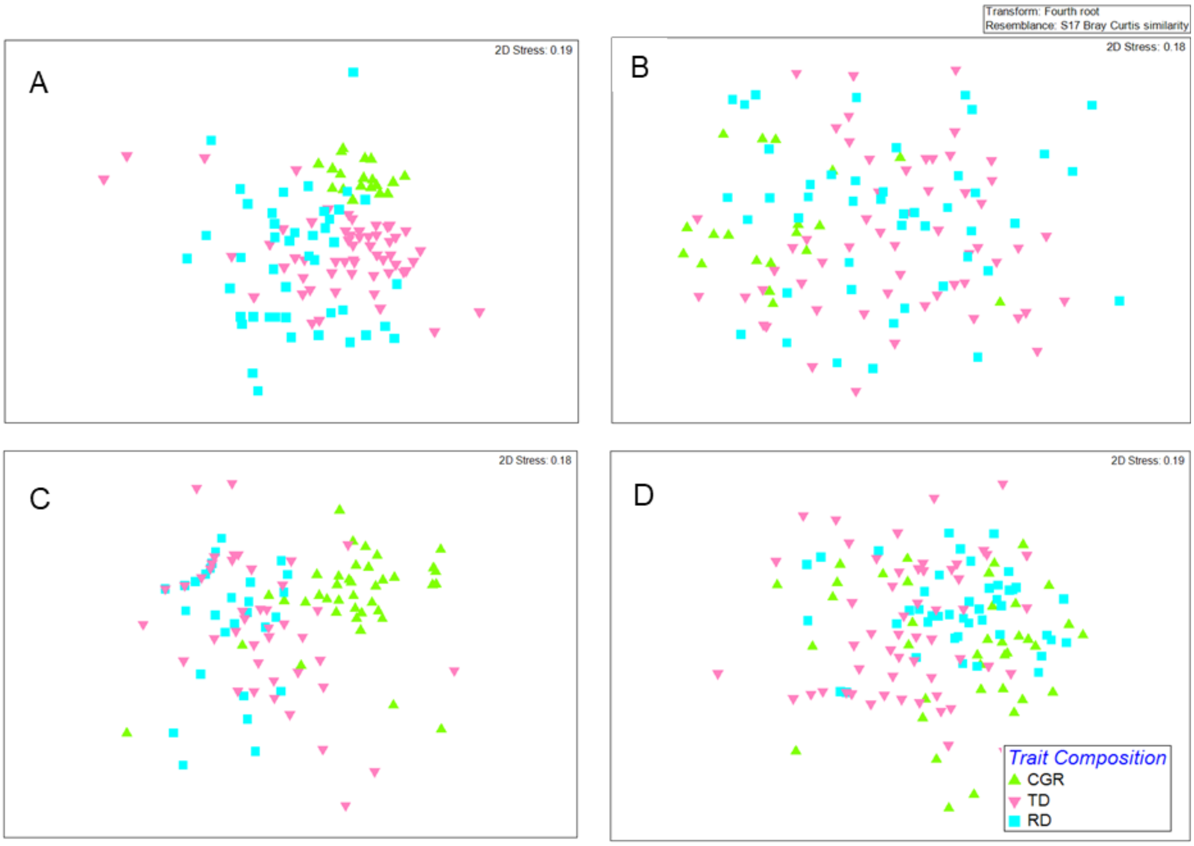

Figure 6.1: Non-Metric Multidimensional Scaling (NMDS) ordinations of plant functional trait assemblages across land-use types before the drought and during drought release (pre-drought: forbs (A), grasses (B); drought release: forbs (C), grasses (D)).

6.3.1.2 Drought effects on trait assemblages

Non-Metric Multidimensional Scaling (NMDS) further revealed that functional trait assemblages differed significantly in response to rainfall variability for both life forms, but more so for grasses (Fig. 6.2, Table 6.2).

Table 6.2: PERMANOVA results indicating significant differences between pre-drought and drought release communities for forb and grass functional traits respectively.

	Forbs		**Grasses**	
	***F*-value**	***p*-value**	***F*-value**	***p*-value**
Combined land-use types	15.59	0.001*	19.15	0.001*
Tailings dam	15.45	0.001*	12.86	0.001*
Rock dump	8.51	0.001*	2.86	0.001*
Cleveland Game Reserve	6.68	0.001*	9.39	0.001*

* Denotes significant variation at $p \leq 0.05$; *F:* measure of effect size relative to variation in the data.

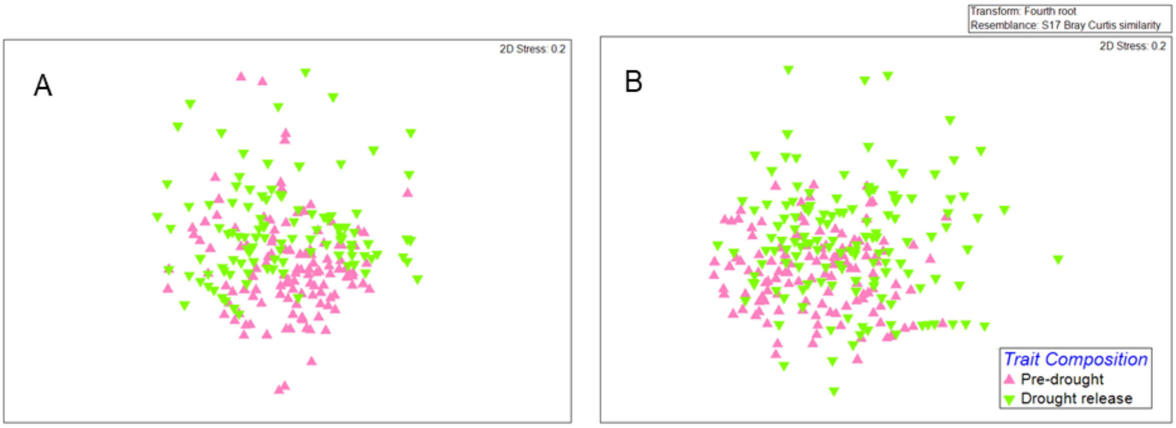

Figure 6.2: Non-Metric Multidimensional Scaling (NMDS) ordinations indicating plant functional trait assemblage shifts in response to drought for forbs (A) and grasses (B), irrespective of land-use type.

After separating land-use types to assess drought effects on community assemblages under different initial environmental conditions, forb trait assemblages revealed stronger clustering on mine dumps, while grass trait assemblages revealed stronger clustering in the protected area (Fig. 6.3, Table 6.2).

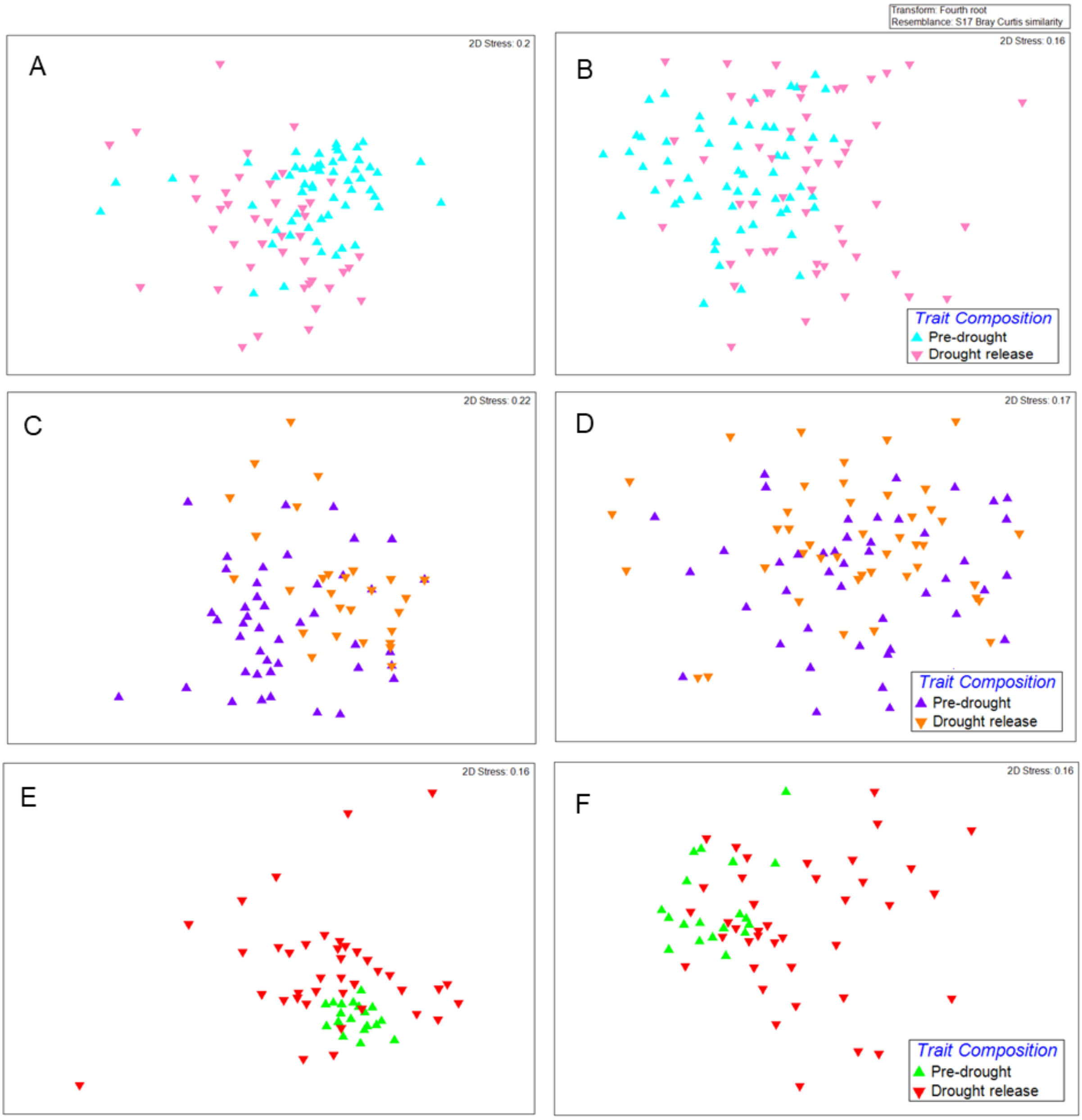

Figure 6.3: Non-Metric Multidimensional Scaling (NMDS) ordinations indicating plant functional trait community shifts in response to drought for forb and grass life forms at each land-use type, tailings dam (TD), rock dump (RD) and Cleveland Game Reserve (CGR). TD - forbs (A), grass (B); RD - forbs (C), grass (D); CGR - forbs (E), grass (F).

6.3.1.3 Plant functional trait diversity

Forb trait richness (Margalef) and diversity (Shannon) were significantly affected by drought and land-use effects respectively, but no significant interaction effect was revealed. Margalef grass trait richness and Shannon diversity were significantly affected by land-use only, and not by rainfall variability, nor its interaction (Table. 6.3). Total grass trait richness and evenness revealed significant rainfall and land-use type interactions, suggesting that grass traits responded significantly to the combined effects of drought and anthropogenic disturbances, especially the total complement of grass traits, as well as how they dominated.

Table 6.3: Two-way ANOVA type Hierarchical Linear Modelling (HLM) tests for differences in plant functional trait diversity index values of species across land-use types in response to drought.

Fixed effects:	**Forbs**		**Grasses**	
Rainfall year : Land-use				
	F_{df}	P	F_{df}	P
Total traits				
Rainfall year	50.50_1	< 0.001*	15.28_1	< 0.001*
Land-use	31.86_2	< 0.001*	12.63_2	< 0.001*
Rainfall year: Land-use	1.86_2	0.158	3.87_2	0.022*
Margalef's species richness				
Rainfall year	18.56_1	< 0.001*	29.97_1	0.314
Land-use	17.68_2	< 0.001*	58.71_2	< 0.001*
Rainfall year: Land-use	0.18_2	0.838	26.37_2	0.582
Shannon diversity				
Rainfall year	36.93_1	< 0.001*	2.80_1	0.095
Land-use	13.45_2	< 0.001*	3.57_2	0.030*
Rainfall year: Land-use	2.25_2	0.108	1.49_2	0.227

Pielou’s evenness				
Rainfall year	7.37_1	0.007*	27.29_1	< 0.001*
Land-use	1.19_2	0.306	5.77_2	0.004*
Rainfall year: Land-use	2.60_2	0.077	3.28_2	0.039*

* Indicates significant *p* - values at $p \leq 0.05$; *F:* measure of effect size relative to variation in the data; df: degrees of freedom.

Forb and grass traits responded differently to drought (Fig. 6.4). Stronger drought effects were revealed for forb functional trait diversity index values than grasses (Bonferroni, $p < 0.05$; Appendix E, Table E1). These effects were only observed on the mine dumps (Bonferroni, $p < 0.05$; Appendix E, Table E1), as no significant differences in diversity indices for forb functional traits were apparent in the protected area (Fig. 6.4A, C, E, and G). No significant declines in grass functional type richness (Margalef’s richness; Fig. 6.4D) or diversity (Shannon diversity; Fig 6.4F) were observed, although the number of grass traits declined significantly in the protected area and the TD (Fig. 6.4B, Bonferroni, $p < 0.05$; Appendix E, Table E1). Plant functional trait evenness presented a significant increase at the TD for both life forms, and at CGR for grass traits (Fig. 6.4G, H; Bonferroni, $p < 0.05$; Appendix E, Table E1).

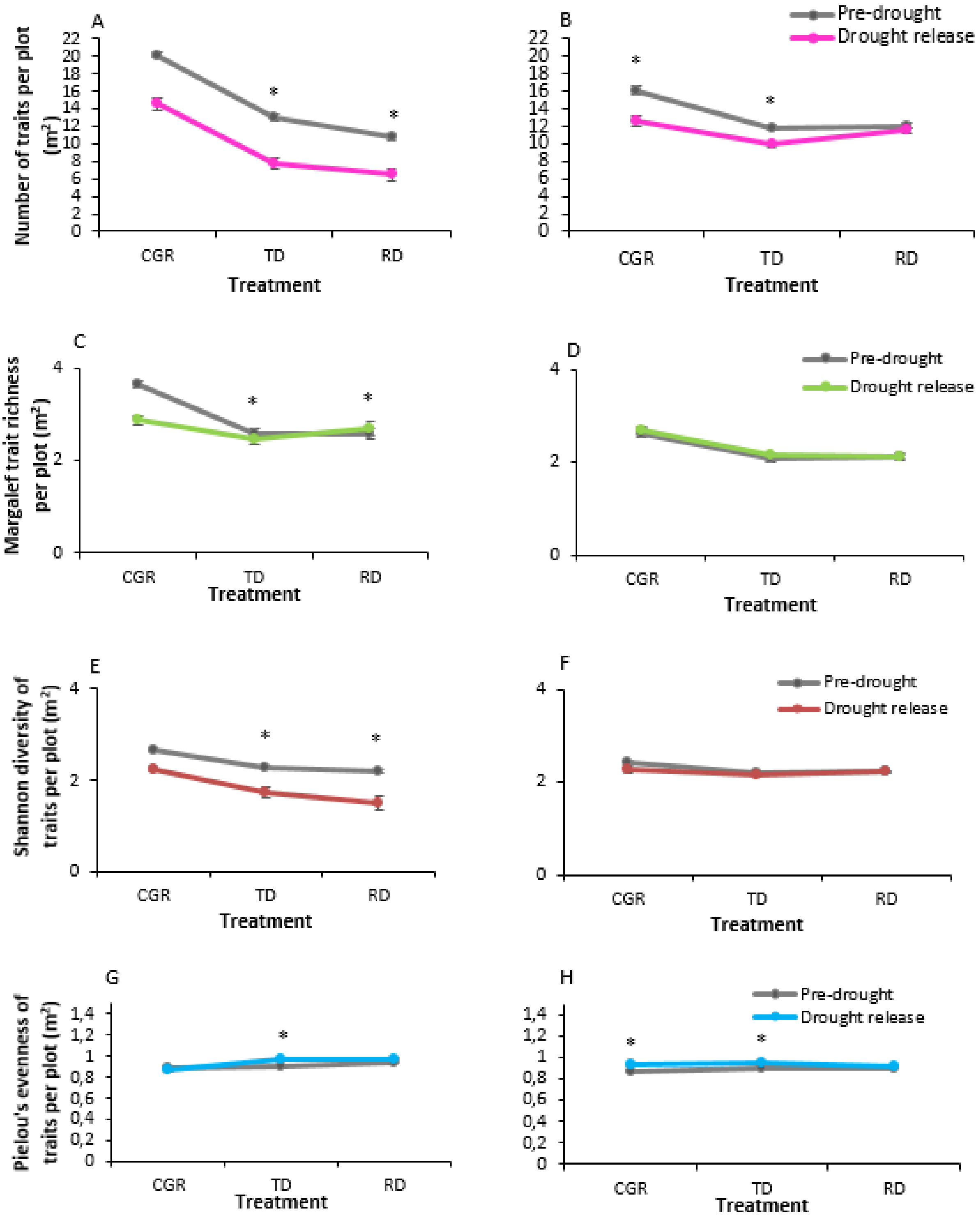

Figure 6.4: Diversity indices for herbaceous plant functional traits (PFT's) before drought and during drought release for across land-use types (Mean number of traits: forbs (A), grasses (B); Margalef's richness: forbs (C), grasses (D); Shannon diversity: forbs (E), grasses (F); Pielou's evenness: forbs (G), grasses (H)). * indicates significant differences in PFT indices between rainfall years (Appendix E, Table E1).

6.3.2 Plant functional types

6.3.2.1 Classification of functional types

Annual grasses

Unweighted Pair Group Method with Arithmetic Means (UPGMA) analyses for annual grasses revealed three distinct terminal groups which were interpreted as three distinct plant functional types (PFT's; Type I, II and III) (Fig. 6.5). PFT's were separated at two hierarchical trait-levels. The first level separation was induced by shade tolerance, palatability and leaf area. Dispersal mode explained the second hierarchical trait-level separation (Fig. 6.5). Type III was the dominant annual grass PFT consisting of four species (Fig. 6.5; Table 6.4).

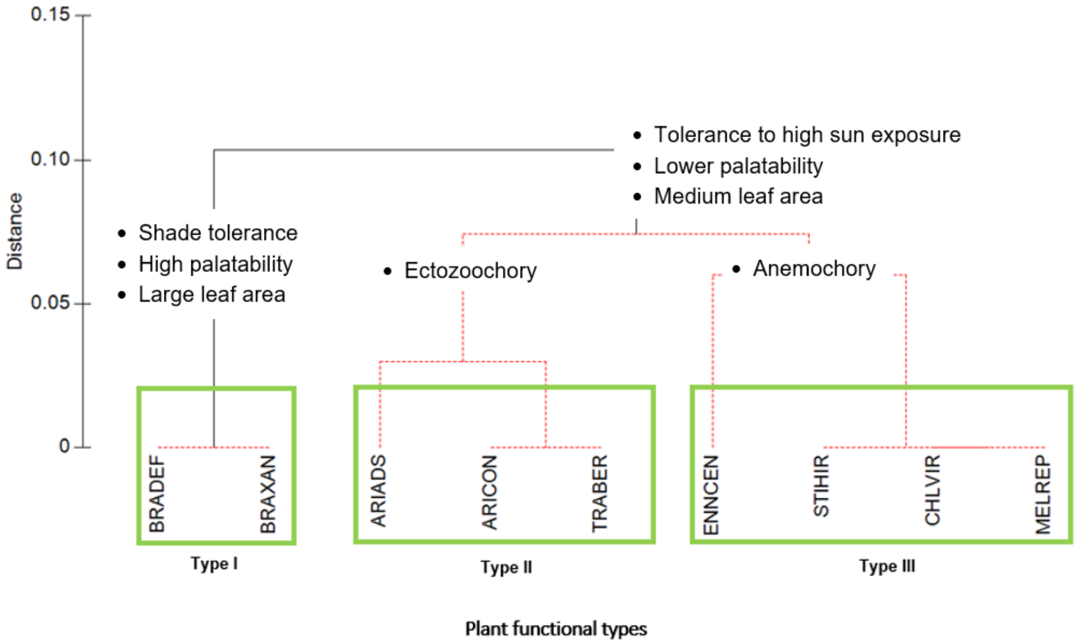

Figure 6.5: Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis based on Modified Gower distance measure indicating annual grass functional types (PFTs). (See species names represented by six-letter species codes in Appendix B, Table B1).

Perennial grasses

UPGMA analyses for perennial grasses revealed four distinct plant functional types (Fig. 6.6). The four PFT's were separated at two hierarchical trait-levels. The first level separation was based on vegetative growth, where after the lineage without vegetative growth was split according to palatability (2nd level) and the vegetative growth lineage was split according to dispersal mode (2nd level) (Fig. 6.6). Type IV and VI were the most dominant perennial grass PFT's, consisting of 11 species each (Fig. 6.6; Table 6.4)

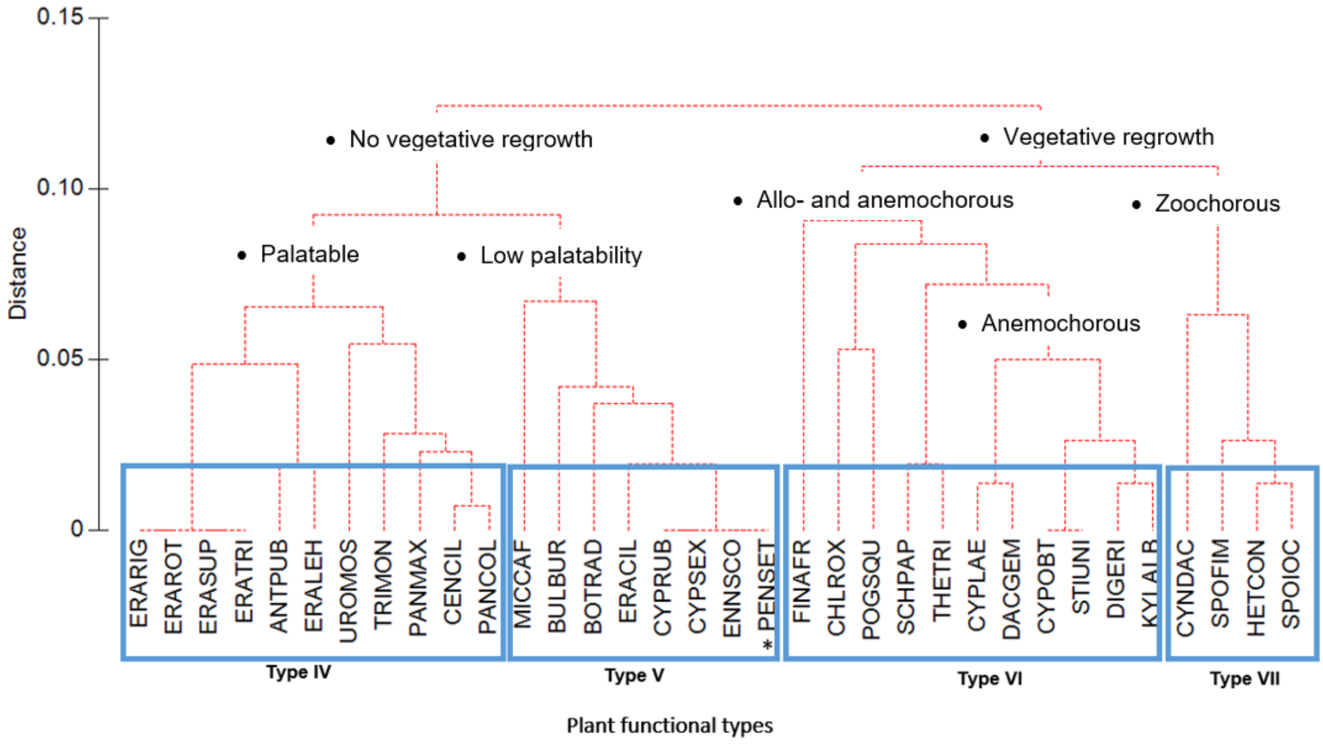

Figure 6.6: Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis based on Modified Gower distance measure indicating perennial grass functional types (PFTs). (See species names represented by six-letter species codes in Appendix B, Table B1). * = Exotic species

Annual forbs

UPGMA analyses for annual forbs revealed four distinct plant functional types (PFT) (Fig. 6.7). Three hierarchical trait-levels were discernible for annual forbs. The first trait-level separation was based on dispersal mode, where after allochorous species were split according to growth form (2nd level). The PFT containing erect species also contained nitrogen-fixers (Type IX), while absent from the prostrate group (Type VIII). Species with specialized dispersal modes (not allochory) split according to palatability (2nd level), and palatable species separated into a third hierarchical level according to growth from (Fig. 6.7). The most dominant annual forb PFT was Type IX, comprising of 19 species (Fig. 6.7; Table 6.4).

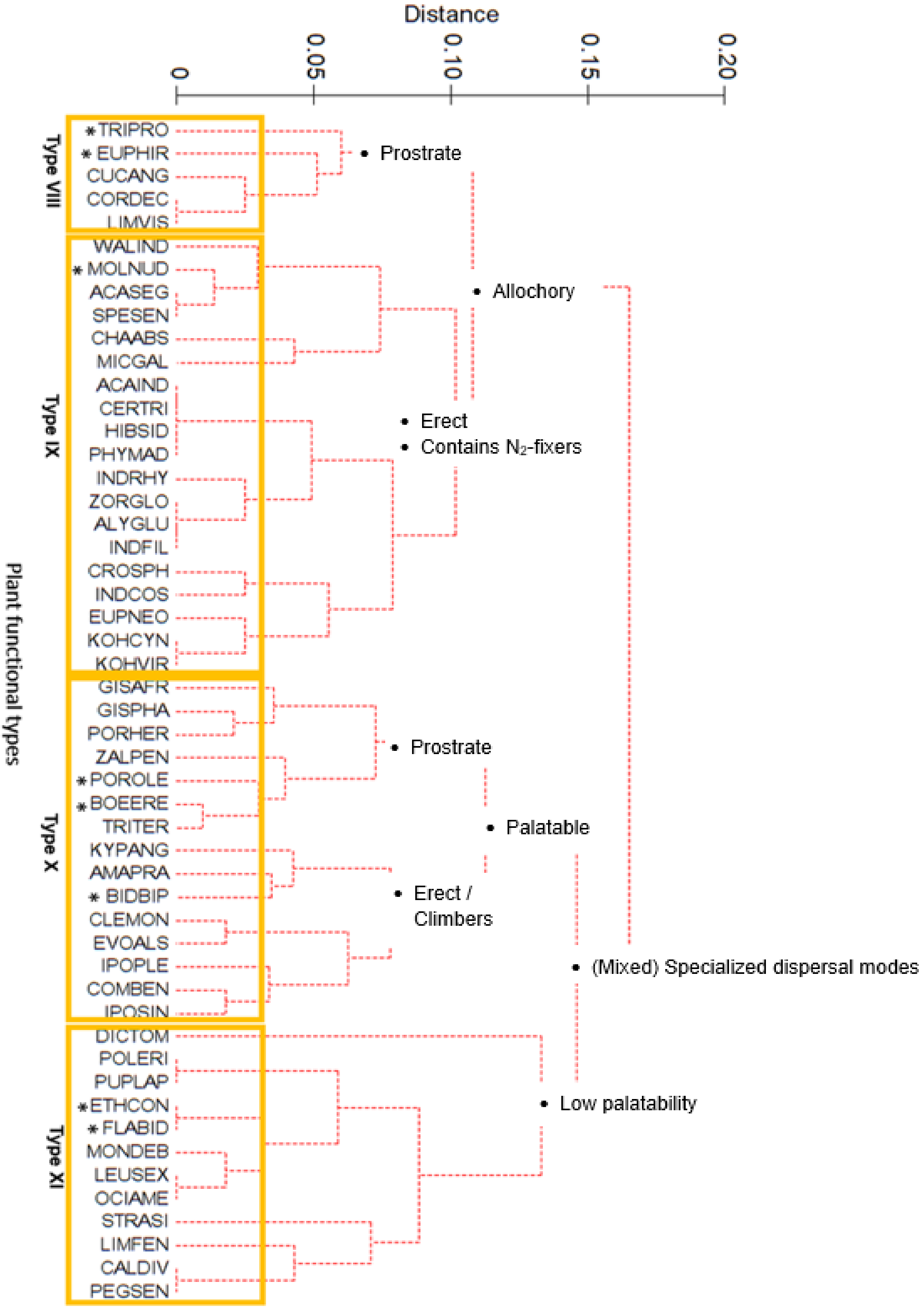

Figure 6.7: Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis based on Modified Gower measure indicating annual forb functional types (PFTs). (See species names represented by six-letter species codes in Appendix B, Table B1). * = Exotic species

Perennial forbs

UPGMA analyses for perennial forbs revealed five distinct plant functional types (PFT) (Fig. 6.8). Perennial forbs separated according to three hierarchical trait-levels. As with annual forbs, the first level separated according to dispersal mode, with species that have specialized dispersal modes separating according to palatability (2nd level) and palatable species separating according to growth form (3rd level) (Fig. 6.8). However, for the purpose of this study, the allochorous lineage was split according to indistinct traits (2nd level), and then again according to nitrogen fixing ability (3rd level). The indistinct 2nd level group was grouped together with the non-nitrogen-fixers (Fig. 6.8). The dominant perennial forb PFT was Type XIV with 19 species (Fig. 6.8; Table 6.4).

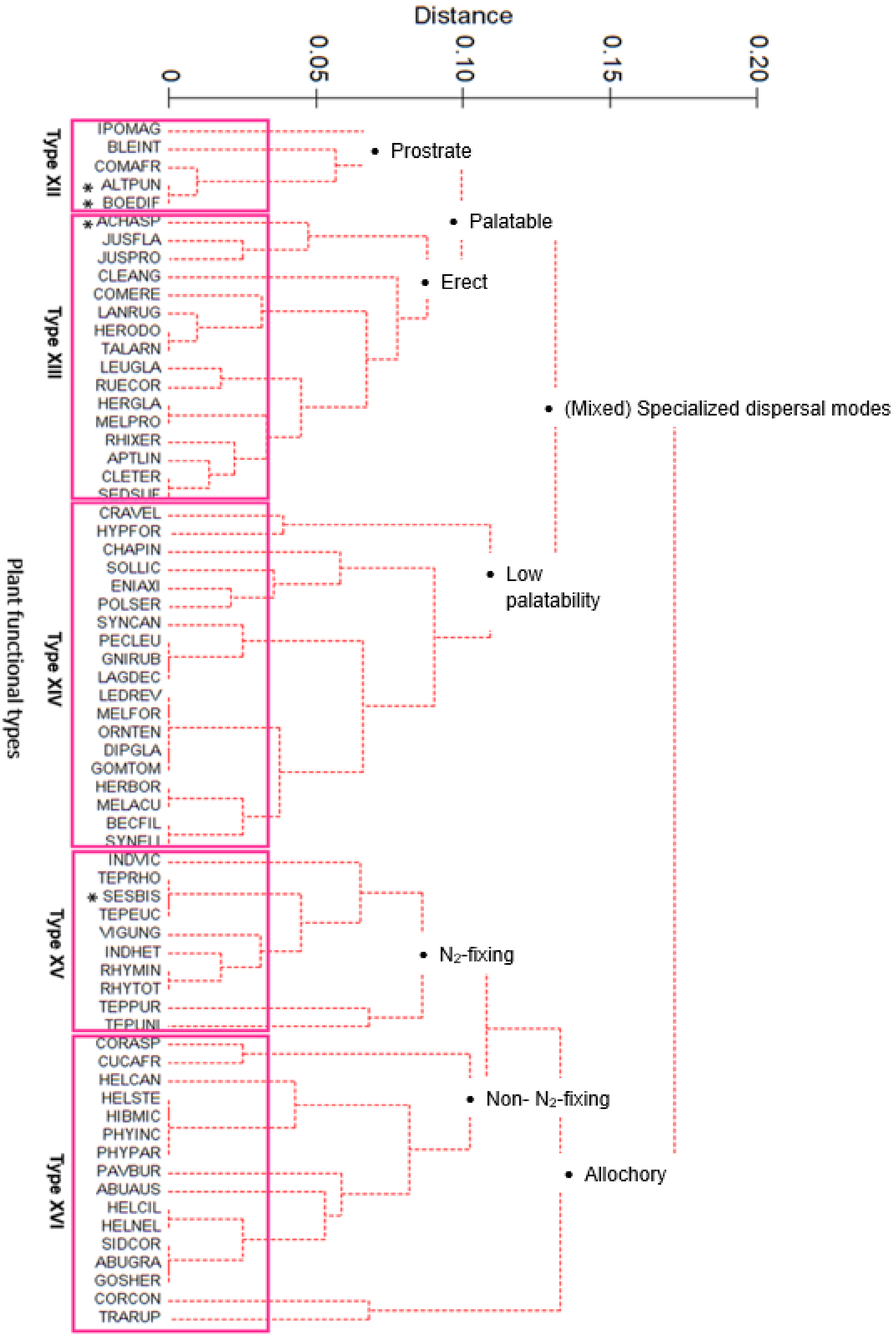

Figure 6.8: Unweighted Pair Group Method with Arithmetic Mean (UPGMA) cluster analysis based on Modified Gower distance measure indicating perennial forb functional types (PFTs). (See species names represented by six-letter species codes in Appendix B, Table B1). * = Exotic species

Table 6.4: Summary of plant functional types (PFT's) and their attributes obtained from Unweighted Pair Group Method with Arithmetic Mean (UPGMA) results. See Appendix E, Table E2 for a detailed list of species corresponding to PFTs in this table.

PFT	**Description**		
Type I	Annual	Grass	Shade tolerant; endozoochorous; high palatability
Type II	Annual	Grass	Tolerant to sunlight; ectozoochorous; low palatability
Type III	Annual	Grass	Tolerant to sunlight; anemochorous; low palatability
Type IV	Perennial	Grass	Non-clonal/resprouting; high palatability
Type V	Perennial	Grass	Non-clonal/resprouting; low palatability
Type VI	Perennial	Grass	Clonal/resprouting; allo- and anemochorous
Type VII	Perennial	Grass	Clonal/resprouting; zoochorous
Type VIII	Annual	Forb	Allochorous; prostrate
Type IX	Annual	Forb	Allochorous; erect, nitrogen (N_2) fixing
Type X	Annual	Forb	(Mixed) Specialized dispersal; high palatability
Type XI	Annual	Forb	(Mixed) Specialized dispersal; low palatability; erect
Type XII	Perennial	Forb	(Mixed) Specialized dispersal; high palatability; prostrate
Type XIII	Perennial	Forb	(Mixed) Specialized dispersal; high palatability; erect
Type XIV	Perennial	Forb	(Mixed) Specialized dispersal; low palatability; erect
Type XV	Perennial	Forb	Allochorous; nitrogen (N_2) fixing
Type XVI	Perennial	Forb	Allochorous; non-nitrogen (N_2) fixing

6.3.2.2 Plant functional type composition shifts in response to drought

6.3.2.2.1 Cleveland Game Reserve

The protected area revealed an increase in annual grasses (Type I, II and III) and decline in dominant perennial grasses (Type VI) in response to drought (Fig. 6.9A, B). Increasing PFT’s predominantly consisted of traits such as zoochory and anemochory, tolerance to sunlight, and low palatability (Table 6.4). Decreasing grass PFT’s mainly consisted of perennial, clonal/resprouting species (Table 6.4).

Annual, allochorous, nitrogen-fixing forbs (Type IX; Table 6.4) increased three-fold during drought release, along with an increase in palatable annual forbs with specialized dispersal modes (Type X) (Fig. 6.9C, D). This increased the frequency contribution of annuals in the forb PFT community from 47 % to 80 % in response to drought.

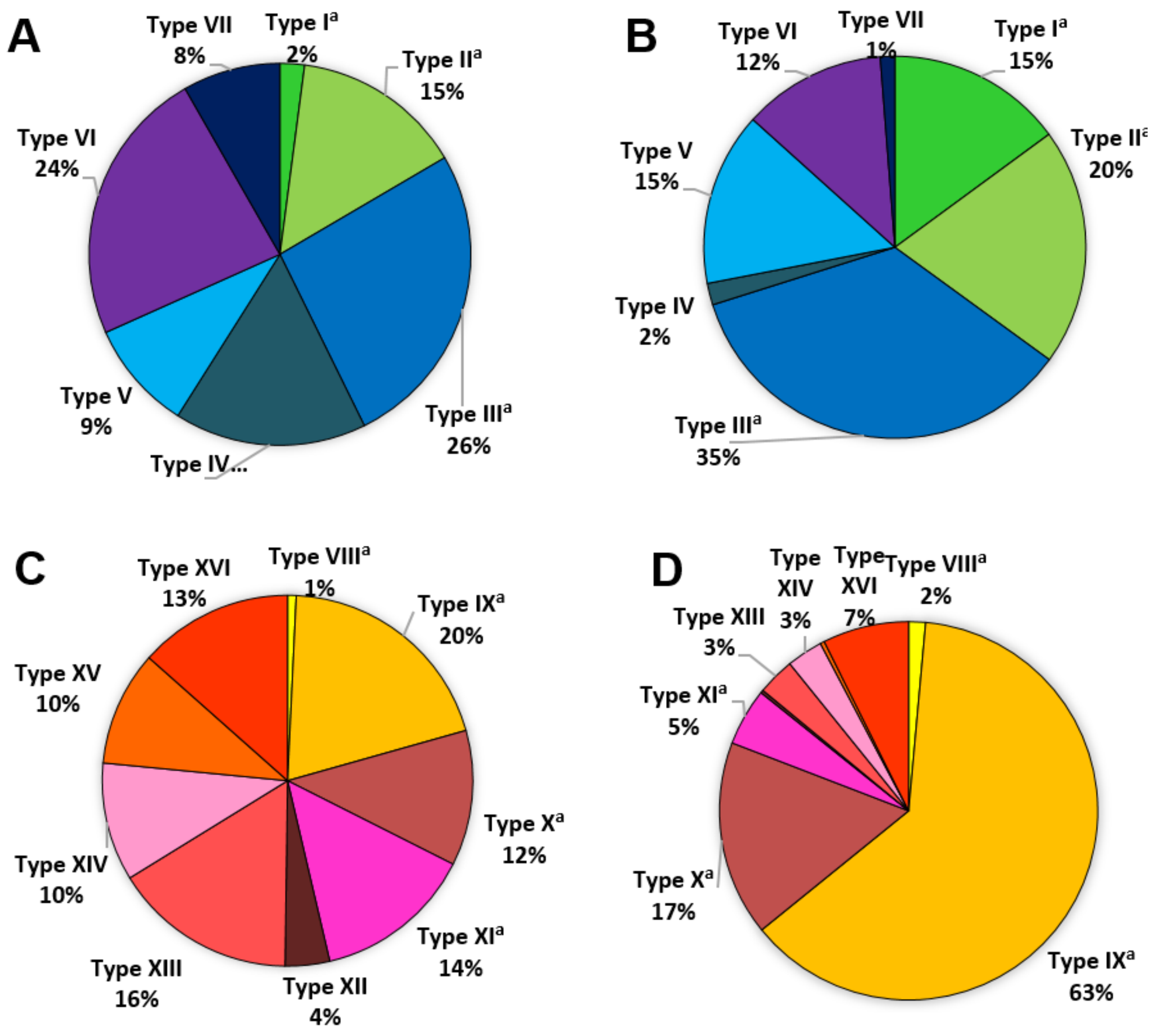

Figure 6.9: Frequency of plant functional types within the protected area (CGR) before the drought and after drought release. (Grass: A = Pre-drought, B = Drought release; Forbs: C = Pre-drought; D = Drought release)
ᵃ represents annual PFT's.

6.3.2.2.2 Mine dumps

On the mine dumps, the dominant PFT's (Type II, III and IV) remained dominant regardless of rainfall variability, although a shift from perennial to annual grass PFT dominance was evident (Fig. 6.10A, B). The dominant grass PFT's consisted of annual, sun tolerant species with a low palatability, and non-clonal/resprouting, palatable perennials that were reduced to half of their pre-drought frequency contribution (Fig. 6.10A, B; Table 4).

Perennial, allochorous, nitrogen fixing forbs (Type XV) made up 62 % of the overall PFT frequency contributions on the mine dumps before the drought (Fig. 6.10C). Perennial, allochorous nitrogen-fixers (Type XV), were reduced to 46 % in response to drought, while annual, allochorous nitrogen fixers (Type IX) increased during drought release (Fig. 6.10B).

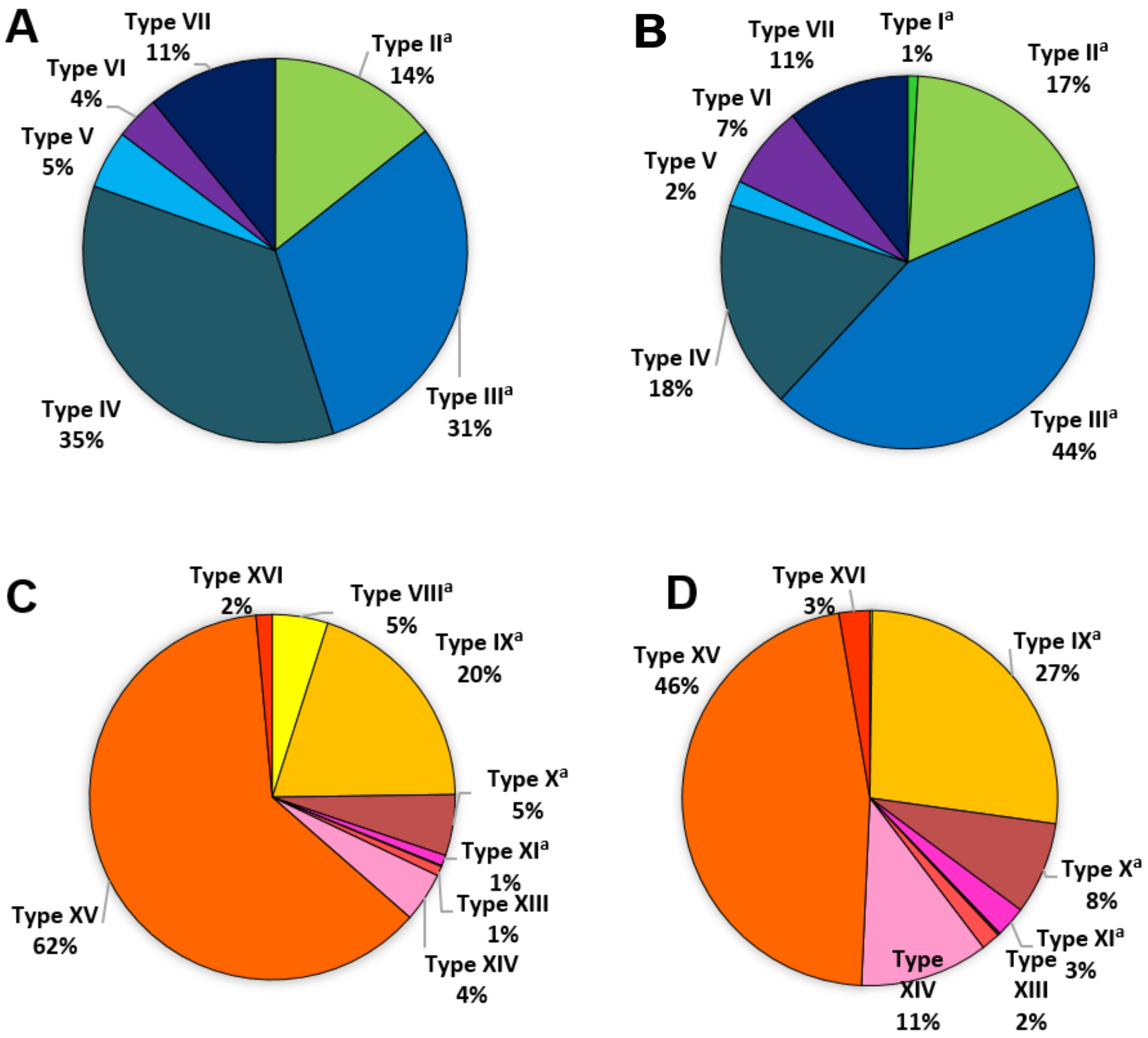

Figure 6.10: Frequency of plant functional types at both transformed areas combined (TD, RD), before the drought and after drought release. (Grass: A = Pre-drought, B = Drought release; Forbs: C = Pre-drought; D = Drought release).
PFT's with frequencies < 1, but > 0 excluded from C include: Type XII
PFT's with frequencies < 1, but > 0 excluded from D include: Type VIII and Type XII
See Appendix E, Fig. E1 and E2 for separated diagrams of transformed areas.
^{a} represents annual PFT's.

6.3.2.3 Functional type responses to land-use and drought

The PCA analyses revealed a strong land-use effect on the first Principle Component (Axis 1), with the mine dump plots clustering to the left of the biplot and the protected area plots to the right (Fig. 6.11B, Fig. 6.12). However, the second Principle Component (Axis 2) may be related to an environmental variable that was not tested for in this study. Pre-drought grass PFT's separated more on Axis 2 (Fig. 6.11A), although most of the variation was still attributed to land-use effect (Table 6.5). Axis 1 and 2 explained less than half of the variation observed in the data, and other components (Axis 3 and 4) may further explain variation seen in the PCA's.

Table 6.5: Eigenvalues attributed to the first two Principle Components (Axis 1 and 2) for forbs and grasses at each land-use in response to rainfall variability.

	Pre-drought			Drought release		
	Eigenvalue Axis 1	Eigenvalue Axis 2	Observed variation (%)	Eigenvalue Axis 1	Eigenvalue Axis 2	Observed variation (%)
Forbs	0.339	0.128	45	0.332	0.137	46
Grass	0.230	0.208	43	0.246	0.186	42

Pre-drought grass PFT's separated into two main groups on Axis 2, based on land-use type (Fig. 6.11A). The RD and TD correlated more with sun tolerant, anemochorous and non-clonal/resprouting grass PFT's (Type III, IV), while the protected area correlated with shade tolerant, highly palatable grass PFT's and mixed dispersal mechanisms (Type I, V, VI) (Fig. 6.11A).

The drought release TD and CGR grass PFT communities were strict opposites on Axis 1, while the RD PFT community was situated at a right angle (90°) to both TD and CGR PFT communities (Fig. 6.11B). During drought release the perennial, non-clonal/resprouting, highly palatable PFT (Type IV) remained associated with the mine dumps (Fig. 6.11B, Table 6.4). The RD became more associated with sun tolerant, ectozoochorous annuals with a low palatability (Type II) and clonal/resprouting, zoochorous perennial grasses (Type VII) (Fig. 6.11B, Table 6.4). The two PFT's closely associated with CGR included highly palatable annual species with a tolerance to limited sunlight and endozoochorous dispersal, as well as non-clonal/resprouting perennials with a low palatability (Fig. 6.11B, Table 6.4).

Before the drought, three main associations of forb PFT's could be distinguished apart from some plots clustering in the middle of the biplot (Fig. 6.12A). The RD was associated with allochorous, prostrate annuals (Type VIII), and the TD with perennial, allochorous nitrogen fixers (Type XV) (Fig. 6.12A, Table 4). Some plots on the TD also associated with the annual, allochorous, nitrogen fixers (Type IX) (Fig. 6.12A, Table 6.4).

After the drought, two main groups could be differentiated, and both mine dumps strongly associated with perennial, allochorous nitrogen fixers (Type XV, Table 6.4) (Fig. 6.12B). Mine dumps were the least associated with annual forb PFT's that had one specific mode of dispersal combined with a low palatability and erect growth form, that were allochorous and did not have the ability to fix nitrogen (Type XI and XVI; Table 6.4). These PFT's, along with highly palatable forb PFT's correlated the most with CGR (closest correlation to the right of Axis 1) (Fig. 6.12A, B). Type X and XIII were also closely linked to CGR, and consisted of highly palatable species with a single specialized dispersal mode (Fig. 6.12A, B; Table 6.4).

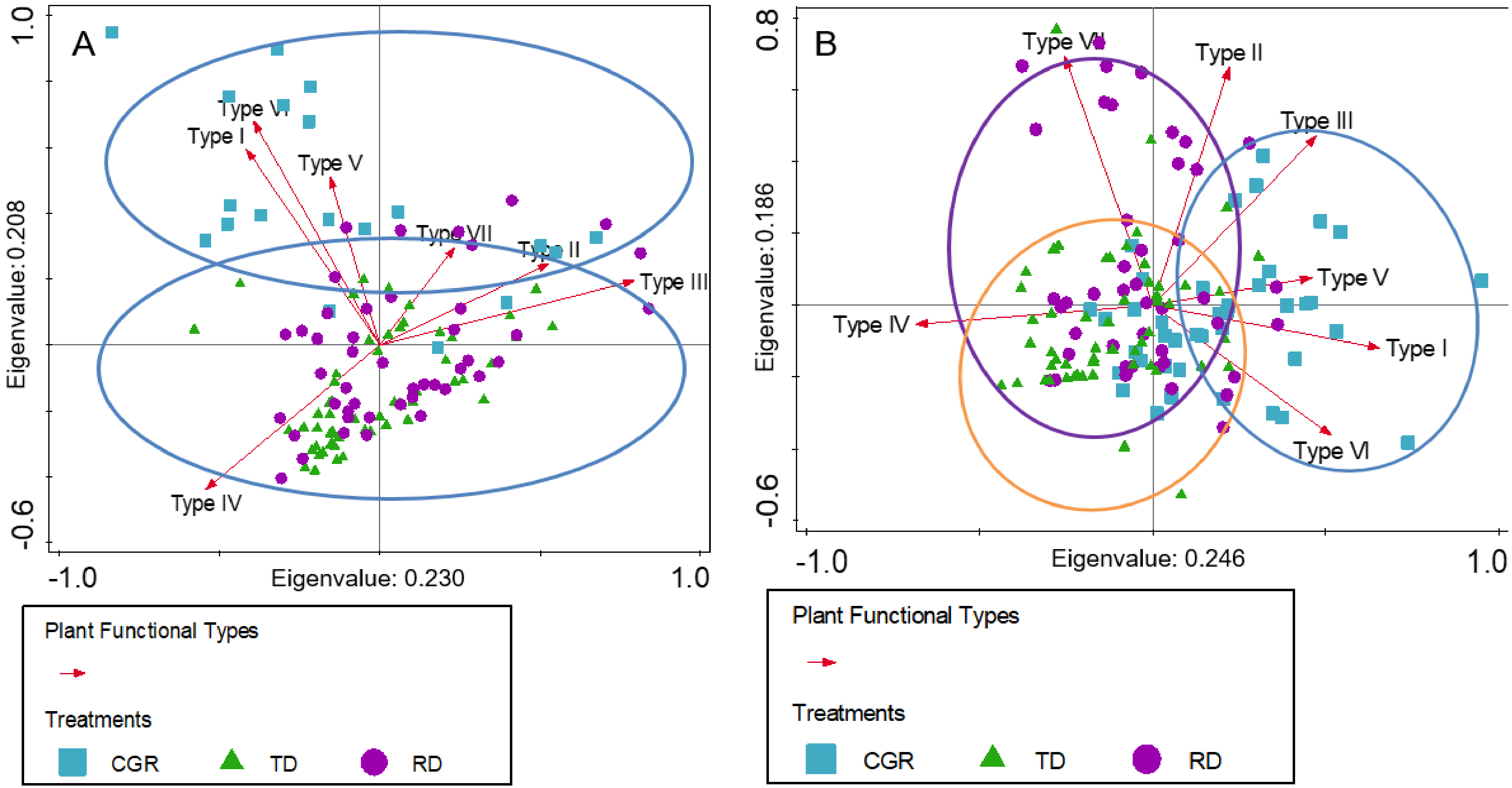

Figure 6.11: Principal Component Analysis (PCA) of grass functional types across protected (CGR) and transformed (RD, TD) areas before the drought (A) and during drought release (B). Trait abundance data were square root transformed.

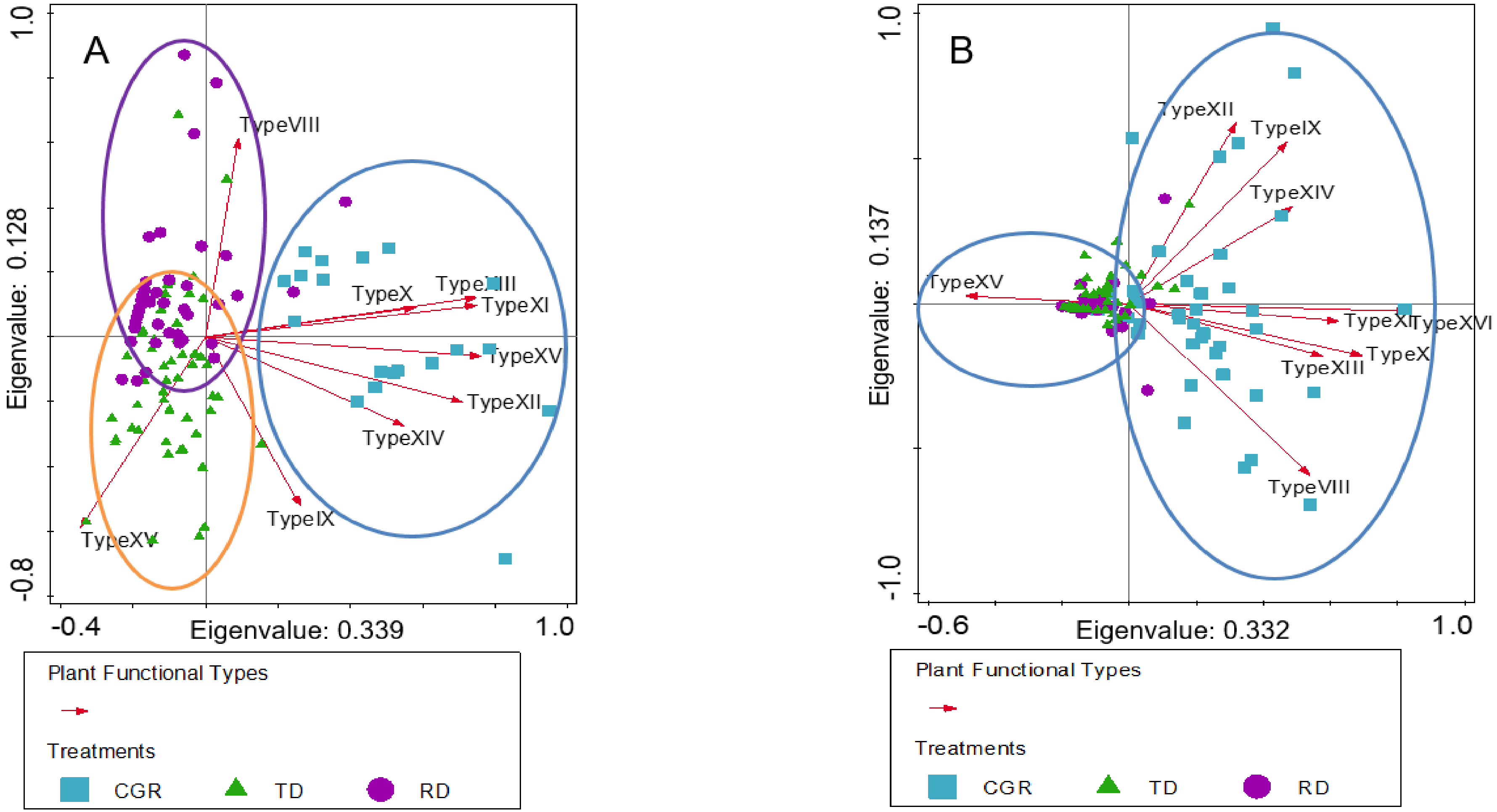

Figure 6.12: Principal Component Analysis (PCA) of forb functional types across protected (CGR) and transformed (RD, TD) areas before the drought (A) and during drought release (B). Trait abundance data were square root transformed.

CHAPTER 7

Discussion

7.1 Herbaceous community composition shifts in response to drought

7.1.1 Drought effects on herbaceous species composition

7.1.1.1 Anthropogenic effects

Mining practices resulted in compositional shifts for both herbaceous species and plant functional traits in response to drought. The weak clustering of forb traits on CGR relative to grass traits suggest that forbs provide trait-based redundancy, suggesting that Mopaneveld ecosystems are resilient to drought through specific forb trait types (Klem, 2018). However, traits possessed by the grass species which dominated on the mine dumps conferred higher tolerance to drought for herbaceous communities, despite the low diversity of forbs. This suggests that grasses can be considered an important life form in mine rehabilitation.

Distinct species assemblages in the land-use types could be attributed to edaphic factors (McIntyre *et al*., 1995; O'Connor, 1999). Semi-arid ecosystems are naturally limited in terms of soil water and nutrients, which affects establishment of seedlings, and thus species distributions and community composition (Soliveres *et al.,* 2012). The rock dump and tailings soils, being deficient in nutrients and rich in toxic heavy metals (Huang *et al.,* 2011), would further impede establishment and persistence, as plants generally take up heavy metals from the soil (Howard-Williams, 1971; Ernst, 1972). These metals could be toxic to many species from the regional species pool, resulting in the absence of these species on the mine dump (Overesch, *et al*., 2007; Mapaure *et al*., 2011). The topography on mine dumps also differed from that of the protected area. Soil and topography are determinants of forb community composition in natural systems (Augustine, 2003; Masunga *et al.,* 2013; Linstädter *et al*., 2016; Clegg and O'Connor, 2017) and may be the leading cause for differences observed in forb species communities. Although not tested for in this study (composition differences between terraces and slopes), a possible explanation for changes could be that mine dump terraces hold a higher concentration of phosphorus (P) (Smith, 2016) which favours grass species, while limited P favours forbs (Siebert and Dreber, 2019).

7.1.1.2 Effects of drought

Decreasing plant cover caused by drought may result in soil erosion and lower water-use efficiency in plants in protected and transformed ecosystems, which further alters species composition (Illius and O'Connor, 1999). In this study, forb species were more responsive to rainfall variability than grasses across land-use types. However, the grass community was more affected by drought in the protected Mopaneveld compared to the mine dumps, while forbs were more affected on the mine dumps. Herbaceous species occurring on the mine dump prior to the drought (predominantly grass species) appear to possess adaptations that enable them to persist under harsh conditions, similar to conditions occurred during the drought, such as high temperatures and low water and nutrient availability (Sheoran and Sheoran, 2010). This can explain why these species were relatively less impacted on mine dumps than in in the protected Mopaneveld. These grass traits that were pre-selected for include fibrous root systems (to stabilise mine soils and delay erosion), tolerance to drought, low nutrient requirements, and reliable germination, establishment and rapid growth rate (Helm, 1995; Sheoran *et al*., 2010, Nurtjahya and Franklin, 2017). The careful selection of grass species with such traits may contribute to the stability of grass trait composition on the mine. Forb species are known to vary in their response to drought, and for large inter-annual variations in response to the amount, frequency and timing of rainfall (Dreber and Esler, 2011).

Both life forms revealed site-specific communities, which was indicative of a strong land-use type effect on herbaceous communities in the Mopaneveld. Sensitive forbs (i.e. only present in the protected area) and tolerant forbs (i.e. only present on mine dumps) dominated over grasses regardless of rainfall variability, but resistant forbs and grasses (i.e. present in protected area and on mine dumps) were equal. This suggests that forb communities were more site-specific than grasses, likely a result of forbs being precursors of change in herbaceous vegetation, especially after disturbance and drought (Van Coller and Siebert, 2015). Herbaceous trait assemblages, especially grass traits, did not respond in the same way. An overall shift in plant functional trait composition and a stronger negative effect of drought on the mine dump plant functional trait composition was anticipated. Shifts in trait assemblages observed during drought release varied between life forms. These results suggest that herbaceous life forms do not only reveal dynamic shifts in dominance in response to rainfall variability (Van Coller *et al*., 2018), but also on a functional level, whereby grass traits were more stable under mining conditions and forb traits persisted in the protected area. Introduced grass species are selected for due to specific traits that aid in restoration (Helm, 1995; Sheoran *et al*., 2010, Nurtjahya and Franklin, 2017). Therefore, the stability of grass traits may be a result of introduced grass species, which would then indicate successful restoration effort when considering that a primary aim of restoration is prevent erosion and establishment of grass species provides soil stability (Helm, 1995; Singh *et al*., 2002). Forb species are well adapted to natural stress conditions of Mopaneveld and make up a considerable contribution to savanna herbaceous community variation particularly during drought (Jordaan *et al*., 2004; Rutherford *et al*., 2012; Siebert and Dreber, 2019). Although a distinct trait composition which would allow species to persist during harsh conditions on the mine dumps was expected after the drought, clustering of traits were not as prominent as expected, even though forbs did present more clustering than grasses. This may indicate that grass traits are more redundant than forb traits, although weak clustering of functional traits of both life forms suggest trait-based redundancy in this transformed Mopaneveld.

The protected area revealed much stronger response patterns to drought on species- and functional trait-levels compared to mined sites, highlighting the dynamic nature of the Mopaneveld (Skarpe, 1992; Siebert *et al*., 2003a; Bond, 2005). Furthermore, forbs on the TD displayed trait-based redundancy, despite strong drought effects on forb species community responses. RD species- and trait communities remained stable in response to drought. The RD was intermediate between the protected area and TD, since it was neither protected, nor was its soil chemistry transformed to the extent of the TD. The TD soil has a high metal concentration originating from the copper ore, which easily leaches into the soil due to its fine particle size (Eriksson and Destouni, 1997; Hansen *et al.,* 2013; Smith, 2016), while rocks on the RD have been removed to expose the ore body (Eriksson and Destouni, 1997; Smith, 2016) and are still subject to natural weathering. This could explain the herbaceous species and functional responses revealed on the different land-use types.

Dissimilarities in herbaceous species community assemblages on mine dumps in response to drought were mainly driven by forbs belonging to the Fabaceae family, known for its ability to fix nitrogen, which are particularly important in mine dump restoration practices (Zhang *et al.,* 2001; Sheoran *et al.,* 2010; Behura *et al.,* 2015). Prevalence of the Fabaceae family agreed with Wagner *et al*. (2016) who reported that nitrogen-fixing herbaceous legumes may increase in abundance after disturbances in dry savanna rangelands. Leguminous forbs are often introduced on mine dumps to fix nitrogen as it is a limited resource on mine dumps, and necessary for growth and persistence of vegetation. Nitrogen fixers may therefore fertilize soil (Sheoran *et al.,* 2010), although the use of grass species in restoration practices is generally more emphasised (Chaulya *et al*., 1999; Ekka and Behera, 2001; Sheoran *et al*., 2010, Nurtjahya and Franklin, 2017). Management may benefit from planting legumes along with such grass species to further aid in restoration process. Declines in perennial forb species and increases in annual forb species drove dissimilarities in the protected area. Annual species are more stress tolerant and typically the first to colonize an open niche created by disturbance (Grime 1979; Tilman *et al*., 1988; Behura *et al.,* 2015). Grass abundance is strongly driven by rainfall variability (O'Connor 1999; Van Coller *et al*., 2018) and contributed to the community dissimilarities due to declines in mean abundance of dominant species across all land-use types. The specific selection of grass species for mine dump restoration may contribute to the abundance of grass species seen on the mine dumps in this study, as well as the stability of grass trait composition (Helm, 1995; Chaulya *et al*., 1999; Ekka and Behera, 2001; Sheoran *et al*., 2010, Nurtjahya and Franklin, 2017). As a nurse crop, grasses are considered particularly important in the initial stages of succession on mine dumps (Helm, 1995; Ekka and Behera, 2001; Sheoran *et al*., 2010).

Changes in natural semi-arid ecosystems is periodic, resulting in species composition being stable for a long period and then shifting to an alternate compositional state for a period of time due to disturbance events (Westoby *et al*., 1989; Siebert and Van Wyk, 2001). It may be possible that the protected area was in a temporary alternate state, however, after sufficient rainfall the drought release community at the protected area may return to the pre-drought state.

7.2 Diversity responses to rainfall variability

7.2.1 Herbaceous species diversity

The herbaceous species richness and –diversity of the protected area and the TD responded similarly, revealing a significant decline in response to drought. In contrast, the species richness and –diversity remained stable on the RD. Aside from being under restoration (planting of tolerant species like *Cynodon dactylon*, *Cenchrus ciliaris*, and *Digitaria eriantha*) (Surmon, 2018b), soil on the RD is composed of more organic matter and nutrients compared to tailings dam soil (Sheoran and Sheoran, 2010), which will contribute to the stability of species diversity patterns.

Plant species richness in the natural Mopaneveld typically peaks for a brief period as a result of the rapid colonization by annual herbaceous species after drought release (Siebert *et al*., 2003a). Accordingly, an increase in annual species was evident for this study, although species richness still remained lower during drought release than before the drought. Herbaceous species richness and diversity responses to disturbance events are dynamic. A study investigating the effects of heavy grazing on rangeland systems (Rutherford *et al.* 2012), revealed that species richness remained stable on heavily utilized areas, whilst increased species richness on heavily utilized patches were observed by Shackleton (2000). In contrast to the rangeland studies, mine dumps (transformed, heavily disturbed) in this study were more stable in terms of species richness and diversity compared to the protected area, although forb species richness and diversity did decrease significantly on the TD. Species richness and diversity did not increase in response to drought, which was inconsistent with findings of Shackleton (2000). Furthermore, the recovery of species richness on mine dumps may not necessarily involve the return of rare species which once occurred at the pre-mined landscape (Zhao *et al*., 2016).

Spatial and temporal heterogeneity in soil resources and microclimate drives plant species diversity (Bartels and Chen, 2010), and has significant impacts on herbaceous species richness (Zhao *et al.,* 2016). This heterogeneity causes significant differences in species richness and diversity across study areas and vegetation types (Zhao *et al*., 2016), as could be observed in this study with natural undulating Mopaneveld in the protected area, and slopes, terraces and nutrient-poor soils on mine dumps. Although soil fertility does not confer forb diversity *per se* (Mlambo *et al.,* 2005; Muvengwi *et al.*, 2017), variability in habitat conditions and with increased rainfall could enhance forb diversity and richness (Shackleton, 2000; Augustine, 2003; Siebert and Dreber, 2019).

Lack of pre-adaptation to drought for introduced mine dump species was expected to result in a decrease in trait diversity on the mine dumps, whilst this would not be the case with natural vegetation in the protected area (Balachowski and Volaire, 2018). Grass trait diversity remained unaffected by drought, however, forb trait diversity in the current study suggests trait-based redundancy, and therefore, enhanced resilience of the protected Mopaneveld herbaceous layer. Plant functional trait diversity in grasses was more stable across land-use types in response to drought, compared to forb trait diversity. The results of this study, especially for forbs were in accordance with previous findings, indicating that disturbance resulted in a decline in functional trait richness and diversity, leading to a decline in functional redundancy (Flynn *et al*., 2009, Laliberte *et al*., 2010; Pakeman, 2011).

Generally, some species tend to be much more abundant than other species on the mine dumps for both forbs and grasses, generally resulting in lower species evenness. Low richness and evenness could lead to lower species diversity (Mapaure *et al*., 2011). For example, in heavily grazed versus lightly grazed Mopaneveld systems, low evenness was shown to result in a decrease in species richness and diversity at the heavy grazed site, though not significantly (Rutherford *et al.* 2012). In this study, the pool of surrounding vegetation in protected areas and presence of seed banks improved the likelihood of species colonisation and may have increased species richness and evenness on mine dumps (Martinez-Ruiz *et al.,* 2001; Martinez-Ruiz and Fernandez-Santos, 2005). Although a lower evenness was observed at the mine dumps compared to the protected area, evenness increased in response to drought. However, as in Rutherford *et al.* (2012), no significant changes were observed for species evenness.

The significantly lower species richness and diversity in mining areas compared to protected areas observed in this study was consistent with other studies (Mapaure *et al.,* 2011). Moreover, ecosystems in the southern part of Africa are known to experience dramatic shifts in vegetation structure and diversity as a result of climate change and the concentration of atmospheric CO_2 (Lehmann *et al.,* 2011; Bond and Midgley*,* 2012; Moncrieff *et al.,* 2014).

The protected area was resilient to drought in terms of functional diversity and richness, as opposed to species richness and diversity which declined. The functions performed by species that were lost in response to drought could be performed by remaining species in the protected area, since functional richness and diversity was not lost in response to drought. However, both species diversity and richness, and functional diversity declined significantly on the TD in response to drought. Trait evenness on the TD increased in response to drought, indicating that the functioning of the herbaceous system on the TD was not completely altered. Increased evenness may result from species that emerged after the drought event such as legumes and drought-tolerant grasses. Forb traits on the RD exhibited a significant decline, which was offset by the increase in grass indicator species on the RD. The overall RD community remained stable, since evenness remained the same, even though grass biomass increased significantly.

An increase in trait evenness was revealed for both life forms, however, increases in forb trait evenness was only significant at the TD and grass trait evenness at the protected area and the TD. Previous studies indicated an increase in evenness with increased disturbance (Biswas and Mallik, 2010; Pakeman, 2011). Species spanning a range of different functional traits that have similar abundances would be indicative of highly disturbed communities (Pakeman, 2011). Low levels of competition are characteristic of disturbed areas which increase evenness (Pakeman, 2011). A higher evenness of functional traits among species could potentially confer better reciprocity, better resource distribution and higher production (Mouillot *et al*., 2005).

7.3 Changes in herbaceous productivity in response to drought

7.3.1 Biomass

The significant decline in mean herbaceous biomass at the protected area compared to mine dumps was not expected since natural vegetation has been shown to be more resistant to drought and be less variable in terms of biomass production compared to species-poor areas such as mine dumps (Tilman and Dowing, 1994; Tilman, 1996). Nevertheless, it is known that drought results in loss of productivity (Illius and O'Connor, 1999).

Biomass production is strongly dependent on water and nutrient availability (Augustine, 2003; Ludwig *et al.,* 2004; Muvengwi *et al.,* 2017). Water and nutrients are limited on mine dumps, and although viable seedlings have previously been found in mine soils of other studies, seedlings can not necessarily establish successfully in mined areas (Salemaa *et al.,* 2001), which not only leads to lower biomass production but also lower species diversity (Mapaure *et al*., 2011). This was especially evident in the pre-drought sampling year, however, the protected area had the lowest mean biomass after the drought event, which was not consistent with the findings of Mapaure *et al*. (2011). Under pre-drought conditions, forb biomass production may be curbed by competition with grasses (Masunga *et al.,* 2013), however, under drought and grazed conditions, the abundance of grasses was reduced, leading to less competition for forb species and a subsequent increase in forb biomass (Jacobs and Naiman, 2008; Buitenwerf *et al.,* 2011; Gilo and Kelkay, 2017).

Additionally, increased tree cover and nutrients as found in the protected area, increases forb biomass (Belsky *et al.,* 1989; Ludwig *et al*., 2004). Higher forb biomass, in comparison with grasses, was also observed under increased soil nutrient availability, shade and low water availability conditions (Belsky *et al.,* 1989; Van der Waal *et al.,* 2009). Mine dumps lack abundant tree cover and nutrient-rich soils favourable to forb species, whilst both tree cover and nutrient availability were higher in the protected area. Results revealed by this study, i.e. significantly higher grass biomass on the mine dumps and higher forb biomass at the protected area, was therefore an expected outcome in terms of functional type analyses. Functional type analyses support these findings as the number of shade-tolerant forb species was higher at the protected area and PCA's revealed a close association of shade-tolerant PFT's with the protected area and not with the mine dumps. Grass species that occur ouside of canopy are generally less productive than under tree canopy grasses (Treydte *et al*., 2009), however, management practices may have altered this finding, since grass species with a high biomass (e.g. *Pennisetum setaceum*) have been planted on the mine dumps. Additionally, grass productivity has been shown to be suppressed by *Colophospermum mopane* trees at high densities (Smit, 2005).

7.3.2 Cover

Negligible differences in herbaceous cover at the RD may be a result of the occurrence of tolerant species and more favourable soil conditions in comparison with the TD. The significant decline in herbaceous cover stems from the significant grass mortality in the protected area.

On the TD, mine silt mixed with water is frequently added on top of the tailings dam, increasing the amount of water in tailings soil during drought, which may have led to an advantage for plant species on the TD. Nevertheless, total herbaceous cover still decreased on the TD.

The increase in bare soil in the protected area may be a result of the significant decline in grass cover observed. The observed loss of perennial grass individuals led to less competition with forbs and a relative increase in forbs during the drier period (Buitenwerf *et al*., 2011), possibly attributing to forb cover not revealing any decreases in response to drought in the protected area. Functional traits and –groups conferring drought tolerance

7.4 Functional traits and –groups conferring drought tolerance

7.4.1 Life span

Annual species are generally tolerant to stressed environments (Grime 1979; Tilman *et al.,* 1988; Behura *et al.,* 2015) and typically increase in abundance following a drought episode (O'Connor, 2015). The increase and dominance of annual species and -functional types was expected, since annual species are known to persist in unfavourable conditions (Waaland and Allen, 1987; Jordaan *et al*., 2004; Castro *et al*., 2010; Olsson and Ödman, 2014) and possess adaptations which promote their success during droughts, such as dehydration avoidance and escape (Geber and Dawson, 1990, 1997; Stanton *et al*., 2000; McKay *et al*., 2003; Heschel and Riginos, 2005; Sherrard and Maherali, 2006). Indicator values (IndVal) supported this since a shift in dominance of perennial indicator species to annual indicator species occurred across all land-use types. Before the drought, the abundance of perennial PFT's made up more than half of the herbaceous component (59 %), but perennial forbs and grass PFT's decreased, in equal amounts, to 30 % in response to drought. Under unfavourable environmental conditions, annual species provide ecosystem functions that produce conditions for the successful establishment of later successional species and perennial (Prach, 1987; Wilcox, 1998). Sensitive forbs (i.e. only present in the protected area) were dominated by annual species during drought release, while surprisingly only perennial sensitive grasses were present during drought release. This may indicate that grasses occurring at the protected area are pre-adapted to typical semi-arid savanna conditions (Theron and Booysen 1966). Perennial grass species are typically depleted after disturbance such as over-grazing or severe drought, resulting in the dominance of forbs and annual grasses in semi-arid savannas (Jordaan *et al*., 2004; Buitenwerf *et al.,* 2011; Rutherford *et al*., 2012; O'Connor, 2015). The dominance of annual forbs and grasses is considered an unstable state, as the proportions of contributions to composition and cover fluctuate according to rainfall variability as well as soil condition (Jordaan *et al*., 2004). Forbs and annual grass dominance following drought is expected to last for several years in the Mopaneveld savanna (Jordaan *et al*., 2004; O'Connor, 2015). Multiple consecutive years of above-average rainfall is needed to reverse the effects of a severe drought on herbaceous vegetation in the Mopaneveld, especially for the recovery of perennial grass species (O'Connor, 1999; Buitenwerf *et al*., 2011; O'Connor, 2015). Although another study in a different vegetation type, Abbas *et al.* (2019) (i.e. Hluhluwe-iMfolozi Park, predominantly SVI 20 Zululand Lowveld), showed a vigorous increase in perennial grasses following drought, this study still coincides with that observed by O'Connor (2015) (i.e. Venetia-Limpopo Nature Reserve, SVmp 1 Musina Mopane Bushveld and SVmp 2 Limpopo Ridge Bushveld), whereby a vigorous increase in annuals are evident. Perennial grass responses to rainfall variability are highly dependent on substrate type (i.e. water retention and nutrient availability in soil) and the loss of perennials results in further nutrient deficiencies due to lack of organic litter and soil cover (Scholes, 1985; Frost *et al*., 1986; O'Connor, 1999). This may hinder future establishment of both annual and perennial species, leading to a decline in both species and functional diversity, which could lead to the eventual loss of ecosystem function.

7.4.2 Life form

Forb species dominated the Mopaneveld herbaceous layer before and after drought, which is typical of Mopaneveld ecosystems (Jordaan *et al.,* 2004; Siebert *et al.,* 2010). Therefore, drought release forb dominance could be explained by the initial abundance of forbs before the drought event. In contrast to Mopaneveld, other semi-arid systems are co-dominated by forb and grass species, which may alternate in dominance as a result of changes in the environment (Illius and O'Connor, 1999; Koerner and Collins, 2014; Van Coller *et al*., 2018). Additionally, forbs and annual grasses have been shown to dominate the Mopaneveld herbaceous layer for multiple decades following the late 1950-1960 drought event (Jordaan *et al.,* 2004). Prolonged below-average rainfall generally results in an increase in forb species (O'Connor, 1999; Rutherford *et al*., 2012). For this reason, the high number of forb species and forb individuals was expected. Thus, forbs make up an intricate part of the Mopaneveld vegetation type (Rutherford *et al*., 2012), and the high proportion of forbs cannot simply be attributed to severe land degradation or transformation alone (Rutherford *et al*., 2012). Grass species present on the mine dumps may be better adapted to harsh conditions associated with mining as grasses are selected to withstand mining impacts and aid in restoration (Helm, 1995; Chaulya *et al*., 1999; Ekka and Behera, 2001; Sheoran *et al*., 2010, Nurtjahya and Franklin, 2017). Change in climatic conditions is the leading driver of forb dynamics in semi-arid savannas, which is exacerbated by additional drivers (O'Connor, 1995; Jacobs and Naiman, 2008; Buitenwerf *et al.,* 2011). As a result of their drought-tolerant traits, forbs can make a sound recovery following a drought event (O'Connor, 1999; Siebert and Dreber, 2019). In fact, forb recovery can often be faster than that of grasses as a result of reduced competition from grasses (Van Coller and Siebert, 2015).

Similar to results found in this study, the Poaceae family is generally dominant on mine dumps, which reveals the colonizing ability of grasses in unfavourable conditions that accompany mining activity (Ekka and Behera, 2011; Behura *et al.,* 2015). The colonising ability of grass species can be attributed to drought tolerance, and their ability to tolerate low nutrient availability (Helm, 1995; Skeel and Gibson, 1996). Adventitious roots in grass species are beneficial for stabilizing mine dump soil and water retention (Helm, 1995). Grass species also play an important role as pioneer species in producing favourable conditions for subsequent colonization by other plant species (Ashby *et al.,* 1989; Helm, 1995; Skeel and Gibson 1996). Fabaceae and Poaceae have been shown to dominate recently mined sites whilst and older sites were still dominated by Poaceae (Behura *et al.,* 2015). Grasses have underground meristems as an adaptation to defoliation. As soon as the stressor is alleviated, these meristems are stimulated and therefore grasses present a faster growth rate compared to forbs (Scholes *et al*., 2003).

7.4.3 Nitrogen-fixing

In accordance with Wagner *et al*. (2016) the dominance of nitrogen-fixing PFT's increased with disturbance. The ability to fix nitrogen is effective in arid environments, providing a competitive advantage over non-nitrogen fixing species (Monks *et al.,* 2012). This was especially evident when considering nitrogen-fixing PFT's which outcompeted other PFT's on the nutrient-poor and low-moisture soils on the mine dumps regardless of rainfall variability. Moreover, drought as an environmental disturbance resulted in an increase in nitrogen-fixers in the protected area. The strong association between nitrogen-fixing PFT's and mine dumps before drought and during drought release was also supported by PCA analyses. Nitrogen fixers are more efficient in taking up essential inorganic nutrients (e.g. Nitrogen and Phosphorus) from the soils, which promotes plant growth and persistence (Cornelissen *et al.,* 2003; Kotschy, 2013). This is especially beneficial in nutrient-poor soils (Ritchie *et al*., 1998; Knops *et al*., 2002). Nitrogen fixers aid restoration practices through improving the structure and chemistry of soils on mine dumps (Sheoran *et al.,* 2010). Nitrogen is limited on mine dumps (Yang *et al.,* 2003), therefore artificial fertilizer and nitrogen-fixing species, such as *T. pupurea* are introduced to increase soil fertility (Zhang *et al.,* 2001; Behura *et al.,* 2015).

7.4.4 Alien species

Most of the dominant forbs on the mine dumps were native. This was contrary to what was found in the semi-arid savanna of Sekhukhuneland (Siebert and Van Wyk, 2001), although alien species did increase in abundance during drought release across all land-use types. Environmental factors associated with increased invasive species include disturbance, severe environmental stress, early successional stages, and low native species diversity (Lodge, 1993; Alpert *et al*., 2000). These attributes generally occur in mining areas, which increases the likelihood of the establishment of invasive species (Lemke *et al*., 2013). Other traits exhibited by invasive species which facilitates their establishment after a disturbance event include rapid establishment, adaptation to nutrient-poor soils and successful growth under unfavourable conditions (Lemke *et al*., 2013).

The only alien grass species among the dominant grass species was *Pennisetum setaceum. Pennisetum setaceum*, which is sown on the dumps at PC, is tolerant to a variety of environmental conditions and is often planted for mine dump stabilization and aesthetic purposes (Rahlao *et al.,* 2014). The dominance of native species in the protected area and mine dumps were substantiated by indicator species of which only 9% of indicator species across all land-use types were alien invasive, with 8% during drought release.

7.4.5 Photosynthetic pathway

C_4 perennial grasses in the Mopaneveld are known to decline as a result of drought, but tend to show increased abundances during and after consecutive years of rainfall (Dye and Spear, 1982; Donaldson *et al*., 1984, O'Connor, 1999; O'Connor 2015). In particular, C_4 grasses are more tolerant to drought conditions and low soil nutrient availability (Sheoran *et al.,* 2010). Some of these species, such as the unpalatable *Bothriochloa radicans, S. pappophoroides, E. cenchroides,* and *S. uniplumis* are relatively well-adapted to drought (O'Connor, 2015), and generally do not exhibit significant changes in response to rainfall variation (O'Connor, 1999). However, under anthropogenic disturbance and drought (drought release, mine dump communities) *B. radicans* was no longer present. Some perennial C_4 grasses increase in response to drought and herbivory, and in this study included *U. mosambicensis* and *Tragus berteronianus* (Abbas *et al*., 2019). As a pioneer, but also perennial, clonal grass *U. mosambicensis* maintained dominance across all land-use types in this study, whilst *T. berteronianus* increased in abundance in response to drought. *T. berteronianus* is indicative of disturbances such as drought (Tainton, 1999). Its emergence was likely inhibited by abundance of other grass species before the drought (Abbas *et al.,* 2019). The majority of annual forbs in this study followed the C_3 photosynthetic pathway. Forb species may increase when C_4 species decline as a result of climate change and increasing CO_2 (Uys, 2006; Trollope *et al*., 2014; Scott-Shaw and Morris, 2015; Siebert and Scogings, 2015).

7.4.6 Dispersal ability

Under grazing pressure in Mediterranean systems, results pertaining to seed dispersal have shown contradicting results, whereby one study revealed specialized dispersal mechanisms is associated with disturbance rather than autochory (Castro *et al.,* 2010), whilst another study indicated the opposite (Peco *et al*., 2005). In this study, allochorous dispersal was the most common mode of dispersal irrespective of rainfall variability, suggesting that multiple modes of dispersal are advantageous for species in semi-arid systems under severe anthropogenic disturbance. If one mode of dispersal does not prove successful, species could still be able to spread in unfavourable environments by means of an alternate dispersal mode. Such trait redundancy enhances ecosystem resilience (Laliberté *et al*., 2010; Mori *et al.,* 2013; Sasaki *et al*., 2015). In addition to allochory, long distance dispersal, such as anemochory, was also favoured. Taller species, with respect to their habitat, typically have anemochorous dispersal mechanisms (Castro *et al.,* 2010), while this is less favoured by- and less common for shorter species (Wilson and Traveset, 2000). In this study zoochorous dispersal, especially ectozoochory, also occurred during drought release. Zoochorous dispersal mechanisms become less important as time since disturbance increases (Castro *et al.,* 2010), which supports the findings in this study. In disturbed forested areas, grass species were found to be associated with anemochory, and non-clonal reproduction (Mabry and Fraterrigo, 2009), this was also found for this study in a semi-arid Mopaneveld savanna.

7.4.7 Palatability

A distinct shift from palatable to unpalatable species in response to drought was observed in this study. Unpalatable forbs and grasses are known to increase in abundance in response to drought (Van Coller and Siebert, 2015). This was expected especially for grass species, where perennial palatable species are known to decrease after a drought event (Savadogo *et al*., 2008; Buitenwerf *et al*., 2011; Tessema *et al.,* 2011; Koerner and Collins, 2014). Forbs provide the system with trait-based redundancy by supplying food source security for herbivores under such conditions (Kallah *et al.,* 2000; Du Toit, 2003; Odadi *et al.,* 2013; Clegg and O'Connor, 2017).

7.4.8 Growth form

Species exhibiting erect growth forms were not expected to be among the dominant PFT's, because it is well known that disturbed environments (especially agricultural disturbance) favour low-growing prostrate or rosette forms (Castro *et al*., 2010; Debussche *et al.,* 1996; De Bello *et al.,* 2005; Peco *et al.,* 2005). Three rare, non-nitrogen fixing forb PFT's were lost from the mine dumps. The two PFT's that were lost from the TD both included palatable, prostrate species. Prostrate growth forms generally do better than erect forms under disturbance (especially grazing pressure) (Díaz *et al.,* 2007). The atypical response of growth form in this study may have resulted from the effect of palatability and the ability to fix nitrogen being more important traits for plant species to persist on mine dumps in the face of drought.

7.4.9 Summary

The drought resulted in a substantial increase in annual species, irrespective of life-form and land-use type. Nitrogen-fixing ability proved to play a significant role in persistence in arid, nutrient-poor soils, making up a significant portion on mine dumps especially. Combinations of traits that conferred persistence and tolerance to drought in grasses included annual life span, long-distance dispersal, tolerance to high sun exposure, and low palatability across all land-use types. Forb trait combinations favoured by protected and transformed Mopaneveld in response to drought include an annual life span, allochorous dispersal, and nitrogen fixing ability. Annuals and perennial nitrogen-fixers made up the majority of the forb PFT's on the mine dumps before drought and during drought release.

Main differences in plant functional traits between land-use types included the association of the protected area with shade tolerant, highly palatable, non-clonal/resprouting grass PFT's and erect, highly palatable, non-nitrogen-fixing forb PFT's with specialized dispersal modes. In contrast with the protected area, mine dumps were associated with sun tolerance, long distance dispersal and allochory, low palatability, nitrogen-fixing ability and vegetative growth.

CHAPTER 8

Conclusions

The effect of anthropogenic transformation on Mopaneveld herbaceous vegetation was expected to be intensified by the recent severe drought. However, species richness and diversity of herbaceous vegetation on the protected Mopaneveld revealed a stronger negative effect of drought than the mine dumps. Furthermore, forb species richness and diversity presented a greater response to drought than grasses, especially at the protected Mopaneveld. The first community-level hypothesis, stating that Mopaneveld herbaceous species richness and diversity will be less affected by drought on a protected area in comparison with that of the mine dumps, was rejected. Evenness was expected to increase on the mine dumps as species that were pre-adapted to drought would persist while other less- adapted species occurring at lower frequencies would be filtered out. The second-community level hypothesis was therefore also rejected since no significant increase in species evenness was revealed for either life form or land-use type.

Forb trait diversity declined significantly on both mine dumps, but not at CGR. This supported the third hypothesis, as there was a decline in trait diversity due to a lack of pre-adapted traits to drought. However, grass trait diversity and richness remained stable, indicating adaptation to severe conditions associated with disturbance for this functional group. Therefore, the third hypothesis was supported by the forb trait results, but was rejected for the grasses. Functional-level analyses revealed that less adapted species (forb PFT’s: perennial life span, specialized dispersal mechanisms, high palatability, prostrate growth form; grass PFT’s: perennial life span, shade tolerant, zoochorous, high palatability) were not necessarily replaced, but further decreased in frequency whilst dominating species (forb PFT’s: annual life span, nitrogen-fixing, allochorous; grass PFT’s: annual life span, sun tolerance, long-distance dispersal, low palatability) that are better adapted to exploit resources and persist in harsh climatic and anthropogenically disturbed environments increased. Therefore, the fourth hypothesis was rejected, since disturbance-sensitive species on mine dumps decreased in frequency and were not necessarily replaced. Since no PFT’s were lost at the protected area or at PC, the Mopaneveld retained its resilience across land-use types and in response to drought through its high trait-based redundancy, which led to the rejection of the final hypothesis.

The responses of the Mopaneveld herbaceous layer provides a better sense of resilience of the overall Mopaneveld ecosystem and contributes to the knowledge gaps pertaining to the combined effect of drought and anthropogenic transformation of Mopaneveld herbaceous communities. Drought in the transformed Mopaneveld affects species diversity, and though functional diversity may remain stable for this study, future species losses may affect functional diversity and ultimately alter ecosystem function. Conservation and restoration efforts on transformed Mopaneveld may benefit from promoting functional diversity and to maintain functional redundancy within an ecosystem by conserving more species with diverging responses to disturbances.

Limitations of this study include the lack of post-drought data, which could have provided information for more accurate comparisons with post-drought studies and provided insights into further variations as the herbaceous communities recovered.

Recommendations for future studies resulting from the current study include further study into the functional significance of plant traits and the recording of clearly defined traits using published methods. Consecutive post-drought studies that incorporate the findings of this study’s pre-drought and drought release outcomes, could capture potentially delayed responses of the transformed Mopaneveld herbaceous vegetation to the severe drought. This would improve comprehension of the long-term dynamics of the various herbaceous species in Mopaneveld ecosystems. Further in-depth investigation of the impact of herbivory on the system would contribute to a broader knowledge of additional drivers that influence Mopaneveld dynamics. Finally, below-ground bud bank surveys could benefit future disturbance studies in the Mopaneveld to assess the regenerative capabilities of forbs and grasses in response to drought.

This study can be compared to studies investigating species- and functional responses of herbaceous vegetation to rainfall variability in semi-arid savannas with poor soil-nutrient content, and studies focussing on the combined effects of anthropogenic disturbance and drought. This is useful since multiple studies have predicted future increases in drought frequency and rainfall variability. Comparisons of studies in different biomes to the current study may contribute to the broader understanding of how different ecosystems respond to drought and will respond to future drought events.

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APPENDIX A: List of abbreviations

Table A1: Abbreviations relevant to this dissertation

Abbreviation	**Meaning**
CGR	Cleveland Game Reserve
GPS	Global Positioning System
HLM	Hierarchical Linear Model
KNP	Kruger National Park
NMDS	Non-Metric Multi-Dimensional Scaling
PC	Palabora Copper
PCA	Principal Component Analyses
PERMANOVA	Permutational Multivariate Analysis of Variance
PFT	Plant Functional Type
RD	Rock Dump
SAEON	South African Environmental Observation Network
SAWS	South African Weather Services
SIMPER	Similarity Percentage Analysis
TD	Tailings dam
UPGMA	Unweighted Pair Group Method with Arithmetic Mean

APPENDIX B: Supplementary table supporting Chapter 3

Table B1: Acronyms and full species names according to Germishuizen and Meyer (2003) for all herbaceous species recorded in the study area.

Abbreviation	Scientific name and authority	Family
ABUAUS	*Abutilon austro-africanum* Hochr.	Malvaceae
ABUGRA	*Abutilon grandiflorum* G.Don.	Malvaceae
ACAIND	*Acalypha indica* L.	Euphorbiaceae
ACASEG	*Acalypha segetalis* Müll.Arg.	Euphorbiaceae
ACHASP	*Achyranthes aspera* Lam.	Amaranthaceae
ALTPUN	*Alternanthera pungens* Humb. Bonpl. and Kunth*	Amaranthaceae
ALYGLU	*Alysicarpus glumaceus* (Vahl) A.DC.	Fabaceae
AMAPRA	*Amaranthus praetermissus* Brenan.	Amaranthaceae
ANTPUB	*Anthephora pubescens* (Hochst.) K. Schum.	Poaceae
APTLIN	*Aptosimum lineare* Marloth and Engl.	Scrophulariaceae
ARIADS	*Aristida adscensionis* L.	Poaceae
ARICON	*Aristida congesta subsp. congesta* L. Roem and Schult.	Poaceae
BECFIL	*Becium filamentosum* (Forssk.) Chiov.	Lamiaceae
BIDBIP	*Bidens bipinnata* L.	Asteraceae
BLEINT	*Blepharis integrifolia* (L.f.) E. Mey. ex Schinz	Acanthaceae
BOEDIF	*Boerhavia diffusa* L.	Nyctaginaceae
BOEERE	*Boerhavia erecta* L.	Nyctaginaceae
BOTRAD	*Bothriochloa radicans* (Lehm.) A.Camus.	Poaceae
BRADEF	*Brachiaria deflexa* (Schumach.) C.E.Hubb. ex Robyns	Poaceae
BRAXAN	*Brachiaria xantholeuca* (Hack. ex Schinz) Stapf.	Poaceae
BULBUR	*Bulbostylis burchellii* (Ficalho and Hiern) C.B.Clarke	Cyperaceae
CALDIV	*Calostephane divaricata* Benth.	Asteraceae
CENCIL	*Cenchrus ciliaris* L.	Poaceae
CERTRI	*Ceratotheca triloba* Benth.	Pedaliaceae
CHAABS	*Chamaecrista absus* (L.) Irwin and Barneby	Fabaceae
CHAPIN	*Chascanum pinnatifidum* (L.f.) E.Mey	Verbenaceae
CHLROX	*Chloris roxburghiana* Schult.f.	Poaceae
CHLVIR	*Chloris virgata* Sw.	Poaceae
CLEANG	*Cleome angustifolia* Forssk.	Capparaceae
CLEMON	*Cleome monophylla* L.	Capparaceae
CLETER	*Clerodendrum ternatum* Schinz	Lamiaceae

COMAFR	*Commelina africana* L.	Commelinaceae
COMBEN	*Commelina benghalensis* L.	Commelinaceae
COMERE	*Commelina erecta* L.	Commelinaceae
CORASP	*Corchorus asplenifolius* Burch.	Tiliaceae
CORCON	*Corchorus confusus* Wild	Tiliaceae
CORDEC	*Corbichonia decumbens* (Forssk.) Exell	Molluginaceae
CRAVEL	*Crabbea velutina* S.Moore	Acanthaceae
CROSPH	*Crotalaria sphaerocarpa* DC.	Fabaceae
CUCAFR	*Cucumis africanus* L.f.	Cucurbitaceae
CUCANG	*Cucumis anguria* L.	Cucurbitaceae
CYNDAC	*Cynodon dactylon* (L.) Pers.	Poaceae
CYPLAE	*Cyperus laevigatus* L.	Cyperaceae
CYPOBT	*Cyperus obtusiflorus* Vahl	Cyperaceae
CYPRUB	*Cyperus rubicundus* Vahl	Cyperaceae
CYPSEX	*Cyperus sexangularis* Nees	Cyperaceae
DACGEM	*Dactyloctenium geminatum* Hack.	Poaceae
DICTOM	*Dicoma tomentosa* Cass.	Asteraceae
DIGERI	*Digitaria eriantha* Steud.	Poaceae
DIPGLA	*Dipcadi glaucum* (Ker Gawl.) Baker	Hyacinthaceae
ENIAXI	*Enicostema axillare* (Lam.) A.Raynal	Gentianaceae
ENNCEN	*Enneapogon cenchroides* (Roem. & Schult.) C.E.Hubb.	Poaceae
ENNSCO	*Enneapogon scoparius* Stapf	Poaceae
ERACIL	*Eragrostis cilianensis* (All.) Janch.	Poaceae
ERALEH	*Eragrostis lehmanniana* Nees	Poaceae
ERARIG	*Eragrostis rigidior* Pilg.	Poaceae
ERAROT	*Eragrostis rotifer* Rendle	Poaceae
ERASUP	*Eragrostis superba* Peyr.	Poaceae
ERATRI	*Eragrostis trichophora* Coss. & Durieu	Poaceae
ETHCON	*Ethulia conyzoides* L.f.	Asteraceae
EUPHIR	*Euphorbia hirta* L.	Euphorbiaceae
EUPNEO	*Euphorbia neopolycnemoides* Pax & K.Hoffm	Euphorbiaceae
EVOALS	*Evolvulus alsinoides* (L.) L.	Convolvulaceae
FINAFR	*Fingerhuthia Africana* Lehm.	Poaceae
FLABID	*Flaveria bidentis* (L.) Kuntze	Asteraceae
GISAFR	*Gisekia africana* (Lour.) Kuntze	Gisekiaceae
GISPHA	*Gisekia pharnaceoides* L.	Gisekiaceae

GNIRUB	*Gnidia rubescens* B.Peterson.	Thymelaeaceae
GOMTOM	*Gomphocarpus tomentosus* Burch.	Apocynaceae
GOSHER	*Gossypium herbaceum* L.	Malvaceae
HELCAN	*Helichrysum candolleanum* H.Buek	Asteraceae
HELCIL	*Heliotropium ciliatum* Kaplan	Boraginaceae
HELNEL	*Heliotropium nelsonii* C.H.Wright.	Boraginaceae
HELSTE	*Heliotropium steudneri* Vatke	Boraginaceae
HERBOR	*Hermannia boraginiflora* Hook.	Sterculiaceae
HERGLA	*Hermannia glanduligera* K. Schum.	Sterculiaceae
HERODO	*Hermbstaedtia odorata* (Burch.) T.Cooke	Amaranthaceae
HETCON	*Heteropogon contortus* (L.) Roem. & Schult.	Poaceae
HIBMIC	*Hibiscus micranthus* L.f.	Malvaceae
HIBSID	*Hibiscus sidiformis* Baill.	Malvaceae
HYPFOR	*Hypoestes forskaolii* (Vahl) Roem. & Schult.	Acanthaceae
INDCOS	*Indigastrum costatum* (Guill. & Perr.) Schrire	Fabaceae
INDFIL	*Indigofera filipes* Benth. ex Harv.	Fabaceae
INDHET	*Indigofera heterotricha* DC.	Fabaceae
INDRHY	*Indigofera rhytidocarpa* Harv.	Fabaceae
INDVIC	*Indigofera vicioides* Jaub. & Spach	Fabaceae
IPOMAG	*Ipomoea magnusiana* Schinz	Convolvulaceae
IPOPLE	*Ipomoea plebeia* R.Br.	Convolvulaceae
IPOSIN	*Ipomoea sinensis* (Desr.) Choisy	Convolvulaceae
JUSFLA	*Justicia flava* (Vahl) Vahl	Acanthaceae
JUSPRO	*Justicia protracta* (Nees) T.Anderson	Acanthaceae
KOHCYN	*Kohautia cynanchica* DC.	Rubiaceae
KOHVIR	*Kohautia virgata* (Willd.) Bremek.	Rubiaceae
KYLALB	*Kyllinga alba* Nees	Cyperaceae
KYPANG	*Kyphocarpa angustifolia* (Moq.) Lopr.	Amaranthaceae
LAGDEC	*Laggera decurrens* Benth.	Asteraceae
LANRUG	*Lantana rugosa* Thunb.	Verbenaceae
LEDREV	*Ledebouria revoluta* (L.f.) Jessop	Hyacinthaceae
LEUGLA	*Leucas glabrata* (Vahl) R.Br	Lamiaceae
LEUSEX	*Leucas sexdentata* Skan	Lamiaceae
LIMFEN	*Limeum fenestratum* (Fenzl) Heimerl	Molluginaceae
LIMVIS	*Limeum viscosum* (J.Gay) Fenzl	Molluginaceae
MELACU	*Melhania acuminata* Mast.	Sterculiaceae

MELFOR	*Melhania forbesii* Mast.	Sterculiaceae
MELPRO	*Melhania prostrata* DC.	Sterculiaceae
MELREP	*Melinis repens* (Willd.) Zizka	Poaceae
MICCAF	*Microchloa caffra* Nees	Poaceae
MICGAL	*Microcharis galpinii* N.E. Br.	Fabaceae
MOLNUD	*Mollugo nudicaulis* Lam.	Molluginaceae
MONDEB	*Monechma debile* (Forssk.) Nees.	Acanthaceae
OCIAME	*Ocimum americanum* L.	Lamiaceae
ORNTEN	*Ornithogalum tenuifolium* F.Delaroche*,* syn*. Albuca virens* (Lindl.) J.C.Manning & Goldblatt	Hyacinthaceae
PANCOL	*Panicum coloratum* L.	Poaceae
PANMAX	*Panicum maximum* Jacq.	Poaceae
PAVBUR	*Pavonia burchellii* (DC.) R.A.Dyer	Malvaceae
PECLEU	*Pechuel-Loeschea leubnitziae* (Kuntze) O.Hoffm.	Asteraceae
PEGSEN	*Pegolettia senegalensis* Cass.	Asteraceae
PENSET	*Pennisetum setaceum* (Forssk.) Chiov.	Poaceae
PHYINC	*Phyllanthus incurvus* Thunb.	Euphorbiaceae
PHYMAD	*Phyllanthus maderaspatensis* L.	Euphorbiaceae
PHYPAR	*Phyllanthus parvulus* Sond.	Euphorbiaceae
POGSQU	*Pogonarthria squarrosa* (Roem. & Schult.) Pilg.	Poaceae
POLERI	*Polygala erioptera* DC.	Polygalaceae
POLSER	*Polygala serpentaria* Eckl. & Zeyh.	Polygalaceae
PORHER	*Portulaca hereroensis* Schinz	Portulacaceae
POROLE	*Portulaca oleracea* L.	Portulacaceae
PUPLAP	*Pupalia lappacea* (L.) A.Juss.	Amaranthaceae
RHIXER	*Rhinacanthus xerophilus* A.Meeuse	Acanthaceae
RHYMIN	*Rhynchosia minima* (L.) DC.	Fabaceae
RHYTOT	*Rhynchosia totta* (Thunb.) DC.	Fabaceae
RUECOR	*Ruellia cordata* Thunb.	Acanthaceae
SCHPAP	*Schmidtia pappophoroides* Steud.	Poaceae
SEDSUF	*Seddera suffruticosa* (Schinz) Hallier f.	Convolvulaceae
SESBIS	*Sesbania bispinosa* (Jacq.) W.F.Wight	Fabaceae
SIDCOR	*Sida cordifolia* L.	Malvaceae
SOLLIC	*Solanum lichtensteinii* Willd.	Solanaceae
SPESEN	*Spermacoce sinensis* (Klotzsch) Hiern	Rubiaceae
SPOFIM	*Sporobolus fimbriatus* (Trin.) Nees	Poaceae

SPOIOC	*Sporobolus ioclados* (Trin.) Nees	Poaceae
STIHIR	*Stipagrostis hirtigluma* (Trin. & Rupr.) De Winter	Poaceae
STIUNI	*Stipagrostis uniplumis* (Licht.) De Winter	Poaceae
STRASI	*Striga asiatica* (L.) Kuntze	Orobanchaceae
SYNCAN	*Syncolostemon canescens* (Gürke) M.Ashby	Lamiaceae
SYNELI	*Syncolostemon elliottii* (Baker) M.Ashby	Lamiaceae
TALARN	*Talinum arnotii* Hook.f.	Portulacaceae
TEPEUC	*Tephrosia euchroa* I.Verd.	Fabaceae
TEPPUR	*Tephrosia purpurea* (L.) Pers.	Fabaceae
TEPRHO	*Tephrosia rhodesica* Baker f.	Fabaceae
TEPUNI	*Tephrosia uniflora* Pers.	Fabaceae
THETRI	*Themeda triandra* Forssk.	Poaceae
TRABER	*Tragus berteronianus* Schult.	Poaceae
TRARUP	*Tragia rupestris* Sond.	Euphorbiaceae
TRIMON	*Tricholaena monachne* (Trin.) Stapf & C.E.Hubb.	Poaceae
TRIPRO	*Tridax procumbens* L.	Asteraceae
TRITER	*Tribulus terrestris* L.	Zygophyllaceae
UROMOS	*Urochloa mosambicensis* (Hack.) Dandy	Poaceae
VIGUNG	*Vigna unguiculata* (L.) Walp.	Fabaceae
WALIND	*Waltheria indica* L.	Malvaceae
ZALPEN	*Zaleya pentandra* (L.) C.Jeffrey	Aizoaceae
ZORGLO	*Zornia glochidiata* DC.	Fabaceae

Table B2: Soil physical- and chemical characteristics of the three different post rehabilitation ages, aspects and topography on the rock dump. This table is adapted from the tables in Smith (2016).

	Age (years)			**Aspect**			**Topography**	
RD	**28**	**32**	**42**	**East**	**South**	**West**	**Terrace**	**Slope**
Sample size	**18**	**18**	**9**	**15**	**15**	**15**	**18**	**27**
Properties								
Macro-elements (mmol/ℓ)								
Ca	0.345±0.025a	0.504±0.060a	0.443±0.024a	0.404±0.030a	0.459±0.031a	0.484±0.078a	0.297±0.013a	0.624±0.043b
Mg	0.189±0.017a	0.249±0.030a	0.203±0.008a	0.218±0.008a	0.224±0.012a	0.214±0.042a	0.176±0.009a	0.268±0.025b
K	0.227±0.015a	0.296±0.028a	0.262±0.011a	0.260±0.018a	0.287±0.021a	0.255±0.028a	0.205±0.009a	0.343±0.020b
Na	0.081±0.007a	0.171±0.057a	0.096±0.009a	0.095±0.007a	0.124±0.012a	0.153±0.081a	0.075±0.004a	0.180±0.050b
PO4	0.005±0.000a	0.005±0.0001a	0.008±0.0007b	0.006±0.000a	0.007±0.001a	0.007±0.001a	0.005±0.000a	0.007±0.001b
SO4	0.024±0.002a	0.289±0.099b	0.049±0.006a	0.042±0.005a	0.117±0.041a	0.279±0.131a	0.032±0.002a	0.269±0.087b
NO3	0.054±0.008a	0.070±0.007a	0.086±0.011a	0.086±0.012a	0.068±0.008a	0.071±0.009a	0.052±0.005a	0.098±0.009b
NH4	0.017±0.002a	0.024±0.002b	0.022±0.001b	0.022±0.001a	0.021±0.001a	0.024±0.003a	0.018±0.001a	0.026±0.001a
Cl	0.039±0.007a	0.046±0.004a	0.043±0.005a	0.041±0.006a	0.049±0.005a	0.037±0.003a	0.039±0.004a	0.048±0.004a
HCO3	1.253±0.090a	1.307±0.070a	1.446±0.060a	1.415±0.077a	1.447±0.061a	1.164±0.073b	1.094±0.049a	1.648±0.029b
Micro-elements (µmol/ℓ)								
Fe	3.505±0.666a	5.795±0.828ab	7.941±1.257b	6.218±0.923a	6.102±1.212a	6.577±1.070a	5.687±0.988a	6.935±0.819a
Mn	0.075±0.018a	0.095±0.026a	0.223±0.034b	0.126±0.023a	0.103±0.027a	0.228±0.045b	0.127±0.026a	0.168±0.028a
Cu	0.209±0.083a	1.407±0.244b	2.004±0.245b	1.350±0.321a	1.448±0.208a	1.520±0.333a	0.465±0.102a	2.540±0.206b
Zn	0.017±0.003a	0.011±0.001a	0.017±0.003a	0.012±0.001ac	0.013±0.001ab	0.020±0.004b	0.016±0.002a	0.013±0.001b
B	3.795±0.869a	4.313±0.610a	5.839±0.629a	4.489±0.764a	4.768±0.631a	5.315±0.709a	3.528±0.460a	6.337±0.593b

Nutrient status (mg/kg)								
Ca	1965.13±158.20a	2646.97±165.21b	3008.48±167.71b	3049.00±204.47ac	2732.13±173.80ab	2235.41±148.58b	2128.06±107.81a	3291.380±141.01a
Mg	668.43±16.36a	529.79±42.44a	553.31±24.62a	628.33±32.52ac	549.86±32.12ab	492.40±38.54b	629.27±15.20a	471.70±35.99b
K	102.13±3.871a	105.11±6.37a	122.79±6.51a	136.85±9.365a	101.94±5.070b	102.16±3.495b	114.97±5.100a	108.38±6.024a
Na	3.367±0.564a	8.157±2.245a	6.343±0.808a	6.188±0.360a	6.236±0.813a	7.400±3.203a	3.822±0.377a	9.650±1.975b
P	12.096±3.232a	17.485±2.554a	11.745±2.143a	12.635±2.142a	12.694±2.266a	17.771±3.320a	20.39±2.479a	7.174±0.368b
Exchangeable cations (cmol(+)/kg)								
Ca	9.806±0.789a	13.209±0.824b	15.012±0.837b	15.215±1.020ac	13.633±0.867ab	11.155±0.741b	10.62±0.538a	16.42±0.704a
Mg	5.090±0.135a	4.360±0.349a	4.554±0.203a	5.171±0.268ac	4.526±0.264ab	4.053±0.317b	5.179±0.125a	3.882±0.296b
K	0.262±0.010a	0.270±0.016a	0.315±0.0167a	0.351±0.024a	0.261±0.013b	0.262±0.009b	0.295±0.013a	0.278±0.015a
Na	0.146±0.002a	0.035±0.010a	0.028±0.004a	0.027±0.002a	0.027±0.004a	0.032±0.014a	0.017±0.002a	0.042±0.009b
Chemical properties								
pH	7.678±0.043a	7.901±0.034b	7.912±0.050b	7.878±0.036ab	7.930±0.046ac	7.763±0.051b	7.685±0.029a	8.070±0.018b
pH$_2$	8.402±0.051a	8.255±0.066ab	8.060±0.062b	8.279±0.075a	8.047±0.068b	8.347±0.047a	8.400±0.043a	7.977±0.052a
pH$_3$	7.723±0.025a	7.518±0.047b	7.385±0.041b	7.450±0.054a	7.489±0.048a	7.562±0.046a	7.665±0.016a	7.313±0.042a
EC	0.140±0.009a	0.201±0.023a	0.169±0.007a	0.163±0.009a	0.181±0.011a	0.184±0.030a	0.126±0.005a	0.235±0.017b
PBray	4.816±0.566a	5.501±0.313ab	6.822±0.478b	5.543±0.589a	5.825±0.334a	6.431±0.527a	4.813±0.301a	7.174±0.368a
OC	0.132±0.018a	0.336±0.041b	0.443±0.044b	0.425±0.069a	0.334±0.030a	0.281±0.047a	0.189±0.018a	0.518±0.040b
CEC	13.22±0.414a	15.48±0.724ab	16.95±0.659b	17.298±0.935a	16.056±0.637a	13.612±0.510b	13.79±0.331a	17.82±0.699b
S	15.17±0.808a	17.87±0.804ab	19.91±0.930b	20.764±1.077a	18.447±0.870a	15.502±0.637b	16.11±0.581a	20.63±0.831b
BS	113.92±2.824a	115.99±1.816a	116.53±2.099a	120.18±2.278a	114.28±2.049a	113.95±1.884a	115.61±1.632a	116.11±1.901a

Soil texture								
Snd$_1$	19.54±1.844a	16.73±0.960ab	14.80±1.207b	17.878±1.355a	14.664±1.190a	17.581±1.150a	20.470±0.797a	11.884±0.788a
Snd$_2$	93.89±0.532a	89.05±1.097a	87.89±1.122a	88.250±1.271a	89.440±1.134a	90.549±1.152a	93.341±0.393a	85.029±1.015b
Silt	5.061±0.662a	7.760±1.058a	9.013±0.941a	8.289±1.013a	8.493±1.093a	6.337±0.906a	4.798±0.461a	11.177±0.933b
Clay	1.045±0.256a	3.188±0.204b	3.092±0.377b	3.467±0.513a	2.067±0.135b	3.114±0.378a	1.861±0.201a	3.794±0.286b

[1] All values ±SEM represent results obtained from sample size (n=85).

[2] Statistical significant differences are indicated by alphabetic letters ($p < 0.05$). The same letters indicate no significant differences while those with different letters indicate significant difference at p.

[3] pH$_2$ = pH(H$_2$O); pH$_3$ = pH(KCl); EC = EC(mS/cm); PBray = P-Bray I (ppm); OC = Organic Carbon (%); CEC = CEC (cmol(+)/kg); S = S-value; BS = Base saturation (%); Snd$_1$ = Sand > 2mm (%); Snd$_2$ = Sand < 2mm (%); Slit = Silt (%); Clay = Clay (%).

[4] EC – electrical conductivity; ppm – parts per million; CEC – cation exchange capacity.

Table B3: Soil physical- and chemical characteristics of the three different post rehabilitation ages, aspects and topography on the tailings dam. This table is adapted from the tables in Smith (2016).

	Age (years)				**Aspect**			**Topography**	
TD	**20**	**24**	**30**	**32**	**East**	**South**	**West**	**Terrace**	**Slope**
Sample size	**12**	**11**	**12**	**11**	**16**	**14**	**16**	**23**	**23**
Properties									
Macro-elements (mmol/ℓ)									
Ca	0.525±0.036a	0.521±0.121a	0.490±0.021a	1.088±0.576a	0.475±0.027a	0.428±0.025a	1.022±0.39a	0.441±0.029a	0.814±0.237a
Mg	0.267±0.015a	0.339±0.110a	0.257±0.011a	0.511±0.248a	0.239±0.012a	0.252±0.014a	0.542±0.19a	0.236±0.011a	0.430±0.114b
K	0.399±0.031a	0.360±0.050a	0.276±0.014a	0.443±0.130a	0.322±0.024ac	0.302±0.022a	0.49±0.09bc	0.298±0.019a	0.435±0.057a
Na	0.114±0.010a	0.104±0.038a	0.068±0.002a	0.157±0.044a	0.086±0.005a	0.068±0.004a	0.175±0.04b	0.095±0.013a	0.122±0.025a
PO4	0.025±0.009a	0.005±0.000b	0.005±0.000b	0.043±0.017a	0.025±0.008a	0.006±0.001a	0.018±0.01a	0.031±0.008a	0.005±0.000b
SO4	0.217±0.049a	0.398±0.277a	0.087±0.010a	1.008±0.918a	0.124±0.030a	0.120±0.018a	1.02±0.649a	0.162±0.030a	0.624±0.394b
NO3	0.292±0.089a	0.174±0.020a	0.253±0.049a	0.386±0.109a	0.238±0.056a	0.192±0.026a	0.378±0.08a	0.249±0.043a	0.288±0.057a
NH4	0.020±0.003a	0.018±0.002a	0.022±0.003a	0.017±0.003a	0.020±0.002a	0.022±0.002a	0.02±0.003a	0.019±0.002a	0.019±0.001a
Cl	0.047±0.005a	0.048±0.008a	0.047±0.009a	0.117±0.050a	0.042±0.004a	0.033±0.004a	0.11±0.033b	0.085±0.020a	0.037±0.007b
HCO3	1.286±0.042a	1.195±0.069a	1.388±0.065a	1.238±0.109a	1.292±0.057a	1.280±0.069a	1.25±0.059a	1.058±0.044a	1.496±0.025b
Micro-elements (µmol/ℓ)									
Fe	3.485±0.942a	6.645±2.004a	3.211±0.657a	27.367±13.74b	12.906±6.303a	3.260±0.669a	8.13±2.396a	17.197±5.622a	0.927±0.112b
Mn	0.104±0.023a	0.107±0.044a	0.116±0.021a	0.183±0.07a	0.129±0.035a	0.072±0.020a	0.158±0.04a	0.218±0.035a	0.029±0.007b
Cu	1.403±0.625a	0.909±0.244a	0.955±0.184a	0.773±0.16a	0.746±0.092a	0.376±0.066a	1.998±0.58b	1.574±0.356a	0.484±0.080b
Zn	0.010±0.000a	0.010±0.000a	0.040±0.007a	0.148±0.04b	0.047±0.018a	0.025±0.007a	0.059±0.02a	0.048±0.018a	0.043±0.009a
B	2.628±0.524a	3.033±0.658a	3.017±0.796a	6.094±1.77a	3.381±0.472ac	1.236±0.128a	5.66±1.31bc	4.989±0.857a	2.071±0.294b

Nutrient status (mg/kg)									
Ca	3154.50±89.88a	2600.32±80.51b	2835.83±48.9bc	3012.16±109.9ac	2962.35±71.14a	2798.80±106.4a	2870.7±75.8a	2771.5±63.8a	3016.46±65.37a
Mg	480.182±37.01a	376.295±36.73a	369.700±37.80a	437.188±33.9a	433.31±23.09ab	469.60±47.69ac	343.35±30.7b	431.63±27.74a	399.16±25.7a
K	113.182±7.61a	85.636±10.67a	68.575±9.71b	97.406±9.04a	97.49±6.190a	100.73±13.20a	74.17±7.64a	110.96±6.532a	71.64±6.172a
Na	5.159±0.80a	2.523±0.27b	2.550±0.33b	3.625±0.50a	3.50±0.474a	2.83±0.440a	3.98±0.544a	4.000±0.452a	2.950±0.353a
P	12.171±2.71a	17.085±2.74a	10.805±2.27a	11.945±2.78a	13.94±2.223a	11.85±2.461a	13.00±2.16a	21.13±1.969a	5.141±0.017b
Exchangeable cations (cmol(+)/kg)									
Ca	15.741±0.45a	12.976±0.402b	14.151±0.244bc	15.03±0.548ac	14.782±0.355a	13.966±0.531a	14.33±0.378a	13.83±0.318a	15.05±0.326a
Mg	3.952±0.305a	3.097±0.302a	3.043±0.311a	3.598±0.279a	3.566±0.190ab	3.865±0.393ac	2.826±0.252b	3.552±0.228a	3.285±0.211a
K	0.290±0.020a	0.220±0.027a	0.176±0.025b	0.250±0.023a	0.250±0.016a	0.258±0.034a	0.190±0.020a	0.285±0.017a	0.184±0.016a
Na	0.022±0.003a	0.011±0.001b	0.011±0.001b	0.016±0.002a	0.015±0.002a	0.012±0.002a	0.017±0.002a	0.017±0.002a	0.013±0.002a
Chemical properties									
pH	7.918±0.047a	7.755±0.074a	7.967±0.033a	7.790±0.106a	7.841±0.053a	7.892±0.066a	7.860±0.062a	7.668±0.052a	8.051±0.011b
pH$_2$	8.144±0.029a	8.357±0.043b	8.141±0.029a	8.090±0.055a	8.175±0.029a	8.223±0.048a	8.188±0.046a	8.236±0.039a	8.146±0.020b
pH$_3$	7.752±0.045a	7.891±0.043b	7.917±0.085b	7.718±0.055a	7.736±0.031ac	7.885±0.082ab	7.907±0.051b	7.7670.036a	7.883±0.047a
EC	0.213±0.012a	0.222±0.055a	0.187±0.006a	0.388±0.181a	0.188±0.009a	0.176±0.007a	0.383±0.127a	0.181±0.010a	0.307±0.077b
PBray	4.602±0.163a	4.519±0.185a	4.778±0.186a	4.438±0.188a	4.721±0.134a	4.546±0.170a	4.430±0.171a	4.040±0.130a	5.141±0.017b
OC	0.317±0.045a	0.311±0.031a	0.378±0.046a	0.681±0.250a	0.375±0.033a	0.290±0.033a	0.590±0.212a	0.446±0.028a	0.391±0.130a
CEC	15.226±0.416a	13.062±0.323b	13.107±0.328b	14.28±0.328a	14.035±0.322a	14.079±0.451a	13.59±0.309a	13.68±0.292a	14.15±0.285a
S	20.006±0.702a	16.303±0.475b	17.381±0.42bc	18.89±0.47ac	18.614±0.496a	18.102±0.654a	17.358±0.48a	17.68±0.467a	18.53±0.416a
BS	130.84±1.31b	124.95±2.08a	132.70±0.89b	132.31±1.34b	132.295±0.872a	128.547±1.84ab	127.70±1.78b	128.85±0.870a	131.11±1.399a
Soil texture									
Snd$_1$	22.684±1.566a	12.602±1.787b	12.708±2.592b	18.26±2.94ab	18.680±1.679a	18.592±2.318a	11.59±2.046b	20.544±1.414a	12.521±1.67b
Snd$_2$	88.978±0.860a	91.989±1.304a	91.016±0.678a	87.825±2.96a	91.095±0.605a	90.404±1.318a	88.303±2.07a	91.685±0.572a	88.485±1.36b

Silt	8.120±0.955a	5.588±1.297a	6.898±0.499a	9.675±2.732a	6.296±0.622a	7.342±1.314a	9.201±1.899a	5.519±0.604a	9.339±1.239a
Clay	2.902±0.291a	2.423±0.053a	2.087±0.364a	2.500±0.483a	2.609±0.245a	2.254±0.239a	2.495±0.315a	2.796±0.239a	2.176±0.191a

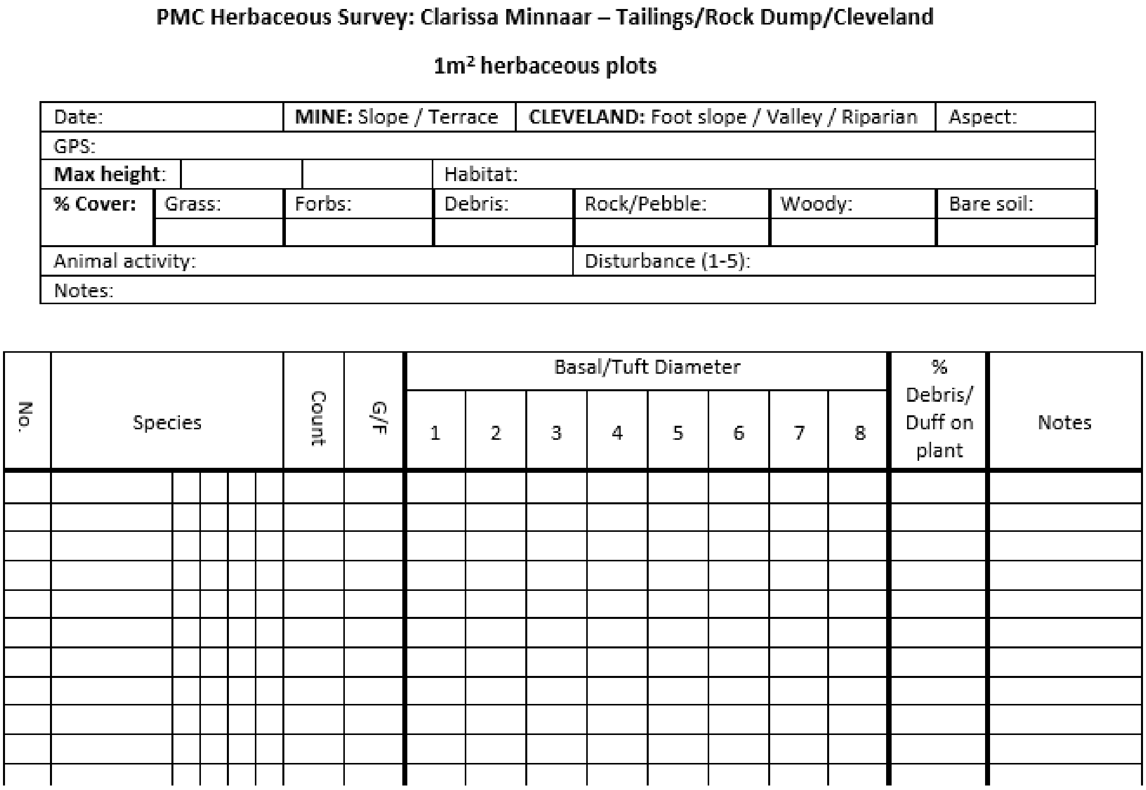
[1] All values ±SEM represent results obtained from sample size (n=85).

[2] Statistical significant differences are indicated by alphabetic letters ($p < 0.05$). The same letters indicate no significant differences while those with different letters indicate significant difference at p.

[3] pH_2 = pH(H_2O); pH_3 = pH(KCl); EC = EC(mS/cm); PBray = P-Bray I (ppm); OC = Organic Carbon (%); CEC = CEC (cmol(+)/kg); S = S-value; BS = Base saturation (%); Snd_1 = Sand > 2mm (%); Snd_2 = Sand < 2mm (%); Slit = Silt (%); Clay = Clay (%).

[4] EC – electrical conductivity; ppm – parts per million; CEC – cation exchange capacity.

APPENDIX C: Supplementary figure supporting Chapter 4



PMC Herbaceous Survey: Clarissa Minnaar – Tailings/Rock Dump/Cleveland

1m² herbaceous plots

Date:		**MINE:** Slope / Terrace		**CLEVELAND:** Foot slope / Valley / Riparian		Aspect:
GPS:						
Max height:			Habitat:			
% Cover:	Grass:	Forbs:	Debris:	Rock/Pebble:	Woody:	Bare soil:
Animal activity:				Disturbance (1-5):		
Notes:						

No.	Species	Count	G/F	Basal/Tuft Diameter								% Debris/ Duff on plant	Notes
				1	2	3	4	5	6	7	8		

Figure C1: Example of field data sheet used to record floristic and environmental data at Palabora Copper and Cleveland Game Reserve.

APPENDIX D: Supplementary tables supporting Chapter 5

Table D1: *Post hoc* Bonferroni tests indicating significant differences (p < 0.05) in indices across land-use types in response to drought.

Rainfall year : Land-use	**Total species**		**Margalef's richness**		**Shannon diversity**		**E_{var} evenness**	
	Forbs	**Grass**	**Forbs**	**Grass**	**Forbs**	**Grass**	**Forbs**	**Grass**
2018:CGR - 2014:CGR	<0.001 *	<0.001 *	<0.001 *	0.027 *	<0.001 *	0.041 *	1.000	1.000
2014:RD - 2014:CGR	<0.001 *	<0.001 *	<0.001 *	0.008 *	<0.001 *	0.140	0.256	1.000
2018:RD - 2014:CGR	<0.001 *	<0.001 *	<0.001 *	0.002 *	<0.001 *	0.016 *	0.285	1.000
2014:TD - 2014:CGR	<0.001 *	<0.001 *	<0.001 *	<0.001 *	<0.001 *	0.001 *	0.231	1.000
2018:TD - 2014:CGR	<0.001 *	<0.001 *	<0.001 *	<0.001 *	<0.001 *	<0.001 *	0.125	1.000
2014:RD - 2018:CGR	<0.001 *	0.965	<0.001 *	1.000	<0.001 *	1.0000	1.000	0.863
2018:RD - 2018:CGR	<0.001 *	1.000	<0.001 *	1.000	<0.001 *	1.0000	1.000	1.000
2014:TD - 2018:CGR	<0.001 *	1.000	<0.001 *	1.000	<0.001 *	1.0000	1.000	0.023 *
2018:TD - 2018:CGR	<0.001 *	0.200	<0.001 *	0.045 *	<0.001 *	0.218	0.835	1.000

2018:RD - 2014:RD	0.159	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2014:TD - 2014:RD	0.156	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2018:TD - 2014:RD	0.120	<0.001 *	0.257	0.086	1.000	0.020 *	1.000	1.000
2014:TD - 2018:RD	<0.001 *	1.000	0.635	1.000	0.026 *	1.000	1.000	1.000
2018:TD - 2018:RD	1.000	0.015 *	1.000	0.413	1.000	0.353	1.000	1.000
2018:TD - 2014:TD	<0.001 *	0.004 *	0.020 *	1.000	0.005 *	1.000	1.000	1.000

*Denotes significant differences at $p < 0.05$.

Table D2: *Post hoc* Bonferroni tests indicating significant differences ($p < 0.05$) in total biomass across land-use types in response to drought.

Rainfall year : Land-use	**Total biomass**
2018:CGR - 2014:CGR	<0.001 *
2014:RD - 2014:CGR	1.000
2018:RD - 2014:CGR	0.389 *
2014:TD - 2014:CGR	1.000
2018:TD - 2014:CGR	0.017 *
2014:RD - 2018:CGR	<0.001 *
2018:RD - 2018:CGR	<0.001 *
2014:TD - 2018:CGR	0.001 *
2018:TD - 2018:CGR	0.037 *
2018:RD - 2014:RD	1.000
2014:TD - 2014:RD	1.000
2018:TD - 2014:RD	0.624
2014:TD - 2018:RD	1.000
2018:TD - 2018:RD	1.000
2018:TD - 2014:TD	1.000

Denotes significant differences at $p < 0.05$

Table D3: *Post hoc* Bonferroni tests indicating significant differences ($p < 0.05$) in mean biomass between life forms across land-use types during drought release.

Life form : Land-use	**Total biomass**
Grass:CGR - Forb:CGR	0.387
Forb:RD - Forb:CGR	<0.001 *
Grass:RD - Forb:CGR	0.006 *
Forb:TD - Forb:CGR	<0.001 *
Grass:TD - Forb:CGR	0.310 *
Forb:RD - Grass:CGR	0.001 *
Grass:RD - Grass:CGR	<0.001 *
Forb:TD - Grass:CGR	0.175
Grass:TD - Grass:CGR	<0.001 *
Grass:RD - Forb:RD	<0.001 *
Forb:TD - Forb:RD	1.000
Grass:TD - Forb:RD	<0.001 *
Forb:TD - Grass:RD	<0.001 *
Grass:TD - Grass:RD	1.000
Grass:TD - Forb:TD	<0.001 *

Denotes significant differences at $p < 0.05$

Table D4: *Post hoc* Bonferroni tests indicating significant differences in cover estimations across land-use types and rainfall year.

	Forbs	**Grass**	**Bare Soil**	**Debris**	**Total herbaceous cover**
2018:CGR - 2014:CGR	1.000	<0.001 *	<0.001 *	0.188	<0.001 *
2014:RD - 2014:CGR	<0.001 *	<0.001 *	1.000	0.699	<0.001 *
2018:RD - 2014:CGR	<0.001 *	0.034 *	1.000	1.000	0.014
2014:TD - 2014:CGR	0.006 *	<0.001 *	1.000	0.005	<0.001 *
2018:TD - 2014:CGR	<0.001 *	<0.001 *	1.000	0.104	<0.001 *
2014:RD - 2018:CGR	<0.001 *	<0.001 *	1.000	1.000	<0.001 *
2018:RD - 2018:CGR	<0.001 *	<0.001 *	0.006 *	1.000	<0.001 *
2014:TD - 2018:CGR	<0.001 *	0.001 *	1.000	1.000	<0.001 *
2018:TD - 2018:CGR	<0.001 *	0,028 *	0.017 *	1.000	<0.001 *
2018:RD - 2014:RD	1.000	1.000	0.028	1.000	1.000
2014:TD - 2014:RD	1.000	0.283	1.000	0.128	1.000

2018:TD - 2014:RD	1.000	0.097	0.072	1.000	<0.001 *
2014:TD - 2018:RD	0.275	0.003 *	0.002 *	0.033	1.000
2018:TD - 2018:RD	1.000	0.001 *	1.000	0.935	<0.001 *
2018:TD - 2014:TD	0,612	1.000	0.007	1.000	<0.001 *

* Denotes significance at $p < 0.05$

APPENDIX E: Supplementary tables supporting Chapter 6

Table E1: *Post hoc* Bonferroni tests indicating significant differences ($p < 0.05$) in plant functional trait indices across land-use types in response to drought.

Rainfall year : Land-use	Total species		Margalef's richness		Shannon diversity		Pielou evenness	
	Forbs	**Grass**	**Forbs**	**Grass**	**Forbs**	**Grass**	**Forbs**	**Grass**
2018:CGR - 2014:CGR	0.612	0.001 *	0.830 *	1.000	1.000	0.314	1.000	0.001 *
2014:RD - 2014:CGR	<0.001 *	1.000	<0.001 *	0.156	<0.001 *	1.000	1.000	1.000
2018:RD - 2014:CGR	1.000	1.000	1.000	0.058	1.000	1.000	0.021 *	1.000
2014:TD - 2014:CGR	<0.001 *	0.019 *	<0.001 *	0.052	0.007 *	1.000	1.000	0.275
2018:TD - 2014:CGR	1.000	1.000	1.000	0.007 *	1.000	1.000	1.000	1.000
2014:RD - 2018:CGR	<0.001 *	<0.001 *	<0.001 *	0.071	<0.001 *	0.199	1.000	0.001 *
2018:RD - 2018:CGR	0.014 *	0.001 *	0.038	0.031 *	1.000	0.301	1.000	0.054
2014:TD - 2018:CGR	<0.001 *	<0.001 *	<0.001 *	0.030 *	<0.001 *	0.007 *	1.000	<0.001 *

2018:TD - 2018:CGR	0.223	<0.001 *	0.073	0.006 *	1.000	0.122	1.000	0.075
2018:RD - 2014:RD	<0.001 *	1.000	0.009 *	1.000	<0.001 *	1.000	0.020 *	1.000
2014:TD - 2014:RD	0.505	0.120	1.000	1.000	0.526	1.000	1.000	0.181
2018:TD - 2014:RD	<0.001 *	1.000	0.001 *	1.000	<0.001 *	1.000	1.000	1.000
2014:TD - 2018:RD	0.001 *	0.007 *	0.100	1.000	0.006 *	1.000	0.960	0.001 *
2018:TD - 2018:RD	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2018:TD - 2014:TD	<0.001 *	0.012 *	0.015 *	1.000	<0.001 *	1.000	1.000	<0.001 *

*Denotes significant differences at $p < 0.05$.

Table E2: Summary of plant functional types (PFT's) and their attributes obtained from Unweighted Pair Group Method with Arithmetic Mean (UPGMA) results.

PFT	**Description**			**Species**
Type I	Annual	Grass	Shade tolerant; endozoochorous; high palatability	*Brachiaria deflexa, Brachiaria xanthophloea*
Type II	Annual	Grass	Tolerant to sunlight; ectozoochorous; low palatability	*Aristida congesta, Aristida adscensionis,* *Tragus berteronianus*
Type III	Annual	Grass	Tolerant to sunlight; anemochorous; low palatability	*Enneapogon cenchroides, Stipagrostis uniplumis, Chloris virgata, Melinis repens*
Type IV	Perennial	Grass	Non-clonal/resprouting; high palatability	*Anthephora pubescens,* *Eragrostis lehmanniana, Eragrostis rigidior, Eragrostis rotifer, Eragrostis superba,* *Eragrostis trichophora, Cenchrus ciliaris, Urochloa mosambicensis, Panicum coloratum* *Panicum maximum, Tricholaena monachne*

Type V	Perennial	Grass	Non-clonal/resprouting; low palatability	*Bothriochloa radicans, Bulbostylis burchellii, Cyperus rubicundus, Cyperus sexangularis, Enneapogon scoparius, Pennisetum setaceum, Eragrostis cilianensis, Microchloa caffra*
Type VI	Perennial	Grass	Clonal/resprouting; allo- and anemochorous	*Cynodon dactylon, Schmidtia pappophoroides, Themeda triandra, Pogonarthria squarrosa, Digitaria eriantha, Dactyloctenium geminatum, Kyllinga alba, Chloris roxburghiana,*
				Cyperus laevigatus, Cyperus obtusiflorus, Stipagrostis uniplumis
Type VII	Perennial	Grass	Clonal/resprouting; zoochorous	*Fingerhuthia africana, Sporobolus ioclados, Sporobolus fimbriatus*, *Heteropogon contortus*
Type VIII	Annual	Forb	Allochorous; prostrate	*Corbichonia decumbens, Cucumis anguria, Euphorbia hirta, Limeum viscosum*,
				Tridax procumbens
Type IX	Annual	Forb	Allochorous; erect, nitrogen (N_2) fixing	*Acalypha indica, Acalypha segetalis,*

				Alysicarpus glumaceus, Ceratotheca triloba, Chamaecrista absus, Crotalaria sphaerocarpa, Euphorbia neopolycnemoides, *Hibiscus sidiformis, Indigastrum costatum, Indigofera filipes, Indigofera rhytidocarpa, Kohautia cynanchica, Kohautia virgata, Microcharis galpinii, Mollugo nudicaulis, Phyllanthus maderaspatensis,* *Spermacoce sinensis, Waltheria indica*, *Zornia glochidiata*
Type X	Annual	Forb	(Mixed) Specialized dispersal; high palatability	*Amaranthus praetermissus, Bidens bipinnata, Boerhavia erecta, Cleome monophylla, Commelina benghalensis, Evolvulus alsinoides, Gisekia Africana, Gisekia pharnaceoides, Ipomoea plebeian, Ipomoea sinensis, Kyphocarpa angustifolia, Portulaca hereroensis, Portulaca oleracea, Tribulus terrestris,* *Zaleya pentandra*

Type XI	Annual	Forb	(Mixed) Specialized dispersal; low palatability; erect	*Calostephane divaricate, Dicoma tomentosa, Ethulia conyzoides, Flaveria bidentis,* *Leucas sexdentata, Limeum fenestratum, Monechma debile, Ocimum americanum, Pegolettia senegalensis, Polygala erioptera, Pupalia lappacea*, *Striga asiatica*
Type XII	Perennial	Forb	(Mixed) Specialized dispersal; high palatability; prostrate	*Alternanthera pungens, Blepharis integrifolia, Boerhavia diffusa, Commelina Africana*, *Ipomoea magnusiana*
Type XIII	Perennial	Forb	(Mixed) Specialized dispersal; high palatability; erect	*Achyranthes aspera, Aptosimum lineare, Cleome angustifolia, Clerodendrum ternatum, Commelina erecta, Hermannia glanduligera, Hermbstaedtia odorata, Justicia flava,* *Justicia protracta, Lantana rugose,* *Leucas glabrata, Melhania prostrata, Rhinacanthus xerophilus, Ruellia cordata, Seddera suffruticosa, Talinum arnotii*
Type XIV	Perennial	Forb	(Mixed) Specialized dispersal; low palatability; erect	*Becium filamentosum, Chascanum pinnatifidum, Crabbea velutina, Dipcadi glaucum,*

				Enicostema axillare, Gnidia rubescens, Gomphocarpus tomentosus,
				Hermannia boraginiflora, Hypoestes forskaolii, Laggera decurrens, Ledebouria revolute, Melhania acuminate, Melhania forbesii, Ornithogalum tenuifolium,
				Pechuel-Loeschea leubnitziae,
				Polygala serpentaria, Solanum lichtensteinii, Syncolostemon canescens,
				Syncolostemon elliottii
Type XV	Perennial	Forb	Allochorous; nitrogen (N_2) fixing	*Indigofera heterotricha, Indigofera vicioides, Rhynchosia minima, Rhynchosia totta,*
				Sesbania bispinosa, Tephrosia euchroa, Tephrosia purpurea, Tephrosia rhodesica, Tephrosia uniflora, *Vigna unguiculata*
Type XVI	Perennial	Forb	Allochorous; non-nitrogen (N_2) fixing	*Abutilon austro-africanum,*

Abutilon grandiflorum, Corchorus asplenifolius, Cucumis africanus, Gossypium herbaceum, Helichrysum candolleanum,

Heliotropium ciliatum, Heliotropium nelsonii, Heliotropium steudneri, Hibiscus micranthus, Pavonia burchellii, Phyllanthus incurvus, Phyllanthus parvulus, Sida cordifolia,

Corchorus confuses, *Tragia rupestris*

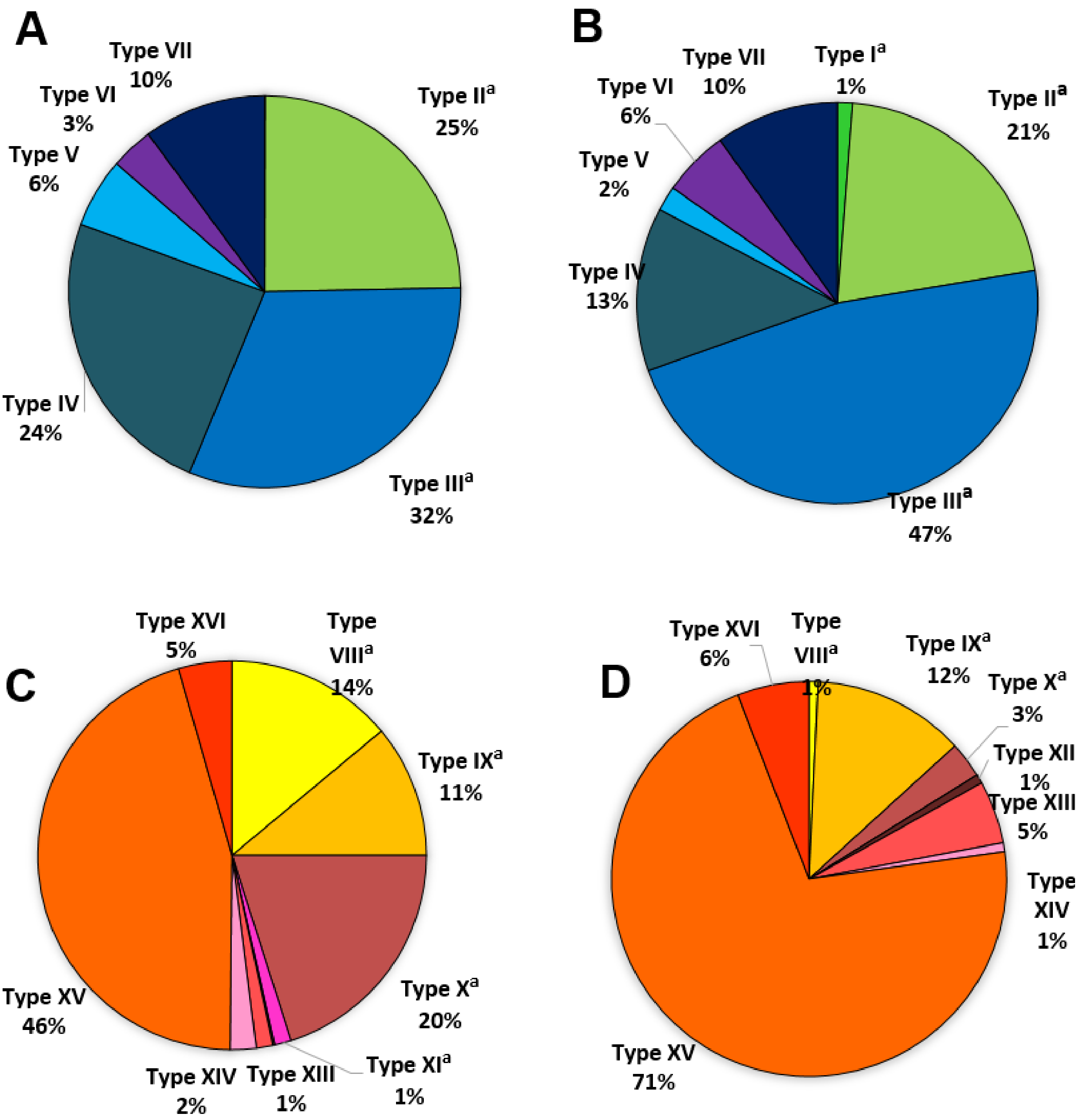


Figure E1: Frequency of plant functional types (PFT’s) on the RD before the drought and after drought release. (Grass: A = Pre-drought, B = Drought release; Forbs: C = Pre-drought; D = Drought release)

[a] represents annual PFT’s.

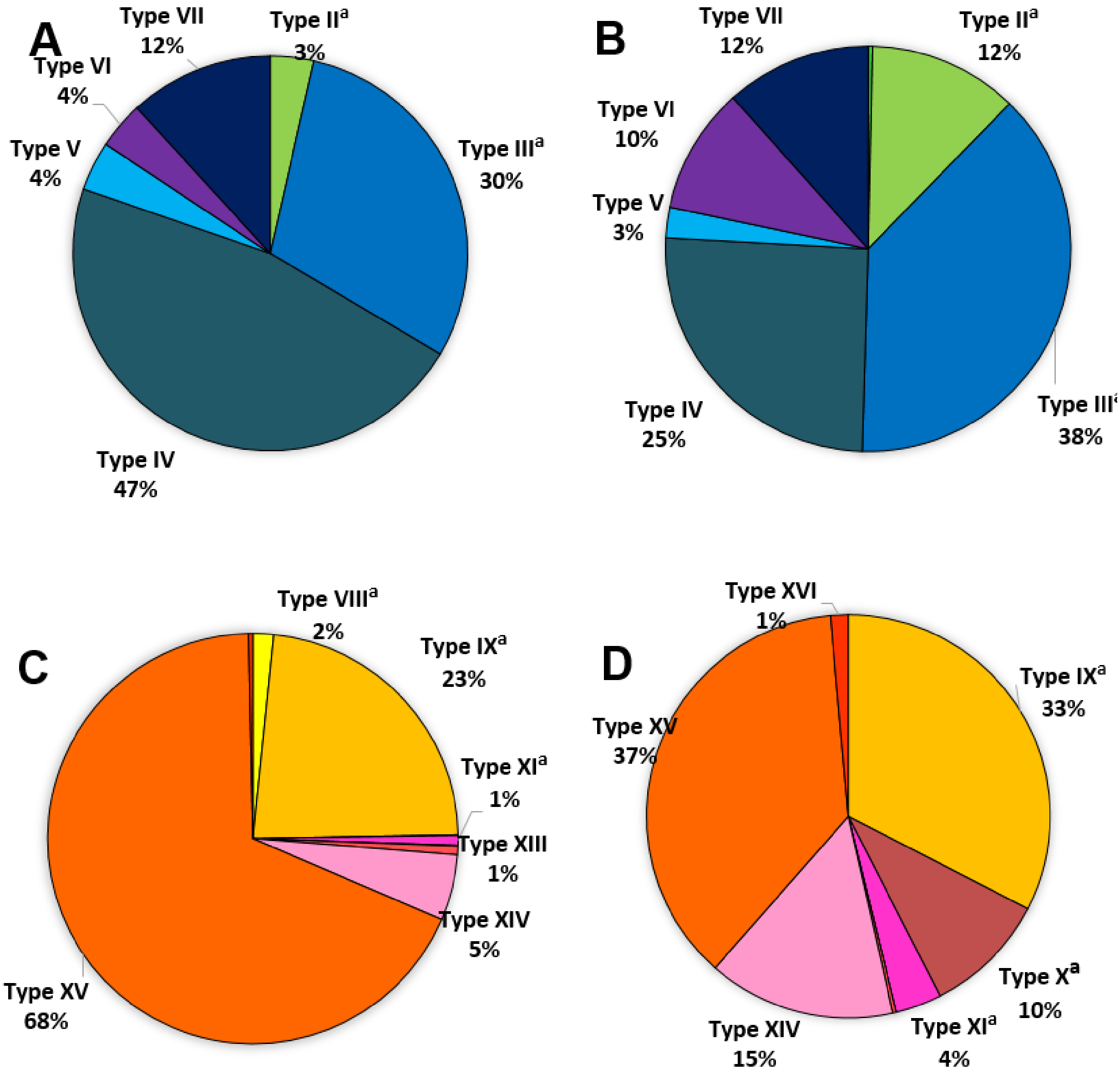


Figure E2: Frequency of plant functional types on the TD before the drought and after drought release. (Grass: A = Pre-drought, B = Drought release; Forbs: C = Pre-drought; D = Drought release)

^{a} represents annual PFT's.