BEAUTY FROM ASHES: SHORT-TERM POSTFIRE REGENERATION OF DUNE FYNBOS-THICKET VEGETATION IN THE SOUTHEASTERN CAPE FLORISTIC REGION

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BEAUTY FROM ASHES: SHORT-TERM POSTFIRE REGENERATION OF DUNE FYNBOS-THICKET VEGETATION IN THE SOUTHEASTERN CAPE FLORISTIC REGION

By

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DECLARATION

I, *Sinenjongo (212250515)*, hereby declare that the *thesis* for *Masters of Science in Botany to be awarded* is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

...... (Signature)

Sinenjongo Gcina

Contents

Acknowledgments	1
Structure of the thesis	2
Abstract	3-4
Chapter 1 - Literature review	5-27
Chapter 2 - BEAUTY FROM ASHES: Understanding the short-term (12 month)	postfire
ecology on coastal dune systems	28-46
Chapter 3 - A survey of belowground bud banks in coastal dune systems	47-73
Chapter 4 – Successes and challenges that come with filling in the gaps of coasta	al dune
systems	74-80
Appendix A, B, C	81-86

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Structure of the Thesis

This thesis is comprised of four connected chapters that are written as stand-alone studies (for publication). Thus, there is some overlap in the contents, particularly in the introduction and description of the study system. Chapter 1 is the literature review that includes the background description of the study system and introduces the major themes presented in Chapter 2 and Chapter 3.

Chapter 2 is a descriptive study on the short-term (12-month) postfire ecology of the fynbosthicket vegetation on a coastal dune system in the southeastern Cape Floristic Region. The resprouters and reseeders present in the system are highlighted in this chapter. A comparison between the proportion of reseeders versus resprouters (in coastal dune systems) is made with the inland fynbos. Potential postfire specialists are also discussed.

Chapter 3 presents a study of the belowground bud banks (BBBs) in coastal dune systems and the classification of these BBBs using the scheme of Pausas et al. (2018). The aim is to assess these growth forms and the disturbance response across a range of species from thicket and fynbos communities in the coastal dune systems after the November 2019 fire on the Mandela University Reserve. This section of the thesis also highlights that coastal dune systems have provided an environment in which a range of species has adapted to form extensive underground lateral expansion to enable them to persist in these fire-prone ecosystems.

Finally, Chapter 4 provides a short overview of the successes and challenges faced while collecting data for this study (especially for Chapter 2) and possible solutions for such challenges.

Abstract

Aim

This study aims to provide an understanding and a description of the short-term postfire regeneration and ecology of the fynbos-thicket vegetation on a coastal dune system in the southeastern Cape Floristic Region. Another aim is to assess the recovery of the vegetation community by assessing the growth forms and the disturbance response across a range of species from thicket and fynbos communities and to provide a belowground bud bank classification for each of these species in the coastal dune systems.

Location

The study site was the Mandela University Reserve and the Noordhoek dune fields, situated in Gqeberha, Eastern Cape, which is part of the south-eastern Cape Floristic Region. The study site hosts thicket-fynbos mosaic vegetation type that occurs in a Mediterranean-Climate Ecosystem (MCE).

Methods

Firstly, field observations and photographs of plant species were taken weekly to assess and identify the species that were emerging and persisting in the dune system in the first 12 months postfire. Phenological events of the species that emerged (e.g., flowering, fruiting, leaf growth, leaf yellowing, and leaf abscission) were also observed and reported on. Secondly, an excavation of 21 species (e.g., *Jamesbrittenia microphylla, Euclea racemosa, Olea exasperata, Searsia laevigata*) was conducted to classify the species into their belowground bud bank types.

Results

There was a rapid emergence of resprouters (facultative resprouters and obligate resprouters) in the first 12 months postfire. This was followed by their growth; primarily occurring after the rainfall events. The dominant resprouting species (facultative resprouters and obligate resprouters) entered the system two weeks after the fire. There was a significant difference in the time to the first emergence of the different regeneration groups postfire (P < 0.001): on average, obligate sprouters (OS) appeared 1 month after fire – two months earlier than facultative sprouters (FS) and four months earlier than non-sprouters (NS). There was no statistical evidence to suggest that the FS and non-sprouters NS emerged at different times postfire; however, most NS species were observed in the system 5 months after fire.

3

Exceptions were the NS species *Pelargonium grossularoides and Mesembryanthemum aitonis, both annuals that emerged 1 month after fire.* A wide range of OS species that appeared earlier in the system (e.g., *Euclea racemosa, Olea exasperata, Searsia laevigata,* and *Lauridia tetragona*) exhibit underground lateral growth with belowground bud banks (BBBs) from which they recover after disturbance. In total, six BBB types were recorded in this study, namely: bud-bearing root, rhizome, rhizophore, woody rhizome, stem tuber, and corms. The bud-bearing root from woody species was the dominant BBB in this system.

Main conclusion

The return of species that occurs in the first year after fire occurs rapidly in the first 2 months as resprouting species (primarily OS) appear in the system. Following this, the rate of return of species decreases as reseeding species (primarily NS) gradually reestablish and occupy the gaps in the dune fynbos-thicket vegetation. This study has shown that plant species in this ecosystem are adapted to fire disturbance as their populations are able to reestablish through various regeneration strategies, including resprouting from different types of BBB.

Chapter 1 - Literature review

Description of study system

In this thesis I will explore postfire vegetative regeneration in the dune system of Mandela University Reserve and surrounds, occurring south of Gqeberha in Nelson Mandela Bay, South Africa. This dune system supports a coastal thicket-fynbos mosaic vegetation and appears in the southeastern Cape Floristic Region (CFR), a Mediterranean-Climate Ecosystem (MCE) of plant hyperdiversity (Fowler et al., 2018). This study system's climate is slightly different from that of other Mediterranean-type ecosystems, as this system is more in the transition zone between a Mediterranean climate system and the neighboring summer precipitation climate system. As a result, the study area is in a year-round rainfall zone (i.e., not a true Mediterranean climate system) but is still classified as an MCE (Marais, 2012). Fire plays a key role in these systems as they are significant drivers and disturbance factors in the dune systems. The attributes of this system are discussed below in more detail.

Mediterranean-Climate Ecosystems

There are five Mediterranean-Climate Ecosystem (MCE) regions in the world where the climate is characterized by hot, dry summers and cool, wet winters (Cowling, et al., 1996; Marais, 2012, Rundel, et al., 2016) with rainfall levels that support and maintain plant growth during winter and spring (Marais, 2012, Marais et al., 2014, Strydom et al., 2021). Another unifying factor is the dominance of evergreen sclerophyllous shrubs (Cowling et al., 1996), which dry out sufficiently in the hot and dry summers to create highly fire-prone landscapes with a predictable wildfire season. Plants in these environments display an extraordinary array of adaptations to fire (Keeley & Bond 1997; Marais, 2012; Fowler et al., 2018).

These fire-prone MCE regions of the world are hotspots of biodiversity and are characterized by exceptionally high numbers of plant species and levels of endemism (Paula & Pausas, 2011; Fowler et al., 2018). Mediterranean ecosystems' productivity and aridity levels provide dry fuel loads that promote recurrent fires during the dry season (Pausas & Bradstock 2007; Paula & Pausas, 2011). However, plants in these regions have adapted to fire through their long relation with fire, consequently most species of these require fire for germination or the release of seeds (Fowler et al., 2018). Changes in fire frequency due to anthropogenic ignitions and climate change are factors threatening these regions' plant diversity (van Wilgen et al., 2010; Marais, 2012).

Resource availability and disturbances are major factors driving plant functioning and traits associated with these two factors define the range of strategies for plant coexistence. In Mediterranean conditions, the topsoil water content during the dry season is drastically reduced, sometimes to less than 1%, which is close to the permanent wilting point estimated for xerophytes (Padilla & Pugnaire, 2007; Paula & Pausas, 2011). Consequently, plant traits related to water uptake are important to explain plant persistence in Mediterranean-type ecosystems (Paula & Pausas, 2011). High water stress tolerance at the seedling stage is especially significant in species where population persistence relies entirely on seedling recruitment (non-sprouters). This explains their higher survival rates under summer drought (Pratt et al. 2008). Seedlings of non-sprouters show greater water transport efficiency, allowing for faster growth and earlier maturity (Pausas et al., 2004; Pratt et al., 2008; Paula & Pausas, 2011).

There are two main mechanisms for postfire persistence at population level in Mediterraneantype ecosystems: firstly, the regeneration of the above-ground biomass after being scorched (i.e., resprouting), and secondly, the recruitment of new individuals from a fire-resistant seed bank, the parent plants of these individuals do not survive and are killed in the fire (Paula & Pausas, 2011; Pausas & Keeley, 2014). Each of these mechanisms is strongly associated with vegetative and reproductive functional traits, and they define two contrasting life histories: resprouters and non-sprouters (reseeders) (Bond & Midgley, 2001; Paula & Pausas, 2011; Pausas & Keeley, 2014).

Vegetation of the Cape Floristic Region

Vegetated dune ecosystems are situated under forests, grasslands, or shrublands and have transformed during the past global climate changes that have occurred on Earth (Barchyn and Hugenholtz, 2013). These dune ecosystems differ in vegetation cover and may be fixed, active, or partially active, mainly as a function of the wind regime and vegetation cover (Yizhaq et al., 2009). At a specific critical vegetation cover, dunes can become completely immobilized. Changes to dunes, either by them being stable or fixed, result in various hybrid states, in which portions of a dune system are covered by vegetation (Barchyn and Hugenholtz, 2013; Bucksey, 2017).

Dune systems undergo a shift whereby they move from being in a stable state to an active state, and this process is referred to as reactivation. There are two processes in which vegetation cover in dune fields can be reduced (Barchyn and Hugenholtz, 2013; Bucksey, 2017). The first occurs when a direct disturbance destroys the vegetation, for example, a fire,

which would expose the underlying sediment. The second includes dune advancement, causing the sediments' erosion and deposition to occur faster than the vegetation can survive and grow. The first process usually is the cause for the second process occurring (Barchyn and Hugenholtz, 2013).

Coastal dune ecosystems are diverse, vulnerable, as well as dynamic environments. These systems are formed by geologically young (late-Pleistocene and Holocene age), sandy sediments of marine origin, exposed to change by winds and sea storms. On some of these dunes, particularly dune systems that are included in the coastal vegetation of South Africa, one will find species from the following growth forms; succulent shrubs, low shrubs, herbaceous climbers, trees, and herbs (geophytic and succulent herbs) (Mucina et al., 2006).

South Africa is rich in biomes (Rutherford et al., 2006), namely, Fynbos, Thicket, Grassland, Savanna and Forest, to name a few. A wide range of environmental and biotic factors influence the distribution of these biomes (Bond et al., 2003). For example, the species predominantly found in the fynbos are highly dependent on regular crown fires, stimulating recruitment from persistent soil and canopy-stored seed banks of relatively short-lived species. In other biomes, such as the forest and scrub, plants regenerate mainly from short-lived, bird-dispersed diaspores that produce shade tolerant seedlings that require long fire-free intervals for recruitment into fynbos (Cowling et al., 1997).

The coexistence of these biomes results from the differences in fire, soil nutrients, soil moisture and other disturbances, such as wind or large herbivores (Strydom et al., 2020). The Holocene dunes of the Cape Floristic Region (CFR) support a mosaic of dune fynbos and subtropical dune thicket vegetation (Cowling, 1984). These two vegetation types appear roughly in equal proportions throughout the extent of this small and fragmented coastal landscape.

Coastal dune systems

Coastal dune systems are some of the most dynamic, valuable, and aesthetic ecosystems we have on earth (Mucina et al., 2006). The establishment of these ecosystems has taken place for millions of years. These ecosystems have been subjected to sea level changes as they mark the transition between land and sea (Abuodha, 2000; Prisco et al., 2016). These systems are best established in sub-humid, warm-temperate to subtropical climates and are abundant in Mediterranean-Climate Ecosystems (MCEs), especially the Cape Floristic Region (CFR) (Tinley, 1985). These systems are categorized by plant communities that are highly biodiverse

and are important, because of the great value in aesthetics and of ecosystem services they provide, such as recreation and restorative activities, providing aesthetic beauty, tangible goods, as water purification, carbon storage and coastal defense and/or mitigation of hazards or climate change-related impacts (e.g., sea level rise and saltwater intrusion). These dune systems are also natural buffers between land and sea (Rust, 1991; Nehren et al., 2016; Prisco et al., 2016; Urbis et al., 2019; Carranza et al., 2020). The plant communities that colonize these dune systems are crucial because they ensure the morphological mobility and stability of the dunes (Abuodha, 2000). These plant communities are one of the vital features of coastal dunes, since they play a role in the high ecological value of these systems (Prisco et al., 2016).

South Africa's southern Cape dunes are characterized by a mosaic of fynbos-thicket vegetation (Cowling & Pierce, 1985). This fynbos-thicket vegetation is a product of thicket species, namely, *Euclea racemosa, Searsia laevigata, Olea exasperata* and *Rapanea gilliana*, invading and establishing in fynbos (Tinley, 1985; Cowling & Pierce, 1985). These thicket species are vigorous resprouters and when they invade fynbos, they can form many ramets from sympodial lateral growth (Tinley, 1985; Cowling & Pierce, 1985). These thicket species provide perches for birds as they invade the fynbos, which quickens the spread of thicket (Cowling et al., 1987). Other vegetation types also contribute to the plant communities formed in these coastal dunes: thicket, fynbos, grassland, and some exposed rocky shelf communities. Soil depth, soil drainage and the fire history of these dunes systems, are the main drivers of these vegetation types, especially when considering the distribution of the thicket, fynbos, and grassland vegetation types (Cowling & Pierce, 1985).

Most thicket species can resprout from basal and aerial bud banks when it comes to the postfire regeneration of thicket species. Still, the degree in which the resprouting ability of these species varies is related to the severity of the fire disturbance that took place (Strydom et al., 2020). However, in the fynbos, postfire regeneration of the species is promoted by high-intensity fires, which promote the regeneration of non-sprouters and less resprouting species. Fynbos resprouters require low-intensity fires to regenerate (Strydom et al., 2020).

Major drivers and disturbance factors in the dune systems

Understanding the factors determining species diversity and distribution is important in ecology. Disturbance is a major driver for diversity, and it, together with succession has been a primary focus for ecology for more than a century (Pausas and Ribeiro, 2017).

1. Fire

Fire occurrence is an important characteristic in more than 50% of the world's terrestrial ecosystems, yet it is one of the most widespread and important forms of disturbance globally (Wilson et al., 2015). Fire is a disturbance with a very long evolutionary history. Macroevolutionary studies have shown that fire is an important factor when it comes to the diversification of some plant lineages, plant species distribution and diversity worldwide (e.g., woody plants) (Pausas & Keeley, 2009; Sauquet et al., 2009; Keeley, et al. 2011; Pausas and Ribeiro, 2016; Teixeira et al. 2020).

Fire-related characteristics are properties that predominantly occur in fire-prone environments, but whether they result from fire selection is unclear (Lamont et al., 2018). Fire has driven the evolution of a collection of plant traits in fire-prone environments, such as fire-resistant tissues or sunken meristems insulated against fire heat, above and belowground plant responses, serotiny (on-plant seed storage with fire-stimulated seed release), fire-stimulated flowering and germination of soil-stored seeds (Lamont et al., 2018).

Regarding fynbos and thicket, fire intensity and frequency are the primary determinants of dune landscapes' co-occurrence and relative abundances (Cowling et al., 1997; Cowling & Potts, 2015; Strydom et al., 2020). There will be times when high-intensity burns destroy mature thicket shrubs, whereas frequent fires tend to kill young thicket plants established in fynbos (Strydom et al., 2020). The fine fynbos fuels are more flammable and burn at higher intensities than thicket fuels (Burger & Bond, 2015). However, during extreme fire conditions, thicket can burn at intensities that sometimes exceed those in fynbos (Kraaij et al., 2018).

According to Strydom et al. (2022), fire exposure has an influence on the species composition in these dune systems. At high fire exposure, thicket species consist of a diverse array of hedge formers that are characterized by many relatively thin and low shoots arising from robust underground stems (Grobler & Cowling, 2021). These hedge formers are said to be geoxylic species, which persist in high fire-exposed dune thicket (Strydom et al., 2022). In high fire exposure the geoxylic structure of certain hedge formers, such as, *Euclea racemosa, Olea exasperate, Rapanea gilliana,* and *Searsia laevigata* is an adaptative trait to recurrent fire (Maurin et al., 2014; Lamont, He & Pausas, 2017; Strydom et al., 2022).

In the case of moderate fire exposure, some of these geoxylic species are replaced by lateral spreaders. Lateral spreaders are the species that generally invest more in aboveground shoots but still retain fire resilience (Strydom et al., 2022). In dune thicket, certain species that are mainly identified as lateral spreaders, (e.g., *Sideroxylon inerme* and *Mystroxylon*

aethiopicum) have high phenotypic plasticity (Strydom et al., 2021), enabling them to persist in low, moderate and high fire exposure environments. Chapter three of this study provides futher details on these lateral spreaders.

According to Strydom et al. (2022), at low fire exposure, thicket is invaded by vertical-growing forest tree species, which establish from bird-dispersed propagules (Cowling et al., 1997; Strydom et al., 2022). Under low fire exposure these species are dominant and can shed lateral branches in favor of fewer vertical branches, shifting from a lateral spreader to a vertical grower via architectural modification (Strydom et al., 2021; Strydom et al., 2022).

Observations have been made on the postfire regeneration in fynbos, such as early secondary successional patterns in fynbos on calcareous coastal dunes in the southeastern Cape (Cowling & Pierce, 1988). When it comes to the fire ecology of dune thicket communities, little is known, due to the limited research that has been done on this topic. Fortunately, Chapter 2 of this thesis focuses on the describing short-term (within a year) postfire ecology of the fynbos-thicket vegetation on a coastal dune system in the southeastern Cape Floristic Region.

2. Wind erosion

The Eastern Cape coast is one of the windiest parts of southern Africa coastline (Avis, 1992). The winds in the regions found along this coastline are primarily westerlies or south-westerlies in the winter and easterlies in the summer. Wind is one of the most important environmental factors in this coastal region since it influences dune formation (Avis, 1992). Strong winds, mostly those parallel to the coast, often during dry conditions, cause extensive sand movement and changes in dune formations. Pioneer plants can survive in these mobile sands, with the help of rapidly elongating stems, rhizomes, roots, or runners. However, wind-blown sand is so great that entire communities may be buried (Avis, 1992).

Wind erosion can play a large role in burnt-out areas (Ravi et al., 2007). Wind erosion processes are not as well studied as soil erosion induced by rainfall and fluvial sediment transport (Wagenbrenner et al., 2013). After a fire has occurred, the soil in the area is vulnerable to particle entrainment caused by the wind, as fire removes the protective ground cover, soil organic matter, and the stabilizing root systems. Fire can also cause more damage by decreasing aggregate stability, reducing soil water repellency, and destroying the soil surface crusts (structures that help limit dune mobility) (Wagenbrenner et al., 2013; Bucksey, 2017).

Erosion crusts are formed from a single layer enriched with fine soil particles. This crust is formed when wind or overland flow removes coarse particles from the surface. In sandy soils along a slope, the structural crusts usually occur upslope, the erosion crusts on the midslope, and the depositional crusts are usually found downslope (Valentin and Bresson, 1992; Bucksey, 2017). Certain types of algae and fungi can strengthen erosion and deposition crusts. Erosion and deposition crusts play a key role in soil stability. Soil crusting is another way to limit the mobility of dunes (Bucksey, 2017). However, wind erosion and thus dune mobility can be reduced by the presence of vegetation.

3. Dune mobility

Vegetation in coastal dune systems is one of the most effective and common sand stabilizers (Durán and Hermann, 2006). Vegetation can inhibit sand erosion and movement and enhance sand accretion. Conversely, sand dynamics such as sand movement can influence the growth of plants since strong winds severely erode non-cohesive sand. This can uncover plant roots, resulting in root erosion (roots being eroded) (Durán and Hermann, 2006), which increases the evaporation from deeper layers (Durán and Hermann, 2006; Bucksey, 2017).

4. Herbivory

Megaherbivores, such as elephant, greater kudu and black rhinoceros browsed in dune landscapes during colonial times (Boshoff & Kerley, 2001; De Villiers et al., 2005; Radloff, 2008). These megaherbivores browse the thicket canopy shrubs and trees in the dune landscapes, influencing plant architecture. Top-down browsing by herbivores can reduce tree height from 5–6 m to 2–3 m and increase the branching density of certain species (Stuart-Hill, 1992; Davies et al., 2018; Strydom et al., 2021). These herbivores do not destroy the structure of thicket where it exists in stands of thicket, therefore their impact in areas where thicket forms a mosaic with fire-prone shrublands, still need to be studied (Strydom et al., 2020).

Strydom et al. (2020) described fire as a disturbance and its effects on the Postfire regeneration of thicket shrubs growing in clumps amongst highly fire-prone fynbos in coastal dune landscapes of the south-eastern CFR. This study deduced that all species were capable of Postfire resprouting from basal buds, but to differing degrees. The extent to which this response has its roots in fire or herbivory is a subject that still needs to be explored. Consequently, dune thicket provides an interesting case where plant lineages adapted primarily to browsing by megaherbivores are exposed to fire (Strydom et al., 2021).

Postfire vegetative regeneration

Postfire Regeneration Strategies

As mentioned above, there are two broad mechanisms by which plant populations persist under recurrent disturbances: resprouting from surviving tissues, and seedling recruitment (Musil & de Witt, 1990; Pausas & Keeley, 2014). Species can have one of these mechanisms or both (Pausas & Keeley, 2014). Many woody plants can resprout, and resprouters dominate many ecosystems. This life history strategy enables plants to persist through disturbances such as fire, flooding, or windstorms (Bowen, 1991; Bond & Midgley, 2001).

Resprouters can grow much faster than non-resprouters as they can quickly reoccupy their gaps. Resprouters can significantly impact the plant population demography by causing decline in the turnover of populations. The presence of resprouters also limits the effects of disturbances, and dependence on seeds for population maintenance can become negligible (Bond & Van Wilgen, 1996; Everham & Brokaw, 1996; Bond & Midgley, 2001). Resprouters generally differ in their ability to resprout, regrow, and to re-establish. The distribution of these species is not hindered or changed, therefore whether a species has a high or low resprouting ability it can still occur in an ecosystem as diverse as a coastal dune ecosystem (Bond & Van Wilgen, 1996; Everham & Brokaw, 1996; Bond & Midgley, 2001).

To have the ability to resprout after experiencing an injury, a plant needs surviving meristems and stored reserves to support regrowth (Bond & Midgley, 2001). Resprouting species need to allocate resources to belowground organs where the active reserves are stored to sustain regrowth. Resprouters use these belowground organs to access more reliable deep water throughout the year (Ackerly, 2003; Paula & Pausas, 2011). The way resources are allocated in resprouters carries a cost traded off against growth or reproduction (Bond & Midgley, 2001). Resprouting is a tolerance trait that confers persistence at the plant level, allowing it to survive diverse disturbance regimes. At the community level, this gives rise to biomes resilient to severe (biomass-depleting) disturbance, such as a fire in savanna. Resprouting ability is determined by the development, protection, and resourcing of a viable bud bank (Clarke et al. 2012; Pausas et al. 2016).

In areas where crown fires are frequent, such as shrublands in the Mediterranean Basin, shrub species are often either directly killed by burning or recover vegetatively from roots or stems (Bond & Midgley, 2001). As mentioned above, some species cannot resprout (non-sprouters), while some have a sprouting ability that increases with size to reach a maximum in adult stages (Bond & Midgley, 2001). Juvenile resprouters can be considered part of the recruitment

strategy after a disturbance, whereas adult resprouters indicate potential persistence after a disturbance (Bond & Midgley, 2001).

The resprouting ability and resprouting rates in plants can sometimes be influenced by anthropogenic changes in atmospheric CO2 (Bond & Midgley, 2001), as a result of this resprouting usually occurs in open disturbed environments rich in resources, where CO2 effects are likely to be greater than in closed communities. In conclusion, resprouting can be identified as a key trait for persistence, influencing the ecology of individuals, populations, and communities (Bond & Midgley, 2001).

In contrast, non-sprouters are subjected to seasonal changes in water availability due to their smaller and shallower roots. Consequently, the water potential of non-sprouters during the dry season is not often observed in resprouting species, as non-sprouters have drought resistance mechanisms, due to exposure to stronger seasonality (Paula & Pausas, 2011). At leaf level, non-sprouters have a higher water use efficiency and leaf mass area ratio (Ackerly 2003). For roots and stems, the low vulnerability to cavitations shown by non-sprouters has been described as a mechanism for water stress tolerance in both adults and seedlings (Pratt et al. 2007a).

Non-sprouters generally have more seeds, larger seed banks, faster growth, and faster maturation rates from seeds. In most cases, they have more seedlings and higher seedling survival than resprouters in matched species comparisons (Bond & Midgley, 2001). According to Bond and Midgley (2001), it has been recorded from a few studies that the emerging idea from fire-prone shrublands and forests is that plants that resprout as adults tend to be poor recruiters. However, non-sprouters play a different game as they tend to recruit more readily.

There have been larger numbers of non-sprouters than resprouters reported for many taxa in Mediterranean type shrublands (Bond & Midgley, 2001). The selection for non-sprouting life histories has played a role in diversification of these rich floras. Although, this great diversity of reseeders found in these many taxa in these Mediterranean type shrublands is not universal. Several genera have equal, or slightly higher, numbers of resprouting species. There are some instances where there are some resprouting and reseeding species that have a closely related. This occurs in many genera in Mediterranean type floras and some species are polymorphic for the trait. Thus, the evolutionary switch from resprouting to reseeding has occurred repeatedly (Bond & Midgley, 2001).

Bud banks and belowground organs

Plants in environments prone to disturbances such as drought, grazing pressure, or fire (Ding et al., 2019), tend to have regeneration strategies put in place to ensure that regeneration or regrowth occurs after the disturbance. Examples of such environments are southern African grassy biomes and fynbos vegetation, driven by fire as a major disturbance (Siebert et al., 2019). As with most plant communities, the maintenance and the renewal of fynbos vegetation depends on the continuous regeneration that plants found in these communities experience (Ding et al., 2019).

Regeneration strategies can be in the form of some plants regenerating from seed, others have aboveground structures, belowground bud banks as well as belowground organs that they use to regenerate, using the resprouting strategy. Belowground bud banks (BBBs) are bud-bearing structures that plants invest their resources into producing, to ensure they can regenerate after a disturbance. BBBs play a crucial role in plant community succession and maintenance of plant communities (Ding et al., 2019). BBBs help mitigate biomass loss and provide stable and sustainable regeneration to be accomplished by the vegetation after a disturbance (Pausas et al., 2018; Ott et al., 2019). BBBs are key players in plant regeneration and recovery after a disturbance and play an important role in ecosystem resilience, plant community structure, and how well the vegetation community deals with drought, grazing pressure, or invasion of alien plant species (Carter et al., 2012; Ding et al., 2019).

The term bud bank was first introduced by Harper (1977). According to Klimešová and Klimeš (2006), Harper was the first to define and characterize bud banks in detail. Harper explained that bud banks formed by an accumulation of dormant meristems formed on rhizomes, corms, bulbs, bulbils, and tubers in the soil. Klimešová and Klimeš (2006) summarized and extended Harpers explanation by suggesting that a bud bank consists of all the bulbs that can potentially undergo vegetative regeneration. The classification of renewal buds is the best example of this. Harper excluded renewal buds (e.g., bulbs) from bud banks because they do not serve as organs for long term storage of meristems. However, Klimešová and Klimeš saw fit to add them in their classification of bud banks, because renewal buds can still take part in the vegetative regeneration of plants, an example of such buds being bulbs (Klimešová & Klimeš, 2006).

Regarding forming bud banks, the buds forming the banks do not necessarily need to be situated in the soil. This is generally true when the disturbance has been low and some aboveground parts of the plant have persisted and are undamaged (Klimešová and Klimeš 2006; Pausas et al., 2018). The formation of a bud bank is usually during stem growth. Still, the formation of buds on either roots, leaves, and stems found outside of the nodes can be produced in some species by injury or fluctuations in nutrient availability (Klimešová & Klimeš 2006).

Belowground bud-bearing organs are stored in roots, root crowns, rhizomes, woody burls, fleshy swellings and belowground caudexes. Mediterranean ecosystem plant species are rich in these types, especially the Cape region, where early hominids consumed bulbs and tubers, and they are now widely used in horticulture (Cowling 2015; Pausas et al., 2018; Botha et al., 2020). Many geophytic species only flower or germinate after fire, and this pyrogenic flowering has been used to trace back the origin of fire-prone ecosystems in the Cape region (Pausas et al., 2018).

Geophytes are herbaceous plants that make us of belowground organs. A defining feature that these geophytic plants have is that they possess buds on their belowground organs that give them the ability to resprout. This feature is especially important to have after a disturbance such as fire occurred as their short-lived aboveground parts are often lost in the fire (Tribble et al., 2021). Resprouting as a means of a regeneration strategy after a disturbance, is common and might also be an ancestral state in woody angiosperms (Bond & Midgley, 2001). Woody plants found mainly in fire-prone areas of Australia, South Africa, the Mediterranean Basin and California also use belowground organs. Many of these plants cope with recurrent fire disturbances by resprouting from lignotubers (Klimešová and Klimeš 2006).

In the case of perennial herbs, these plants use belowground organs by relying on dormant meristems, which are hidden deep in the soil on stems or roots. Seed reproduction in these perennial herbs may be limited and sexual reproduction may be less effective (Klimešová and Klimeš 2006). Resprouting is limited by the interaction of the disturbance regime that diminishes the buds and resources required to ensure resprouting, and by the environment that drives growth and resource allocation (Clarke et al., 2012). Sprouting ability differs among plant species, species' life history stages, and the severity of different disturbances. When the severity of disturbance increases in an area, several plant species will resprout and others will come up from seed (Bond & Midgley, 2001).

Belowground organ traits, such as organ storage capacity, longevity and branching intensity also influence the species resprouting ability, shoot population renewal and clonal growth. Consequently, how the community responds to resource limitation or disturbance may result from differences in the belowground bud-bearing organs (Ott et al., 2019). Examples of these organs are root and stem tubers, rhizomes, and bulbs, while plants on nutrient-poor soils differ

as rhizomes are largely what one will find in these areas (Ott et al., 2019). In the case of coastal dune systems, some of the organs found in these systems are roots, rhizome, rhizophore, woody rhizome, stem tuber, and corms, but very little is known about the dominant belowground bud-bearing organs and which of the belowground bud-bearing organ types are responsible for the maintenance and regeneration of the dune systems after a period of resource limitation or a disturbance, such as fire. I will be investigating this in chapter 3 of this thesis.

Different organs with Belowground bud banks

Roots

Several plants have lateral roots that grow near the soil surface with adventitious buds that produce vertical stems, either root suckers or sprouts. Root suckering has been described in a few angiosperm families, predominantly dicots, a few fern species, and some conifer species. Root suckering is closely linked with lateral spreading, where the ramets remain connected to the parent plant. Root suckering is an efficient resprouting mechanism responding to disturbances, including fire (Lamont, 1988; Hoffmann & Solbrig, 2003; Rodrigues et al., 2004; Pausas et al., 2018). This is because these plants' lateral buds are often well insulated from fires by the soil (Pausas et al., 2018). Root structure is also strongly correlated with physiological traits responsible for the plant's water status (Paula and Pausas, 2011). Plants with vigorously branched roots, characterized by abundant root tips, will have a high water-transport efficiency due to their low overall distance from the tips to the root crown (Paula and Pausas, 2011).

Root crowns

The root crown is the belowground organ situated at the root-shoot transition zone (Pausas et al., 2018). This post-disturbance strategy of resprouting, is one that most resprouting plants use in the regeneration process (Pausas et al., 2018). Trees, including conifers, shrubs, and perennial herbs are some of the plants that benefit from root crown resprouting. This resprouting does not facilitate lateral spreading and colonization, thus it is functionally limited to in-situ persistence after disturbances (Pausas et al., 2018). The root crown has a bud bank located at the cotyledonary region. In this bud bank, clusters of a few buds are formed. With the maturing of the plant comes the increase of the bud bank. This results from the accumulation of axillary buds on basal branches growing from the initial buds (Kauppi et al., 1987; Pausas et al., 2018). In early development, there are plant species that can move the bud bank closer to the soil surface or even belowground, using the root or hypocotyl

contracting or by the bending of the seedling axis; this may increase postfire survival of juveniles that use root crowns as a regeneration mechanism (Pausas et al., 2018).

Woody basal burls

There are instances when the number of buds in the root crown may be restricted for longlived plants if fire recurrence is high. When this is the case, storing many buds at or below ground level may be advantageous. Therefore, many woody plants have acquired basal burls (swollen woody structures), with a disproportionately high concentration of renewal buds (Keeley et al., 2012; Pausas et al., 2018.). Lignotubers are examples of basal burls and often occur in fire-prone ecosystems. The large size of the bud bank and its high degree of protection make lignotubers especially adaptive where high-intensity fires are frequent, therefore they are common in Mediterranean fire-prone ecosystems (Keeley et al., 2012; Paula et al., 2016; Pausas et al., 2018).

Rhizomes

Rhizomes are clonal growth structures formed belowground (Pausas et al., 2018). Many plants have underground stems that grow horizontally from a parent plant without a defined limit. Each stem section is typically called a rhizome and can support aerial shoots and adventitious roots (Pausas et al., 2018). Characteristically, rhizomes are perennial, belowground horizontal stems independent of their woodiness (Pausas et al., 2018).

These structures often grow horizontally at a species-specific depth and, after a while, are orthotropic (growing vertically) and form above-ground shoots, whereby the horizontal part of the rhizome bears bracts. A few roots are developed at the nodes and have long internodes with vegetative spreading that is often fast, extending up to several meters per year. The persistence of the rhizomes that arise at depth can originate at the soil surface and then pulled beneath the soil by contractile roots (Klimešová and Klimeš, 2006; Pausas et al.,2018).

Belowground caudexes

Single-stemmed species, surrounded by persistent dead leaves or leaf bases, as in grasstrees, aloes, palms, cycads and Velloziaceae, have an undivided (monopodial) trunk called a caudex. Despite only having one (apical) bud, they are reliable postfire resprouters (Pausas et al., 2018). Before they emerge, caudexes may remain below ground level for many years, with their buds protected from heat by the soil. For example, the cycad caudex may occur from a depth of 80 cm, with a taproot that pulls it further belowground, resulting in it possibly never emerging from the soil (Lamont, 1984; Pausas et al., 2018).

Corms

Corms are belowground fleshy swelling structures, common in fire-prone ecosystems. They may resprout quickly after fire, sometimes with spectacular postfire flowering (Pausas et al., 2018).

Bulbs, bulbils and tubers

Bulbs are below ground storage organs that comprise storage leaves and a shortened stem base. Bulbs are formed by organs produced within a single season or during several seasons. A bulb represents one renewal bud; in some cases, plants produce smaller bulbs. Bulbs, stem tubercules and root tubers are all small vegetative diaspores (fleshy swellings; Pausas et al., 2018), produced in axils of leaves on stems above-ground or below-ground.

Bulbils are found in the scale leaves, stem tubercules are in the stem part and root tubers are produced on adventitious roots; these soon fall from the parent plant and instantly start to grow, having no dormancy. However, belowground bulbils and tubercules may sometimes postpone their development until spring; young plants regenerating from bulbils and tubercules resemble seedlings in their morphology and size (Pausas et al., 2018).

Phenology

Developing knowledge and understanding and the ability to predict how plants respond to environmental changes is vital in plant ecology. A way to achieve this is to observe the phenology of the plants, as phenology is a good indicator of ecological responses to environmental change (MacKenzie et al., 2020). Phenology is also a plant trait (MacKenzie et al., 2020). Plant phenology research requires monitoring seasonal biological processes such as leaf growth, flowering, fruiting, leaf senescence, leaf abscission, and shoot growth, which are traits among the most visible and observable facets of plant ecology (MacKenzie et al., 2020).

The phenological events for most plant species are generally caused by seasonal climate, which considers the time in which these phenological events occur (MacKenzie et al., 2020). Flowering and fruiting phenology moderate plant-pollinator interactions, seed dispersal, and reproductive success, whereas leaf growth and leaf senescence phenology are phenological traits that moderate herbivory, carbon budgets, and albedo (MacKenzie et al., 2020).

Regardless of the plant phenology research that has been done in the MCE regions of the world, there is still a gap when it comes to understanding postfire phenology (i.e., postfire

flowering, postfire fruiting and other postfire plant responses) and regeneration mechanisms of many of the species concerning the fire regimes they arise in (Marais, 2012). Chapter 2 of this thesis looks at short-term (12 month) postfire phenology.

Conclusion

Studies have been conducted in different areas of coastal dune systems in South Africa: Natal (Moll 1960; Ward 1980), southwestern Cape (Jeffrey and Moll, 1987), and along the Eastern Cape coastline (Dyer and Olivier, 1986; McLachlan et al. 1987; Young, 1987). These studies have focused on the descriptions of dune systems in the Eastern Cape. In 1985, Tinley summarized the dune systems of South Africa and the CSIR undertook a broad survey of coastal vegetation in the Cape Province (Avis, 1992).

The dune fynbos-thicket vegetation of Mandela University nature reserve, situated near Port Elizabeth in the south-eastern CFR, is a fire-prone Mediterranean-type ecosystem rich in plant species, many of which are locally endemic. This reserve is similar to the site near Humansdorp that Pierce and Cowling studied in 1984, therefore it will not be surprising if there are similarities in species composition, when identifying what is found on the Mandela University nature reserve sites observed in this study and what was identified on the site near Humansdorp by Pierce and Cowling (1984). The main aim of this study is to explore the postfire ecology in the coastal dune system. This includes a description of the most dominant and successful species that recover in the system after a disturbance such as fire.

The second chapter in this study compiled a dataset of postfire phenology of the species that emerged and colonized the dune system in the first 12 months after the fire in January 2019 at the Mandela University reserve. Another aim was to classify the plants according to their growth form and Postfire regeneration strategy, which are the fire responses (resprouting and reseeding). These important variables to investigate help us understand the short-term (12 months) postfire ecology on these coastal dune systems.

The third chapter classified the BBB type for a range of common resprouting dune species. The aim was to assess these growth forms and the disturbance response across a range of species from thicket and fynbos communities in the stabilized coastal dune systems.

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Chapter 2 - BEAUTY FROM ASHES: Understanding the short-term (12 month) postfire ecology on coastal dune systems

ABSTRACT

Background

Studies have been done to try and bridge a gap in the lack of knowledge regarding postfire regeneration and the phenological phases of the vegetation found in coastal dunes of the Cape Floristic Region (CFR). This study aims to further the current understanding of postfire ecology, such as to track the postfire regeneration at a fine temporal scale (12 months) and to describe the recovery of the vegetation community in this coastal dune landscape and compare this with inland systems of the Cape.

Methods

Geo-tagged photographs of plant species were taken weekly within sites affected by January 2019 fire in the coastal dune landscape. Observations of species emergence and phenological events (e.g., flowering, fruiting, leaf growth, leaf yellowing, and leaf abscission) took place over the first 12 months postfire.

Results

After the fire, there was a rapid emergence of resprouters, facultative resprouters (FS), and obligate resprouters (OS) species, followed by their growth; this primarily occurred after the rainfall events. Dominant resprouting plant species enter the system two weeks after the fire: woody shrubs (e.g., *Jamesbrittenia microphylla, Searsia laevigata*) and a few grass species (e.g., *Stipagrostis zeyheri barbata, Stenotaphrum secundatum*). Most non-sprouters/obligate seeders (NS) species were observed in the system late, except for *Pelargonium grossularoides* and *Mesembryanthemum aitonis*. There are differences in the proportion of non-sprouters versus resprouters between what is found in the inland fynbos systems and the coastal dune systems. In the first year after fire, the obligate resprouters are the most dominant postfire species in the coastal dune systems as they persist throughout the 1st postfire year.

Keywords: dune systems, fire, regeneration strategy, phenology

INTRODUCTION

Coastal dune systems worldwide have been forming for millions of years (Abuodha, 2000). Studies have been conducted on fossil coastal dunes in several areas around the world, such as along the Kenyan coast (Oosterom, 1988) and in the Netherlands (Jelgersma et al., 1970), to confirm the date of the origin of these ecosystems (Abuodha, 2000). Coastal dunes are located on all continents, except for Antarctica (Grobler et al., 2019). According to Grobler et al. (2019), coastal dune systems are best established in sub-humid, warm-temperate to subtropical climates. According to the classification of Oliver and Fairbridge (1987), Jennings (1964), and Pye (1991) concluded that coastal dunes are less likely to develop in humid tropics (Abuodha, 2000).

In South Africa, the southern Cape coastal dune systems support a mosaic of fynbos, thicket, and forest vegetation, with their relative abundance and position in a landscape dictated primarily by fire exposure (fire frequency) (Cowling and Pierce, 1985; Cowling et al., 2019; Strydom et al., 2021). This study aims to look at the high fire-frequency end of the dune vegetation spectrum, specifically the fynbos-dominated vegetation.

One of the main drivers in the distribution of the vegetation types found in coastal dunes is fire (Keeley et al., 2011; Marais, 2012). The origin of the fire is purported to be tied to the origin of plants (Pausas and Keeley, 2009). It is believed that some of the same fire regimes evident today were present in early land plant communities (Pausas and Keeley, 2009). Fire is an ecological disturbance agent that plays a significant role in the evolution, distribution, and abundance of woody plants worldwide (Pausas and Keeley, 2009; Teixeira et al., 2020). Trees and shrubs present a range of different post-fire responses, strategies, and adaptive traits to persist or re-establish in burnt areas (Teixeira et al., 2020). Consequently, there are several fire adaptations that ensure that plants can persist in fire-prone environments. Fire adaptations are adaptive traits in which natural selection is acting under the current fire-prone environment to shape the trait, which provides a fitness advantage for plants in fire-prone environments (Keeley et al., 2011; Teixeira et al., 2020).

An example of postfire adaptive traits being of value is found in Mediterranean-type climate (MCE) shrublands, specifically, shrublands that are resilient to periodic high-intensity crown fires at intervals of decades or more (Keeley et al., 2011). These shrublands limit the seedling recruitment to the immediate postfire years, which come from the previously dormant soil-stored seed banks or synchronous seed release from serotinous fruits (Keeley et al., 2011).

Resprouting is a trait of adaptive value in fire-prone environments, playing a key role in ensuring that there is plant community resilience to specific fire regimes (Keeley et al., 2011).

Postfire vegetative regeneration

Determining regeneration strategies in plant communities following disturbances such as fire can help ecologists better understand how disturbance affects the structure and diversity of the ecosystem (Fidelis et al., 2021). The regeneration strategies of importance that we consider in this study are postfire regeneration strategies of plant species: resprouting and non-resprouting/obligate seeder. These postfire responses enable plant communities to recover in areas where a fire disturbance has occurred (Teixeira et al., 2020).

Resprouters and non-resprouters (obligate seeders) are favored in different conditions: longer intervals between fires favor non-resprouters, whereas resprouters seem to favor more frequent fires as they thrive under constant removal of aboveground biomass (Fidelis et al., 2021). Non-resprouters also require areas with the availability of open space after a fire has occurred, for reestablishment (Teixeira et al., 2020; Fidelis et al., 2021).

Resprouting is an important post-fire response that enables plants to persist after a fire and is regarded as a key functional trait in woody plants (Teixeira et al., 2020). For example, postfire regeneration of woody species in fynbos shrublands does not only depend on the resprouting of species present at the time of the fire but also on seedling recruitment from species with canopy stored or soil stored seeds (Pierce and Cowling, 1991; Marais, 2012; Strydom et al., 2020). Resprouting species tend to have the ability to start by having vigorous shoots, which non-sprouters cannot compete with. In this way, resprouting have a head start as they avoid the risks related to seedling establishment (i.e., limited dispersion, seed predation, seed desiccation, and the initial and most vulnerable seedling stages) (Teixeira et al., 2020).

Postfire regeneration strategies

There are two broad mechanisms by which plant populations persist under the recurrent disturbance of fire: resprouting from surviving structures and recruitment from seeds. Species can have one of these mechanisms or both (Pausas and Keeley, 2016). The Postfire regeneration strategies focused on in this study are non-sprouters/reseeders (NS), obligate resprouters (OS), and facultative resprouters (FS). Species with reseeding ability are non-sprouters/reseeders (NS) that are killed by the fire and cannot resprout. These species only recruit seedlings from a fire-stimulated seed bank (Keeley and Bond, 1997). Species with a resprouting ability are divided into two types; (1) obligate resprouters (OS), which are species that resprout to persist, as their seeds are killed by fire (Keeley et al., 2006), and (2) facultative

resprouters (FS), which are species that recruit via seedsand have some resprouting ability after the fire (Bond and Midgley, 2001; Marais et al., 2012).

These postfire responses enable plant communities to recolonize areas where a fire disturbance has occurred (Teixeira et al., 2020). A few drivers influence seedling and resprouting regeneration strategy success, for instance, fire frequency and season as well as postfire conditions, such as increased gap availability and reduction of competition for light and nutrients (Fidelis et al., 2021).

The significance of postfire regeneration strategies is demonstrated by the observations that seedlings of non-sprouters and facultative resprouters species are often abundant postfire. Numerous seedlings of these species suffer mortality, and generally, facultative resprouters suffer more significant mortality than non-sprouters (Marais, 2012). Nevertheless, as non-sprouters species depend on reseeding to maintain population stability, their seedlings must be established postfire to replace the adult plants killed by the fire (Marais, 2012). When it comes to the facultative resprouters postfire regeneration strategies, these species have a double strategy (can resprout from surviving below-ground structural organs or recruit from seeds), and several studies observe that facultative resprouters populations generally have a lower postfire resprout survival. This has resulted in a tradeoff between seedling recruitment and postfire resprout survival (Marais, 2012).

The nature of the obligate resprouters postfire regeneration strategy is very different from that of facultative resprouters as obligate resprouter species have heat-sensitive seeds that are short-lived fleshy seeds, lacking the ability to survive a fire (Cowling et al., 1997; Keeley et al., 2006). The pre-fire adults of obligate resprouters need to recruit seedlings, which are often rare and will occur between fires (Cowling et al., 1997). As a result of these tradeoffs and differences in these postfire regeneration strategies, the fitness of obligate resprouter species is proposed to be dependent on resprouting, whereas facultative resprouter species are dependent on their resprouting ability (Marais, 2012). With the gap that is in the knowledge and understanding of postfire regeneration and postfire regeneration strategies of the plant species that recolonize the coastal dunes of the south-eastern CFR, research focusing on the overall population stability and the relative contribution of different strategies (resprouting and reseeding) to long term species survival, after a disturbance such as fire, needed.

Phenology

Plant phenology research involves the observation of seasonal biological processes such as leaf growth, flowering, fruiting, leaf senescence, leaf abscission, and shoot growth. These traits are among the most observable and much-recorded facets of plant ecology (MacKenzie

et al., 2020). Although there has been plant phenology research done in the MCE regions of the world, there is still a gap in the understanding of postfire phenology and regeneration mechanisms of several species (e.g., fynbos species) concerning the fire regimes they arise in (Marais 2012).

Some work has been done regarding fire and the forest and thicket component of these dune systems. For example, Strydom et al. (2020) investigated the influence of fire severity effects on resprouting of subtropical dune thicket of the Cape Floristic Region. However, the postfire recovery in the dune fynbos component of these systems has not been investigated in much detail. This study describes the postfire phenology of multiple (n = 175) plant species associated with the dune fynbos-thicket mosaic vegetation of Mandela University Nature Reserve in the southeastern CFR over 12 months. Additionally, I classify these plant species according to their growth form and postfire regeneration strategies to investigate whether there are differences in postfire responses among these plant types.

METHOD AND MATERIALS

Study site

This study spanned 12 months thus monitoring postfire regeneration on the Mandela University Reserve (34° 47′S, 25° 56′E) and the Noordhoek dune fields, still part of the reserve (34° 02′S, 25° 64′E) (Figure 1), situated in Port Elizabeth, Eastern Cape, which is part of the south-eastern Cape Floristic Region. This study was a natural experiment.



Figure 1: Mandela University nature reserve site (1, 2 and 3)
Vegetation

The Mandela University nature reserve and the surrounding areas support St Francis Dune thicket, which is characterized by clumps of thicket growing within a matrix of dune fynbos (Mucina et al., 2006). Dune fynbos typically grows in sandy soils and coastal calcareous sands. In mosaics of dune thicket and dune fynbos areas, dune fynbos is frequently coupled with fire-prone, edaphically drier areas, whereas the dune thicket tends to grow in areas excluded from fires, such as on, or near, calcrete outcrops. If not burnt, dune thicket will eventually replace dune fynbos (Cowling et al., 1997).

Climate

The seasonality of rainfall is less pronounced in the Eastern Cape compared to other parts of South Africa (Lubke et al., 1988). The Eastern Cape experiences maximum precipitation of 680 mm, of which about 300 mm falls in summer (October-March) and 350 mm in winter (April-September), and average temperatures of 25.1°C - 8.3°C (Mucina et al., 2006). The Eastern Cape is described as a transition zone of climatic types, with Gqeberha receiving the last fronts that bring winter rain to the CFR. Throughout the year, the wind is dominated, in terms of speed and frequency, by west-south-west winds and easterly winds consistently occur in the summer (Lubke et al., 1988; McLachlan et al., 1994).



Figure 2: Annual short term average rainfall data for 2019 for Gqeberha. Data for station [0035209B1] - GQEBERHA AWOS

In 2019 and 2020, which are the years the data of this study was recorded, the rainfall in winter (April-September) was 227 mm with the heaviest rainfall month being July 2019 (68 mm),

whereas the rainfall in summer (October-March) was 181 mm with the heaviest rainfall month being in February 2020 (39 mm) (Figure 2).

Geological setting

A large-scale feature of the Southern Cape coast where this study site is situated, is the presence of asymmetric half-heart bays. These embayment's are bounded by weathering-resistant quartzite sandstone headlands that are filled with less-resistant Cretaceous sandstone and shale. Some examples are the bays associated with Cape St. Francis, Cape Recife (situated to the southeast of the study site), and Woody Cape (Claassen, 2015; Bucksey, 2017). The species, growing on these dune systems, are highly specialised and can withstand extreme conditions. These species may have special morphological and/or physiological features enabling them to grow under adverse conditions (Lubke 1998; Knevel 2001).

The bedrock of the Mandela University nature reserve, Cape Recife, and surrounding areas such as Noordhoek, is made up of the Table Mountain Group Quartzite. This bedrock is typically covered by lime-rich coastal deposits of the Algoa Group. The calcrete of this group can be seen outcropping in places of the Mandela University reserve. This calcrete is covered by the Schelm Hoek Formation that mostly comprises of unconsolidated to semi-consolidated well sorted and fine-grained sands (Claasen, 2015).

Data collection

Three survey routes of approximately 3km each were set up using PVC piping in February 2019. On each site, 10 PVC pipes were placed to mark out the 3km route that was monitored. These pipes were placed in set intervals so that if someone was standing at one of the pipes, they were able to walk for a few meters and they would see the next pipe, to avoid going off the route. These were postfire areas (site 1 at Mandela University Reserve and sites 2 and 3 at Noordhoek) (Figure 1). The first monitoring was conducted on 15 February 2019, 23 days postfire. These routes were monitored weekly. Geo-referenced photos taken of plant species were used for logging results of what was resprouting/reseeding or producing leaves or flowering (Figures 3 and 4). Multiple photographs were taken of all plant species encountered along the routes, and multiple (ca 10) individuals of each species were photographed.



Figure 3: Photographs showing the study sites about two weeks following the fire at Mandela University and Noordhoek.



Figure 4: Photographs showing the study sites about 38 weeks after the fire at Mandela University and Noordhoek.

There were times when errors in the data collection occurred as different people monitored the routes every week. Even though the paths on the sites were clearly marked, from the data it is noted that there were some outliers in the sample (species spotted outside the paths). These were generally the species that were identified or observed in the system once or twice throughout the year.

The species observed less than five times over the study period were eliminated from the "All presence data" (Appendix B). Even though these species did emerge in the system in the first 12 months after the fire, there is an error as there are large temporal gaps between observations of these species, indicating that these species could have been identified off the monitored paths or potential misidentifications. Most of these species were only identified once in the system.

Data analysis

To assign the species into their postfire regeneration groups, facultative resprouters, obligate resprouters and non-sprouters, three sources were used: 1. Dr Adriaan Grobler (personal communication), 2. my own field observations and 3. Grobler and Cowling (2021) (Appendix A).

For the statistical analysis for this study, I used a Kruskal-Wallis rank sum test to test for differences in the time to first emergence (measured in months) between the three postfire regeneration groups (OS, FS, NS) (Appendix A), followed by post hoc pairwise comparisons using Wilcoxon rank sum tests Benjamini-Hochberg correction (Benjamini and Hochberg, 1995) for multiple comparisons.

RESULTS

After 12 months, 175 plant species were observable in the area surveyed. The distribution of the postfire regeneration strategies was as follows: 83 facultative resprouters (FS), 38 obligate resprouters (OS), and 54 non-resprouters (NS). About half (51%) of these species were woody species, and the other half were herbaceous species (mainly geophytes, annuals, and forbs) (Appendix 1).



Figure 5: First emergence of the different post-fire regeneration strategy groups, facultative resprouters (FS), obligate resprouters (OS) and non-resprouters (NS) postfire. Indicated are the median value (horizontal bar), the twenty-fifth and seventy-fifth percentiles (lower and upper bounds of box, respectively), and the range of values that are within 1:5×IQR (interquartile range) of the twenty-fifth and seventy-fifth percentiles (upper and lower bounds of "whiskers"). Each dot represents a species.

The facultative resprouters (FS) and obligate resprouters (OS) species were the early resprouters in this system, and this was especially true in the first month after the fire (Figure 5). There was a significant difference in the time to the first emergence of the different regeneration groups postfire (Kruskal-Wallis test, $\chi 2 = 22.215$, df = 2, P < 0.001). On average, obligate sprouters (OS) appeared two months (median time to first emergence = 1 month, IQR = 1 month) earlier than facultative sprouters (FS) (median = 3 months, IQR = 7 months) (Wilcoxon test, P = 0.0016) and 4 months earlier than non-sprouters (NS) (median = 5 months, ICR = 1 month).

IQR = 7.75 months) (Wilcoxon test, P < 0.001), but there was no statistical evidence to suggest that the facultative resprouters (FS) and non-sprouters (NS) emerged at different times postfire (Wilcoxon test, P = 0.0782).



Figure 6: Percentage of flowering spp. in the first month postfire.

The facultative resprouters (FS) and obligate resprouters (OS) species were not just the first to recover back into the system; they were also the first species to flower. Out of the species that flowered in the first month postfire, about 58% of these species were obligate resprouters (OS). The rest of these early flowering species were facultative resprouters (FS) (42%) (Figure 6). None of the non-sprouters (NS) species that recovered in the first month in the first year flowered.

DISCUSSION

South Africa's southern Cape dunes are characterized by a fynbos-thicket mosaic vegetation type (Cowling, 1984). In this study, the early colonizers that entered the system after a month postfire were predominantly species found in the thicket and fynbos, with one or two coastal and wetland species. This confirms Cowling and Pierce (1985) description of these coastal dunes being formed from a mixture of vegetation types, but the prominent vegetation types being the fynbos and the thicket. After a disturbance such as a fire, the species found in these dune systems undergo postfire vegetative regeneration. It is no surprise that most of the flora found in these coastal dunes is predominantly from the thicket (dune thicket) and fynbos (dune fynbos), as these dunes are a mosaic of these vegetation types. Examples of the flora that one will find on these southern dunes are thicket species such as *Maytenus*

procumbens (OS), Searsia crenata (OS), and some dominant species being Euclea racemosa (OS), Rapanea gilliana (OS), Sideroxylon inerme (OS), Putterlickia pyracantha (OS), Carissa bispinosa (OS), Olea exasperata (OS) and Cussonia thyrsiflora (OS) (Cowling and Pierce, 1985). These dune thicket species recovered back into the surveyed area except for Sideroxylon inerme, an obligate resprouter (OS) identified twice in the 12 months postfire.

In contrast to the thicket dune flora, according to Cowling and Pierce (1985), some examples of the Southern cape dune fynbos species that were most likely to be in the system were Agathosma apiculata, Metalasia muricata (NS), Felicia echinata (NS), Helichrysum teretifolium (FS), Restio eleocharis (FS), Phylica litoralis (NS), Ficinia spp. (FS) and Aspalathus spinosa, to name a few. In this study, these dune fynbos species were observed in the surveyed area.

The dominant species in these coastal dune systems may or may not be the ones that are the first to respond in the surveyed area after the fire. In this study, it was discovered that some dominant species from past studies were among the species that were the early colonizers of the system. The following were some of the main species: *Putterlickia pyracantha, Phylica ericoides, Rhoicissus tridentata, Cussonia thyrsiflora, Maytenus procumbens, Euclea racemosa, Rapanea gilliana,* and *Searsia laevigata,* to name a few. These species do not just dominate and survive in these systems but play a huge role in the vegetation community structure of these systems. These were also some of the first to flower and fruit, supporting what is already known about them (Cowling and Pierce, 1985; Strydom et al., 2021)., that they have; growth through resprouting (Strydom et al., 2021), flowering, and fruiting (Cowling and Pierce, 1985).

When focusing on the species with regards to their postfire regeneration strategies and what the return rate over a short-term period (12 months postfire) is for each postfire regeneration strategy, the main findings are that facultative resprouters (FS) have the highest response rate (first to be observed after the fire). The species that respond in the system first, as well as flowered and fruited first, were predominantly facultative resprouters (FS) and obligate resprouters (OS) (Figure 5, Figure 6). In many cases, obligate resprouters (OS) have no seedlings directly postfire. Still, they have a high adult resprout success, which explains the rapid fruiting and flowering that took place with some of the obligate resprouters (OS), for example, *Asparagus aethiopicus and Searsia laevigata*. The facultative resprouters (FS) have a broad range of seedling recruitment and adult resprouting success; this is what we observe with *Jamesbrittenia microphylla* (Marais, 2012).

In the first month, the first to colonize the system is mainly woody plants with resprouting abilities. These species can resprout due to their belowground structures, i.e., their surviving meristems and stored reserves to support regrowth (Bond & Midgley, 2001). These belowground structural organs enable these resprouters to grow much faster than seedlings and quickly reoccupy their gaps (Bond & Midgley, 2001; Klimešová and Klimeš, 2006).

Some species are no longer observable in the system after a few months, such as *Colchicum eucomoides* (herbaceous geophyte), *Oxalis depressa* (herbaceous geophyte), *Trachyandra divaricata* (herbaceous geophyte), and *Anagallis arvensis* (herbaceous annual) (Appendix A). These species' growth form is probably the reason for their disappearance. Most annuals and geophytes complete their reproductive cycle soon after a fire (Manning et al., 2002). Consequently, these species will often go dormant underground forms (bulbs or seeds) until the next fire (Marais, 2012).

The late comers in this dune system were the non-resprouters (NS) species (Appendix B, Figure 5). Most of the non-resprouters (NS) observed in the surveyed area came in 33 weeks postfire (e.g., *Metalasia muricata, Achyranthemum sordescens, Passerina rigida*), 36 weeks postfire (e.g., *Muraltia squarrosa*) and some in the 38th-week postfire (e.g., *Phylica ericoides*) The 38th week was the last week a survey was done of the system for this study. Non-resprouters (NS) must compete against each other as well as the obligate resprouters (OS) and facultative resprouters (FS) species for resources and light, so that they are re-established back into the system (Bond et al., 1984; Pausas and Bradstock, 2007). It was interesting to see *Metalasia muricata* come in so late into the system, as it is a southern cape dune fynbos species that is frequently present and dominant in this system (Cowling and Pierce, 1985).

In literature, it has been noted that the seeds of non-resprouters (NS) in fire-prone fynbos are directly or indirectly fire stimulated, and germination is restricted to the wet season in the first year postfire (Bond et al., 1984). Since the study area received less rainfall in comparison to past years, this could have affected the germination period of the non-resprouters (NS) species, delaying their recovery back into the area surveyed in the first 12 months postfire, which could explain the low percentage of non-resprouters entering the system in the first few months postfire. However, there were three non-resprouters (NS) that entered the system within the first month and persisted in the system throughout the 12 months. The non-resprouters (NS) were *Pelargonium grossulariodes, Erucastrum strigosum,* and *Mesembryanthemum aitonis.* These are herbaceous annuals in growth form. Fynbos species, mostly annuals, fire ephemerals, and geophytes, frequently complete their

reproductive cycle directly after a fire (Manning et al., 2002), which possibly explains the success in the recovery of these species in the first 12 months postfire. Species that recover in this way often will disappear in the second year postfire. This is what started to happen with *Mesembryanthemum aitonis*.

Species that tell a story:

Searsia species

There are four *Searsia spp.* found on the Mandela University Reserve and surrounds, namely, *Searsia laevigata, Searsia crenata, Searsia glauca*, and *Searsia lucida* (Figure 7, Table 2). These species are all tall woody shrubs and have the regeneration life history strategy of being obligate resprouters. This means these are species that resprout so that they can persist, as their seeds are killed by fire (Marais et al., 2012). In a system prone to fire as a disturbance, it is important to ensure that obligate resprouters (OS) have a chance to have a population that will thrive postfire, and this is made possible from resprouting as well as when the pre-fire adults of the obligate resprouters (OS) recruit seedlings (Marais et al., 2012).

There are many obligate resprouters (OS) in the Mandela University Reserve and Noordhoek dune systems. These species are generally the ones that enter the system first (Appendix B), as well as the ones that undergo flowering and fruiting after a fire. The *Searsia spp.* found in this system are examples of these species. Therefore, it is no surprise that these *Searsia spp.* were observed in the system within the 1st or 2nd month after the fire. *Searsia laevigata* and *Searsia glauca* appeared in the 1st month after the fire, whereas *Searsia crenata* and *Searsia lucida* appeared in the 2nd month after the fire. *Searsia laevigata* was the only species out of the four that flowered and fruited. The first appearance of flowering and fruiting occurred in the 2nd month after the fire (Figure 7, Table 2). This was a very interesting observation, and it led to the following questions: (1) could there be coastal dune systems species that have adapted the fire-triggered flowering postfire strategy like those found in tropical savannas (e.g., Zirondi et al., 2020) and (2) could *S. laevigata* be an example of such a species?

Fire-stimulated flowering are species that have not been investigated in these fire-prone dune systems, even though there might be no better demonstration of a fire-adapted trait than this specific trait, whose presence depends on whether a fire takes place (Lamont and Downes, 2011). Species with fire-stimulated flowering may be separated into a few growth forms, usually woody shrubs and, in some instances, some evergreen herbs, trees, and palm-like

plants (Lamont and Downes, 2011). *Searsia laevigata* falls under this group as it is an obligate resprouting woody shrub.

Mesembryanthemum aitonis

Mesembryanthemum aitonis is an example of a species that stood out in the system. It was one of the early colonizers, but this species persisted and was present throughout the first 12 months postfire and extremely abundant (Figure 8). In this study, I put forth the idea that *Mesembryanthemum aitonis* in these dune systems is a postfire opportunist or short-term postfire specialist. This means that *M. aitonis* had a high return rate in the system as there was a gap for it to do so. *Mesembryanthemum aitonis* was also one of the more dominant flowering species.

Boophone disticha

Boophone disticha was flowering two weeks after the fire (Figure 9). This is because *B. disticha* has an aboveground perennial structure that protects it from fire (Figure 9). *Boophone disticha* is across a vast area of southern, central, and East Africa, and it occurs in many countries, from South Africa to South Sudan (Duncan et al., 2016). The species comprises both summer and winter growing forms. The summer growers dominate a major part of its range.

The winter growers occur in southwestern Namibia and in the southwestern, southern, and southeastern parts of South Africa, including areas on the Langeberg, at Cape Agulhas, Ladysmith, Still Bay, Port Elizabeth, Hamburg, and Chalumna near East London (Duncan et al., 2016). The winter growers flower from late summer to autumn, produce leaves from autumn to spring and remain dormant in summer. The summer growers flower mainly from late winter to early summer, produce leaves from spring to autumn, and remain dormant in winter (Duncan et al., 2016).

In Figure 8, it is noted that in this study, the *B. disticha* we find in the dune system is the winter growers, flowering February-March (late summer/early autumn). This supports the description Duncan et al. (2016) on the winter-flowering form of *B. disticha*, which is that it is restricted to the Greater Cape Floristic Region (i.e., the winter-and all-year rainfall zones of South Africa).



Figure 7: A representation of the presence, flowering, and fruiting of the four *Searsia spp.* in the 1st, 4th, 8th and 12th month postfire that were found on these coastal dune systems.

Table 2: Species of the Searsia genera found on these coastal dune systems

Species	Family	Postfire Regeneration Strategies	Growth Form	Reference	First appearance (postfire)	First flowering (postfire)	First fruiting (postfire)
Searsia laevigata	Anacardiaceae	OS	Woody tall shrub	Grobler and Cowling 2021	February (1 month after fire)	March (2 months after fire)	March (2 months after fire)
Searsia crenata	Anacardiaceae	OS	Woody tall shrub	Grobler and Cowling 2021	March (2 months after fire)	No flowering recorded	No fruiting recorded
Searsia glauca	Anacardiaceae	OS	Woody tall shrub	Cowling et al., 2019; Grobler and Cowling 2021	February (1 month after fire)	No flowering recorded	No fruiting recorded
Searsia lucida	Anacardiaceae	OS	Woody tall shrub	Grobler and Cowling 2021	March (2 months after fire)	No flowering recorded	No fruiting recorded



Figure 8: *Mesembryanthemum aitonis* appearance in the first 12 months after the fire that took place on the coastal dune systems of Mandela University reserve and Noordhoek.





4 months postfire



5 months postfire 6 mor



6 months postfire



7 months postfire



8 months postfire



9 months postfire



10 months postfire



11 months postfire



12 months postfire

Figure 9: Boophone disticha appearance in the first 12 months after the fire that took place on the coastal dune systems of Mandela University reserve and Noordhoek

Plants in these coastal dune systems, particularly the woody species, have adopted survival traits (e.g., resprouting) to ensure postfire persistence (Bond and Midgley, 2001). In this study, facultative resprouters demonstrated the highest recovery percentage compared to the obligate resprouters and non-sprouters. Facultative resprouters have a wide range of seedling recruitment and adult resprout success. In contrast, non-sprouters depend on seedling recruitment and obligate resprouters have no seedlings in the immediate postfire environment which means they depend on adult resprouting success. These results contrast with the findings in inland fynbos. Marais (2012) reported that obligate resprouters were the more successful resprouters in the inland fynbos because of their ability to resprout early and vigorously after fire and to endure the hot, dry summer months.

In this study, 7 out of the 12 species that flowered in the first month postfire were obligate resprouters, whereas, in the inland fynbos, Marais (2012) reported that the obligate resprouters only started flowering during the second year postfire. However, in both systems (inland fynbos and coastal dune system), most of the facultative resprouters flowered in the first year postfire. Marais (2012) reported that many species in the Cape Mountain fynbos flower profusely within the first year or two after a fire. She reported that some of these species, especially species from Iridaceae and Orchidaceae, demonstrate obligate fire-stimulated flowering (Manning 2007; Lamont and Downes, 2011), which resulted in some flowering being enhanced after the fire. This phenomenon has been put forth to explain the rapid flowering observed in *Searsia laevigata* in this study.

CONCLUSION

The observations made in this study provide information for more studies on postfire regeneration strategies and growth forms (the focus of the study in the next chapter of this thesis). Postfire regeneration strategies, namely, obligate resprouters (OS), facultative resprouters (FS), and non-resprouters (NS), and fire dependant regeneration strategies such as fire-stimulated flowering should be included in standard species descriptions to establish a better understanding of plants in fire-dependent ecosystems (Marais, 2012). Postfire regeneration strategies are crucial indicators of resilience to fire as they enable plant communities to recover in areas where a fire disturbance has occurred; these regeneration strategies ensure persistence in fire-prone dune systems.

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45

Chapter 3 - A survey of belowground bud banks in coastal dune systems

ABSTRACT

Background

Little is known about belowground bud banks (BBBs) in the dune vegetation of fynbos-thicket mosaic of coastal dune systems in the southeastern Cape Floristic Region. There is a lot of resprouting taking place in the dune fynbos-thicket mosaic. However, there has been a lack of understanding and knowledge regarding the role of BBBs as a resprouting strategy. In recent years, investigations have been done on these distinctive growth forms in other fire-prone ecosystem such as savannas. This study aims to survey BBBs and the disturbance response across a range of species from thicket and fynbos communities in the stabilized coastal dune systems that possess these growth forms.

Methods

Surveying BBB types in the dune system by excavating 21 species, such as some common Postfire fynbos-thicket mosaic species types (e.g., *Rapanea gilliana, Euclea racemosa, Olea exasperata, Searsia laevigata, Lauridia tetragonia,* and *Jamesbrittenia microphylla*).

Results

А wide range of species (e.g., Euclea racemosa, Olea exasperata, Searsia laevigata, and Lauridia tetragonia) exhibit underground lateral growth from which they recover from disturbance. Several species in these dune systems contain belowground bud banks with belowground organs that enable these species to resprout after a disturbance. Six BBB types are represented in these coastal dune systems: bud-bearing root, rhizome, rhizophore, woody rhizome, stem tuber, and corm. The bud-bearing root from woody species was the dominant BBB in this system.

Conclusion

This study highlights that belowground bud banks consist of belowground structures that can be used for vegetative regeneration, such as rhizomes, tubers, corms, and bulbs that enable plants to resprout after a disturbance such as a fire in the coastal dune systems. Lateral resprouting is another way that woody species in these dune systems can resprout and persist. These types of resprouting mechanisms (BBBs and lateral resprouting) play a crucial role in plant community succession and population and vegetative regeneration and maintenance and the renewal of plant communities after a disturbance such as fire.

Keywords: Coastal dune systems, fire, resprouting, belowground bud banks

INTRODUCTION

Description of the dune system

The dune system that was focused on in this study is a thicket-fynbos mosaic vegetation type system and occurs in a Mediterranean-Climate Ecosystem (MCE) in the Cape Floristic Region (CFR).

After a disturbance, the species found in these dunes undergo vegetative regeneration. When it comes to the postfire regeneration of thicket species, most can resprout from basal and aerial bud banks, but the degree to which the resprouting ability of these species varies concerning the severity of the fire disturbance that took place (Strydom et al., 2020). Other examples of the flora that one will probably find on these southern dunes are thicket species such as *Maytenus procumbens* and some dominant species being *Rapanea gilliana, Putterlickia pyracantha, Carissa bispinosa,* and *Cussonia thyrsiflora* (Cowling and Pierce, 1985).

However, fynbos resprouters require low-intensity fires to regenerate (Strydom et al., 2020). Examples of the Southern cape dune fynbos species that are most likely to be in these systems are resprouters such as *Restio eleocharis, Phylica littoralis, Ficinia* spp., and *Aspalathus spinosa* and a few non-sprouters such as *Agathosma apiculata, Metalasia muricata, Felicia echinata, Helichrysum teretifolium,* to name a few (Cowling and Pierce, 1985). The vegetation in these dune systems acts to decrease aeolian activity and stabilizes the dunes (Bucksey, 2017). After a fire, stabilized dunes can be reactivated and mobile – depending on the regrowth of vegetation (Strong et al., 2010; Bucksey, 2017).

Means of persistence of coastal dune systems

For the vegetation community found in coastal dune systems, one could see regeneration strategies that the plants possess, namely, resprouting/reseeding, belowground bud banks, belowground organs, and fire-related traits (i.e., bud protection, germination stimulated by temperature and smoke, postfire flowering), as being examples of "postfire persistence mechanisms" (Ott et al., 2019; Fidelis et al., 2021).

The ability of plant species to resprout (resprouters) and grow from seed (reseeders) are very important responses to plant ecology. Resprouters, as well as reseeders, play a crucial role in

47

population dynamics and recovery from disturbance. Obligate resprouting (OS) and facultative resprouting (FS) are the two Postfire regeneration strategies of resprouters. Obligate resprouter species must resprout after fire, as their seeds are not fire resistant and seedling recruitment occurs in fire-free periods. In contrast, facultative resprouter species can resprout and recruit seedlings after a fire (Marais 2016).

Marais (2016) found a significant difference in postfire resprouting success between obligate resprouting species and facultative resprouting species, supporting the division of woody resprouting shrubs into these two Postfire regeneration strategies. OS species had minimal fire-related mortality related to their ability to resprout early and vigorously after a fire. The FS species varied in their response to fire and had greater fire-induced mortality than the obligate resprouting species. Postfire mortality (post-sprouting) of facultative resprouters was also greater than obligate resprouting species, especially towards the end of the long dry summer, suggesting a link to water stress (Marais 2016).

Plant communities of the Grassland and Savanna Biomes in South Africa are resilient to disturbances, including fire, herbivory, and rainfall variability, within which they have evolved. The coastal dune vegetation in the southern Cape Floristic Region also has the resilience to such disturbances (Strydom et al., 2021). Since the vegetation dynamics, structure, and function of a few biomes, including the Fynbos of the Cape Floristic Region, are driven by several disturbances (e.g., fire), one would assume there would be several studies that have investigated belowground regeneration strategies (Siebert et al., 2019). However, this is not the case, as studies on belowground traits are limited in the scientific literature, with only a few contributions pertaining to 'belowground bud bank' as the main topic (Pausas et al., 2018; Siebert et al., 2019; Chiminazzo et al., 2021).

Belowground bud banks (BBBs) are an investment strategy in fire-prone environments that plants invest resources into and use to ensure they can regenerate after a disturbance. These belowground bud-bearing structures are stored in roots, root crowns, rhizomes, woody burls, fleshy swellings, and belowground caudexes (Pausas et al., 2018). These structures accomplish lateral spread and colonization functions and have adaptive value in recovering from fire as they protect buds from fire heat (Keeley et al., 2011; Pausas et al., 2018).

Plant bud banks are all the buds that are the source of the vegetative reproduction of plants. These bud banks are connected to the regeneration strategies of plant communities in ecosystems that are frequently subjected to disturbances (Siebert et al., 2019). The accumulation of buds on plants occurs when new nodules are produced on the plant bodies as plant growth occurs. These buds are then used for branching, flowering, and seasonal regrowth or may remain dormant for future use, for example, recovery after being damaged by a disturbance (Klimešová et al., 2019). The buds that remain dormant wait for opportunities to resprout and are generally protected against damage caused by disturbances. These dormant buds are known as the bud bank of a plant (Klimešová et al., 2019).

In most cases, plants that have bud banks can store carbohydrates, which provide energy for the plants to resprout. The stem of the plant is the most important part for plant growth as well as for resprouting as it generally is the organ that contains most of the buds (Klimešová et al., 2019). Consequently, stems need to use growth modifications belowground and store resources where buds that allow resprouting are sheltered from disturbances. A common type of modified stem is the rhizome, which is positioned belowground and provides buds and carbohydrates. Buds may also be formed on roots usually situated deeper belowground than stem-derived rhizomes and are therefore better protected from disturbances that reach upper soil horizons (Klimešová et al., 2019).

In woody plants, the development of buds on stems or roots is usually at the expense of vertical growth. Bud bank size, bud bank fluctuation (temporal change of bud bank size), bud preformation, and bud protection are commonly related to the bud bank and often looked at when describing the bud bank. The frequency and intensity of a bud bank usually influence the bud bank size and bud protection, respectively. In contrast, bud bank fluctuation and bud preformation are relevant to the timing of the disturbance (Klimešová et al., 2019).

Belowground bud banks (BBB) play a crucial role in plant community succession, population regeneration, and maintenance. For example, belowground bud banks comprise an important regeneration strategy for many savanna plant species. Belowground bud banks are crucial in studying how plants adapt to environmental stress, ecological restoration, and succession (Ding et al., 2019; Siebert et al., 2019). In several ecosystems, the size and structures of the aboveground plant richness can give an idea of BBB composition and the population renewal of plants in response to different disturbances and environmental stresses (Ding et al., 2019).

Several studies are being conducted on plant bud banks all over the world. Some look at shrublands subjected to high-intensity fires and how plants resprout after disturbance (Pausas

and Keeley, 2017). Others look at species growing in fire-prone savannas, which usually persist by resprouting from their buds (Chiminazzo et al., 2021). Through these studies, it has been discovered that water availability is one of the key factors affecting the density of belowground buds. The size and composition of plant buds are closely related to precipitation; because of this, the higher the precipitation, the more abundant the bud bank will be. An example of this is found in the density of buds in North American grasslands, which increases significantly with annual average precipitation (Ding et al., 2019).

Resprouting is a common regeneration strategy in these coastal dune systems in the CFR (Chapter 2 of this thesis, Strydom et al., 2020). In this study, the identification of the dominant resprouters that emerged in the first eight months after the fire was made. The excavation of these species was done to find the resprouting for each. These species were then classified into belowground bud bank (BBB) types; determined by the belowground structures that were present, enabling them to resprout, recolonize and persist after the fire disturbance. The BBB types that were present and absent were noted. The following BBB traits were considered while surveying the BBBs of the species: the origin of the buds (where the buds generally are located), bud bank size, bud protection, growth form, and recolonization ability. Lateral resprouting was also observed as it is one of the persistence traits that some resprouters in these sandy dunes perform.

Little is known about the belowground bud banks (surviving structures) that enable plants growing in these fire-prone ecosystems to regenerate after recurrent disturbances such as fire (Pausas, 2018). By surveying these BBBs in the coastal dune ecosystem, the aim isto establish which BBB categories are present, to classify the resprouters (early colonizers) into their BBB types, and to compare the BBBs in this system with those found in other systems.

METHOD AND MATERIALS

Study site

A study was done on the Mandela University Reserve (34° 47′S, 25° 56′E) in Gqeberha, Eastern Cape, which is part of the south-eastern Cape Floristic Region.



Figure 1:Nelson Mandela nature reserve site

Vegetation

The dune vegetation in this dune system consists of a mosaic of dune fynbos and subtropical dune thicket. These two vegetation types appear roughly in equal proportions throughout the extent of this small and fragmented coastal landscape (Vlok et al., 2003; Grobler et al., 2018; Dayaram et al., 2019). Dune thicket is distinguished from other thicket vegetation types by the presence of dune endemics such as *Olea exasperata*, *Searsia crenata*, *Euclea racemosa*, *and Robsonodendron maritimum*, and the dominance of certain canopy-forming shrubs such as *Searsia glauca*, *Sideroxylon inerme* and *Pterocelastrus tricuspidatus* (Cowling, 1984).

The Mandela University nature reserve covers 830 ha. It supports St Francis dune fynbos-thicket, mosaic-type vegetation characterized by tall, dense clumps of dune thicket occurring within a matrix of dune fynbos that is mostly outside the influence of salt spray. Stunted trees dominate these dunes, shrubs, abundant lianas, and sparse herbaceous and grassy undergrowth (Vlok et al., 2003; Mucina et al., 2006; Grobler et al., 2018; Dayaram et al., 2019; Strydom et al., 2020).

Dune fynbos generally grows on coastal calcareous sands. In mosaics of dune thicket and dune fynbos areas, dune fynbos is frequently associated with fire-prone and drier areas. In contrast, dune thicket grows in areas protected from fires, such as near or deep, well-drained fertile soils in the lowlands or steep-walled interdune valleys and dune slacks where moisture lies closer to the surface and where fires typically do not penetrate (Pierce and Cowling, 1984). Under natural conditions, fire return intervals in dune landscapes are believed to range from 16 to 26 years in fynbos and 50 years or more in unbroken stands of thicket. As a result, it may be assumed that dune thicket might, in the long run, replace dune fynbos (Cowling et al., 1997; Kraaij et al., 2013; Cowling and Potts, 2015; Strydom et al., 2021; Cowling and Hoffman, 2021). Along the South African coastline, from west to east, there is a gradual shift from coastal fynbos to thicket and then coastal forest as the rainfall changes from winter to summer (Tinley, 1985). The vegetation in these regions is influenced by the climate, mainly the rainfall and temperature.

Climate

The climate of this study system is somewhat different from that of Mediterranean-type ecosystems, as this system is more in the transition zone between a Mediterranean climate system and the neighbouring climate system.

The seasonality of rainfall is much less noticeable in the Eastern Cape compared to other parts of South Africa (Lubke et al., 1988). The Eastern Cape experiences a non-seasonal temperature regime, having maximum precipitation of 680 mm, of which about 300 mm falls in summer (October-March) and 350 mm in winter (April-September), and average temperatures of 25.1°C - 8.3°C (Mucina et al., 2006). The Eastern Cape is described as a transition zone of climatic types, with Gqeberha receiving the last fronts that bring winter rain to the Western Cape. Throughout the year, the wind is dominated, in terms of speed and frequency, by west-south-west winds and easterly winds consistently occur in the summer (Lubke et al., 1988; McLachlan et al., 1994).

The climate has drastically changed throughout the Eastern Cape in the past few years. The year of sampling in this study was notably drier than average. Unfortunately, long term average

historical data was not obtained and therefore could not be included in Table 1 to make a comparison of the rainfall average in the area over the years. However, Table 1 is a representation of the short-term average rainfall data for 2019-2020, to give an indication of what the conditions were during the study period. The rainfall in summer was 179 mm, with the heaviest rainfall month being in February 2020 (39 mm), whereas the rainfall in winter was 340 mm, with the heaviest rainfall month being Aug 2020 (131 mm) (Table 1). When considering these rainfall data, one can see that there is a decline in the maximum precipitation in this area, with a massive drop of 19,8% in summer and a drop of 1,7% in winter when compared with what was noted in the Coastal vegetation of South Africa, mentioned above (Mucina and Rutherford,2006).

Table 1: Annual short term average rainfall data for 2019 and 2020 for Gqeberha. Data for station [0035209B1] - GQEBERHA AWOS

Year	Month	Average Rain (mm)	
2019	January	21	
2019	February	55	
2019	March	24	
2019	April	50	
2019	Мау	39	
2019	June	28	
2019	July	68	
2019	August	3	
2019	September	37	
2019	October	26	
2019	November	23	
2019	December	18	
2020	January	38	
2020	February	39	
2020	March	35	
2020	April	13	
2020	Мау	89	
2020	June	24	
2020	July	51	
2020	August	131	
2020	September	32	
2020	October	69	
2020	November	48	
2020	December	22	

Geological setting

A large-scale feature of the western part of the Eastern Cape coast where this study site is situated in the presence of asymmetric half-heart bays. These embayments consist of rocky quartzite headlands filled with less-resistant Cretaceous sandstone and shale. Some examples are Cape St. Francis, Cape Recife, and Woody Cape (Claassen, 2015; Bucksey, 2017). The bedrock of the Mandela University nature reserve, Cape Recife, and surrounding areas such as Noordhoek comprises the Table Mountain Group Quartzite. This bedrock is typically covered by lime-rich coastal deposits of the Algoa Group. The calcrete of this group can be seen outcropping in places of the Mandela University reserve. This calcrete is covered by the Schelm Hoek Formation, which mostly consists of unconsolidated to semi-consolidated well-sorted and fine-grained sands (Claassen, 2015). Therefore, the sites that I worked on were both dune sand and calcrete (Fig. 2).



Figure 2: Jamesbrittenia microphylla (facultative resprouter) growing in calcrete on the left, *Pelargonium* grossularioides (non-resprouter) and *Mesembryanthemum aitonis* (non-resprouter) growing in dune sand on the right.

Data Collection

The identification process of the dominant resprouters that were observed entering the system eight months after the fire was conducted. Following the identification process, the resprouters identified were species chosen for excavation. These resprouting species were the early emergence species after the fire. The excavations of 21 species took place in the first eight months after the fire. With the videos and photographs of the excavations, surveying the resprouting strategies used by these species in the system was done.



Figure 3:Three common Postfire fynbos-thicket mosaic species that were identified on the Mandela University reserve three months after the 2019 November fire. A = *Searsia laevigata*, B = *Mesembryanthemum aitonis* C = *Trachyandra divaricata*.

Species	Family	Growth form	No. of excavation	
Rapanea gilliana	Myrsinaceae	Woody low shrub	6	
Euclea racemosa	Ebenaceae	Woody tall shrub	4	
Olea exasperata	Oleaceae	Woody tall shrub	3	
Searsia laevigata	Anacardiaceae	Woody tall shrub	2	
Lauridia tetragonia	Celastraceae	Woody low shrub	4	
Jamesbrittenia microphylla	nesbrittenia microphylla Scrophulariaceae Woody dwarf shrub		10	
Asparagus asparagoides	asparagoides Asparagaceae Woody liana		10	
Gazania krebsiana	Asteraceae	Herbaceous forb	6	
Gazania rigens	Asteraceae	Herbaceous forb	3	
Rubia petiolaris	Rubiaceae	Herbaceous vine	10	
Aizoon canariense	Aizoaceae	Herbaceous annual	10	
Felicia amoena	Asteraceae	Herbaceous annual	6	
Asparagus capensis	Asparagaceae	Woody dwarf shrub	4	
Helichrysum teretifolium	Asteraceae	Woody low shrub	8	
Selago canescens	Scrophulariaceae	Woody dwarf shrub	2	
Trachyandra divaricata	Asphodelaceae	Herbaceous geophyte	10	
Restio eleocharis	Restionaceae	Herbaceous Evergreen hemis	3	
Colchicum eucomoides	Colchicaceae	Herbaceous geophyte	10	
Indigofera sulcata	Fabaceae	Woody low shrub	3	
Hebenstretia integrifolia	Scrophulariaceae	Herbaceous forb	2	
Rhoicissus tridentata	Vitaceae	Woody liana	4	

Table 2: Species excavated to investigate belowground storage organs

These 21 species (Table 2) were excavated to investigate their belowground storage organs. Chapter 2 of this thesis identified some of these species as woody species. From previous studies, it is known that several species, frequently woody species, can survive recurrent disturbance by resprouting. The resprouting ability of these plants often depends on the dormant buds and the type of storage organ (Bombo et al., 2021). The excavation of these species would give us insight into what type of storage organ or BBBs enabled these species to resprout. The individual plants of interest were carefully dug up, ensuring that the underground structures remained intact. For the individuals that could not be fully excavated, an excavation of about 1m-2m was done to get an idea of the BBB type (see Fig. 4).



Figure 4: A Rapanea gilliana excavation (1 m - 2 m) on the Mandela University reserve. Point A is the initial dig point, with B and C being length of the excavated belowground bud bank of Rapanea gilliana

Once excavated, the belowground organs that made up the belowground bud banks (e.g., roots, root crowns, woody basal burls, rhizomes, belowground caudexes, corms, bulbs, bulbils, and tubers) were noted and recorded (Fig. 6).

In the 2018 Pausas et al., provide a classification system (a global Belowground Bud Bank database) to identify major belowground bud bank structures for resprouting after disturbance. This study used this database to classify the resprouting species that were dug up into their BBB types (location of the buds) using the Box 1 key (Pausas et al., 2018). In their study, six plant locations that support belowground buds in fire-prone ecosystems were identified. These plant bud locations were the following: root, root crown, rhizomes (non-woody rhizome, woody rhizome,

and rhizophore), basal burls (woody), fleshy swellings (bulb, corm, root tuber, and stem tuber), and belowground caudexes (Pausas et al., 2018) and were the same plant bud locations that were identified in the plants observed in this study.

Box 1 below is a summary of the characteristics used to assess the BBBs. For each of the species excavated the following traits were observed of their BBBs.

Box 1 Belowground bud bank characteristic assessment

For each belowground bud bank (BBB), the following characteristics were considered:

- **Origin of the bud**, which is the supporting tissues (e.g., root or stem).
- Bud bank size (for the genet: *low*: < 10 buds, *moderate*: 10–100, *high*: > 100; this is correlated with the number of resprouting stems, an easier parameter to observe: *low*: 1, *moderate*: 2–20, *high*: > 20).
- **Bud protection** is when the species protect their buds belowground on specialized organs (*low*: most buds above ground or at the soil surface, *moderate*: most buds < 1 cm below ground, *high*: most buds > 1 cm below ground).
- **Growth form** (e.g., herb: perennial forb or graminoid, suffrutex: woody low or tall shrub).
- **Recolonization ability** is how quickly the species re-enter or recolonize the system.

The species that colonize the system in abundance in the 1st month after postfire were assigned the *Very High* recolonization ability.

The *High* rating is for the species that recolonize the system in small numbers within the 1st month. *Mod-High* is the rating for the species that appear in the 2nd month.

The *Moderate* rating is for the species that recolonize the system in small numbers 3-4 months postfire. The species that appear 4-5 months postfire are rated *Low-Mod*.

The *Low* rating is for the species that recolonize the system in small numbers 5-6 months postfire and the species with the *Very Low* rating are the ones that appear 6-8 months postfire.

Table 3: A summary of the belowground bud bank (BBBs) types on the Mandela University dune systems (Pausas et al., 2018).

BBB type	Stylized diagrams of (BBB)	Location of the buds			
	structures				
Bud-bearing Root	Ro Ro	Lateral roots that give rise to buds (In some cases, root crown is present)			
Rhizome	FR	Non-woody rhizome, i.e., a subterranean non-woody stem that usually grows horizontally			
Rhizophore	Rh	Non-woody subterranean stem with downward-facing shoots that produces roots			
Woody rhizome	WR	A subterranean woody stem that grows horizontally			
Stem tuber	St	Tuber of stem origin			
Corm	 Co	Compressed swollen stem that lacks fleshy scales			

RESULTS

Out of the 12 BBB types (categories) established by Pausas et al. (2018), only half of the BBB types were identified from the sampled species (Table 2). The six categories were: bud-bearing root, rhizome, rhizophore, woody rhizome, stem tuber, and corm (Fig.5, Fig. 6, Table 3). The most represented BBB type in this system was the bud-bearing root, followed by the rhizome, woody rhizome, stem tuber, and lastly, rhizophore and corm BBB types (Fig. 5). Plants with bud-bearing roots (woody shrubs) resprouted profusely after fires and recolonized the system (Table 3, Box 1).



Figure 5: Percentage representation of belowground bud bank types of sampled species.

All species surveyed were able to resprout after the fire. The location of the dormant buds and the BBB type contributed to this resprouting ability. The stem was the origin (bud location) for all the species sampled in this study (Table 4). Out of the sample species, one resprouted from a rhizophore, one species resprouted from a corm, three resprouted from stem tubers, three resprouted from a nonwoody fibrous rhizome (with monopodial arrangement leading to expansive clone), four resprouted from woody rhizomes, four resprouted from a nonwoody fibrous rhizome and five species resprouted from bud-bearing root (Table 4).

The species with the highest recolonization ability (species that recolonized the system in the first month) (Box 1) were *Trachyandra divaricata, Aizoon canariense, Asparagus capensis, Jamesbrittenia microphylla,* and *Searsia laevigata.* Out of all the growth forms, the herbaceous geophytes (*Colchicum eucomoides* and *Trachyandra divaricata*) had a high to very high recolonization ability (Table 4). Regarding bud protection (Box 1), 4/21, 19% showed low protection; 14/21, 67% showed moderate protection; and 3/21, 14% showed high protection (Table 3). The species with low bud bank sizes, such as *Gazania rigens, Gazania krebsiana,* and *Colchicum eucomoides*, had high bud protection) (Box 1, Table 4).

Table 4: Main features of the belowground bud banks in plants from coastal dune system on Mandela University (Pausas et al., 2018).

Species	BBB type	Origin	Bud bank size	Bud protection	Growth form	Recolonization ability
Trachyandra divaricata	Stem tuber	Stem	Low-moderate	Low-high	Herbaceous geophyte	Very High
Gazania rigens	Woody rhizome	Stem	Low	High	Herbaceous forb	Moderate
Gazania krebsiana	Woody rhizome	Stem	Low	High	Herbaceous forb	Moderate
Colchicum eucomoides	Corm	Stem	Low	High	Herbaceous geophyte	High
Indigofera sulcata	Nonwoody fibrous rhizome with a monopodial arrangement leading to expansive clone	Stem	Moderate	Mod-high	Woody low shrub	Low
Selago canescens	Nonwoody fibrous rhizome with a monopodial arrangement leading to expansive clone	Stem	Low	Mod-high	Woody dwarf shrub	Low
Hebenstretia integrifolia	Nonwoody fibrous rhizome with a monopodial arrangement leading to expansive clone	Stem	Low	Mod-high	Herbaceous forb	Low-Mod
Rhoicissus tridentata	Rhizophore (note buds are only supported by the oldest rhizophores)	Stem	Low-moderate	Mod-high	Woody liana	High
Helichrysum teretifolium	Nonwoody fibrous rhizome	Stem	Low	Mod-high	Woody low shrub	Moderate
Restio eleocharis	Nonwoody fibrous rhizome	Stem	Low	Mod-high	Herbaceous Evergreen hemis	High
Rubia petiolaris	Nonwoody fibrous rhizome	Stem	Low	Mod-high	Herbaceous vine	Mod-High
Aizoon canariense	Nonwoody fibrous rhizome	Stem	Moderate	Low-high	Herbaceous annual	Very High
Asparagus asparagoides	Stem tuber	Stem	Low-moderate	Low-high	Woody liana	Mod-High
Asparagus capensis	Stem tuber	Stem	Low-moderate	Low-high	Woody dwarf shrub	Very High
Felicia amoena	Woody rhizome	-	Moderate	Mod-high	Herbaceous annual	Low-Mod
Jamesbrittenia microphylla	Woody rhizome	Stem	Moderate	Mod-high	Woody dwarf shrub	Very High
Searsia laevigata	Bud-bearing root (Root crown)	Stem	Moderate	Mod-high	Woody tall shrub	Very High
Lauridia tetragona	Bud-bearing root	Stem	Moderate	Mod-high	Woody low shrub	Very Low
Euclea racemosa	Bud-bearing root	Stem	Moderate	Mod-high	Woody tall shrub	High
Rapanea gilliana	Bud-bearing root	Stem	Moderate	Mod-high	Woody low shrub	Moderate
Olea exasperata	Bud-bearing root (Root crown)	Stem	Moderate	Mod-high	Woody tall shrub	Very Low



Jamesbrittenia microphylla, (j) bud-bearing root Euclea racemosa, (k) bud-bearing root Rapanea gilliana.

DISCUSSION

This dune vegetation system is a section of the coastal dune landscape of the southeastern CFR that is exposed to intermittent fire (Cowling et al., 2019; Strydom et al., 2020). Resprouting is a common mode of postfire regeneration in these systems (Chapter 2 of this thesis; Cowling and Pierce, 1988; Cowling et al., 2019; Strydom et al., 2020). Several dune endemic species have been observed to resprout readily after a fire (Cowling et al., 2019; Grobler et al., 2020). In fire-prone ecosystems, there are a diversity of ways by which plants successfully conceal their buds below ground which enable them to survive and resprout vigorously after a fire (Pausas et al., 2018).

There are at least six locations where belowground buds can be located (Pausas et al., 2018): roots, root crown, rhizomes, woody burls, fleshy swellings (stem tuber, corm), and belowground caudexes (Table 3, Table 4, Fig. 6). According to Pausas (2017) when you consider the history and function of these BBB types, these organs may be divided into these three groups.

The first group originated in the early history of plants and, at present, is widespread. Plants in this group can act as resprouting sources after several types of disturbance, including fire (Pausas, 2017; Bombo et al., 2021). This group includes the bud-bearing roots and root crown BBB types (Pausas, 2017). According to the results found in this study, this includes *Searsia laevigata, Lauridia tetragona, Euclea racemosa, Rapanea gilliana*, and *Olea exasperata* in these coastal dune systems, which are all bud-bearing root types (Table 4, Fig. 6). These are the species that could be classified as geoxyles. The species in this group have moderate bud bank sizes and moderate to high bud bank protection. Their recolonization ability is variable among these species (fluctuating between Very Low, Moderate, and High) (Box 1).

The second group would have also originated early and spread mainly among ferns and monocots (Pausas, 2017). Several geophytic growth forms characterize this group, and often the plants in this group are linked to seasonal stresses; they have been highly successful under recurrent fire (Pausas, 2017). These include non-woody rhizomes and a wide range of fleshy underground swellings (e.g., stem tubers and corms). In these coastal dune systems, examples of these plants are *Trachyandra divaricata, Selago canescens, Hebenstretia integrifolia, Helichrysum teretifolium, Restio eleocharis, Rubia petiolaris, Aizoon canariense, Asparagus asparagoides* and *Asparagus capensis* (Table 4, Fig. 6). Even though most of the species in this group have non-woody rhizome BBB, it was interesting to discover that about

6/10 of these species were dicots and not monocots, which was a trait noted by Pausas (2017) for this group.

The presence of plants with fleshy underground swellings such as corms and bulbs are highly associated with fire-prone areas as a result of a few of their traits, such as low bud accumulation or size and high bud protection, enabling the plants bearing these structures to survive harsh environmental conditions (Bombo et al., 2021). Out of the sampled species, *Colchicum eucomoides* was the only species that had a corm (Table 4, Fig.6). The low number of this BBB could be because, at high fire frequency sites, softer structures like corms and bulbs tend to be limited (Bombo et al., 2021). *Colchicum eucomoides* had high bud protection and a low bud bank size, which confirms what has been stated in the literature about corms as a belowground bud bank (Bombo et al., 2021).

The third group would have originated later in evolutionary history, and the species in this group are strongly connected to fire-prone ecosystems such as coastal dune systems in the CFR. These are woody rhizomes, lignotubers, and xylopodia (Pausas, 2017). They are characteristic of the geoxyle growth form (Pausas, 2017). These species were classified under the woody rhizome BBB type and included *Gazania rigens, Gazania krebsiana, Felicia amoena*, and *Jamesbrittenia microphylla* (Table 4, Fig.6). It could be assumed that these species would be the ones that have the highest recolonization ability as they are linked to fire-prone ecosystems, but this was not the case. *Gazania rigens* and *Gazania krebsiana* had moderate recolonization ability (appeared in the system 3-4 months postfire and in small numbers), whereas *Felicia amoena* had a low-moderate recolonization ability. *Jamesbrittenia microphylla* (Box 1, Table 4) and was observed within the first-month postfire. Within the second month, individuals of this species were already flowering (Chapter 2). This species has a high return rate.

There seems to be a connection between the BBB types and bud protection. The woody species with woody bud support produce non-swollen bud banks with few stems that arise horizontally or vertically, unrelated to the root collar. These species had high or moderate-high bud protection (Box 1) (Pausas, 2018). For example, plants with woody rhizomes in these dune systems, such as *Gazania rigens, Gazania krebsiana*, and *Jamesbrittenia microphylla*, resprout profusely after fires and colonize space vegetatively with the help of having high bud protection. These results corroborate the patterns observed in Cerrado woody species, which mainly rely upon resprouting from basal or belowground organs (Chiminazzo et al., 2021).
Only 50% of the BBBs provided by Pausas et al. (2018) were present in this system. The following BBBs were absent in this system: root crown, basal burls (woody), lignotuber and xylopodium, fleshly swelling bulb, root tuber, and belowground caudex. According to Pausas et al. (2018), basal burls (woody) lignotubers are generally found in the Mediterranean, warm, temperate, savanna ecosystems, and basal burls (woody) xylopodium are found in plants that grow in savanna (Pausas et al., 2018). The absence of the belowground caudex is no surprise since this BBB is present and more dominant in Mediterranean, warm, temperate, grassland ecosystems (Pausas et al., 2018).

Bombo et al. (2021) focused on belowground bud banks in a semi-arid African savanna. Their study identified the following BBBs: non-woody and woody rhizomes, root crowns, stolons, and bulbs or corms. The proportion and types of BBBs found in their study are the same as what is found in this study, with two exceptions: stolon is not a BBB type identified in this study, whereas for their study, it was, and rhizophore was identified as a BBB type in our study, whereas for them it was absent. This is an interesting observation as, according to Pausas et al. (2018), the rhizophore BBB type is predominantly present in savanna ecosystems. Regarding the BBB types, both studies identified: non-woody rhizomes, corms, root crowns, and woody rhizomes. These BBBs are present in any ecosystem, except for woody rhizomes, which are more prevalent in savanna and Mediterranean, warm, temperate ecosystem types (Pausas et al., 2018; Bombo et al., 2021).

In ecosystems such as the savanna, woody species can resprout postfire by using one of the following strategies: belowground structures; buds protected by the bark; or hairy buds (Chiminazzo et al., 2021). Some savanna species can even use aerial resprouting when trichomes are present to cover the buds and accessory buds of the plant. In cases when the fire has been severe, the savanna resprouters will use basal and belowground resprouting from belowground storage structures (BBBs) (Chiminazzo et al., 2021).

From the observations made in this study, woody species in coastal dune systems are different from savanna species because they resprout postfire by using at least one of the following persistent traits: belowground structures (BBBs) or lateral resprouting. Lateral resprouting is belowground resprouting after a fire that plants perform using their adventitious buds (horizontal roots or lateral roots), which is their resource location (Clarke et al., 2013). Root suckering is a resprouting type (Clarke et al., 2013) strongly associated with lateral resprouting and is an effective resprouting mechanism in response to disturbances, including fire (Rodrigues et al., 2004; Lamont et al., 2018). When plants can undergo lateral resprouting, they have postfire shoots, which in this case are multiple new stems, thinning to many stems.

This gives the plant potential for clonality (Clarke et al., 2013). According to Clarke et al. (2013), lateral resprouting is common in angiosperm forbs, shrubs, *Acacia, Hakea, Isopogon,* and trees (*Banksia*).

Searsia laevigata, Olea exasperata, Lauridia tetragonia, Euclea racemosa, and Rapanea gilliana are woody species that perform lateral resprouting in these coastal dune systems. These species undergo lateral resprouting using their lateral roots, which grow near the soil surface with adventitious buds that produce vertical stems (Pausas et al., 2018; Clarke et al., 2013). This study observed that these woody species had roots that had lateral buds well insulated from the fires by the soil. These roots undergo lateral spreading, whereby the ramets remain connected to the parent plant (Clarke et al., 2013; Pausas et al., 2018). In some cases, species that perform lateral resprouting can resprout from other structures such as root crowns (Pausas et al., 2018). This study confirmed this in woody species such as *Searsia laevigata* and *Olea exasperata*, which had root crown structures (Table 3).

CONCLUSION

Fires are mainly driven by warming and the incidence of drought. In many regions of the world, especially Mediterranean climate systems, the frequency, and severity of wildfires are expected to continue to increase in the coming decades because of warmer and drier weather conditions (Bowman et al., 2009; Wilson et al., 2015; Kraaij et al., 2018). For this reason, surveying the BBB types found in this coastal dune system goes beyond acquiring a classification of the BBBs in this system. This study not only provides knowledge to understand the belowground world of coastal dune systems, but it also provides ways to maintain these systems by providing information on what it is that enables the species found in these dune systems to persist after disturbances such as fire (Durán and Hermann, 2006; Clark and de Villers, 2016).

The vegetation that grows in these coastal dune ecosystems is the most effective and common loose soil or sand stabilizer (Durán and Hermann, 2006). Several woody resprouting plants in these coastal dune systems contain BBBs with belowground structures that play a crucial role in plant community succession, population regeneration, and the maintenance of plant communities. Identifying the diversity of these BBBs and other persistence traits such as lateral resprouting is the foundation for understanding the many evolutionary pathways available for responding to severe recurrent disturbances in coastal dune systems.

This study section highlights that coastal dune systems have provided an environment where a range of lineages have adapted to extensive underground lateral expansion. It also highlights that belowground bud banks consisting of all buds that can be potentially used for vegetative regeneration such as rhizomes, tubers, corms, bulbs, bulbils are structures that enable plants to resprout after a disturbance such as fire in the coastal dune systems. This research helps in acquiring knowledge and understanding of the 'belowground world' and broadening the understanding of the dynamics of coastal dune ecosystems to improve the management and conservation of these highly diverse ecosystems.

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Chapter 4 –Successes and challenges that come with filling in the gaps of coastal dune systems

Introduction

From the very first chapter, the aims of this study have been achieved. Chapter 1, set the tone by delivering all the important information that defines coastal dune systems. This chapter provided information that highlighted the importance of these coastal dune systems for a community, such as being tangible goods, by playing a role in water purification and carbon storage as well as being coastal defense and hazard mitigation tools (Prisco et al., 2016; Nehren et al., 2016). These ecosystems are also important for individuals who see and enjoy the aesthetic beauty and the recreation and restorative activities they provide (Urbis et al., 2019; Carranza et al., 2020).

In most ecosystems a disturbance is generally a factor that will only have a negative impact on the ecosystem, however in this study fire proved that this is not always the case. Instead, in this study fire proved itself to be a key ingredient that these coastal dune systems need to be exposed to, for the regeneration to take place, consequently providing space for more species to re-established themselves back in the system. Fire not only enhances the plant diversity in these coastal dune systems (Pausas and Ribeiro, 2016; Teixeira et al. 2020), but it also stimulates some of the physiological attributes of some of the species found in these dune systems, such as the flowering of some plants; fire-stimulated flowering (Lamont and Downes, 2011; Lamont et al., 2018). An example of a species that seems to have this firestimulated flowering trait observed in this study is, *Searsia laevigata*.

A huge success that was achieved in this study is there is now a classification of what postfire regeneration strategies the species found on these coastal dune systems possess and the measure of the resilience of fire that these dune systems have has been observed. This has been a great study to once again prove that the postfire regeneration strategies that these species have, do ensure persistence in these dune systems.

This last section of the thesis focuses on challenges or errors that occurred in this study when collecting data. This is followed by a small section of the consequences of specific errors and a conclusion of the study as a whole.

Challenges

However, this study has not been without its challenges. When it comes to data collection, data analysis, data processing and data reporting, errors can and do occur (Brown et al., 2018), but getting it right or as close to as right as possible is critical when collecting data.

Data collection, data analysis and processing were achieved with as much accuracy in this study, with a few minor errors.

When it came to data collection, the field assistants were told what to observe and how many pictures needed to be taken of each plant to have the correct identifications for all the species. Unfortunately, there were times when the observed species were species outside the routes/paths being monitored, these were the outliers. To eliminate these outliers having any negative impact on the results, it was decided that if a species appeared on less than five dates, it would be eliminated and not included in the dataset and figures representing presence, flowering, and fruiting of species (Appendix B and Appendix C).

An elimination process was done regarding species that were only identified once in the system, for example, *Withania somnifera*, which was identified on 14/02/2019, about three weeks after the fire (Figure 1).



Figure 1: Species identified and eliminated from the study

Some species were not as well represented in this study which was surprising as they do commonly feature in these coastal dune systems according to other studies (Cowling, 1984; Strydom et al., 2022) and Chapter 3 of this thesis, namely *Gazania krebsiana, Gazania rigens, Sideroxylon inerme, Searsia lucida, Searsia crenata, Aspalathus recurvispina, and Ficinia dunesis.* It is important to consider that this is a short-term post-fire ecology study, so there are possibly some species that would only colonize the system in the 2nd year after the fire or

after a few years. Flowering also played a crucial role in identifying the observed species, as many of these species were identified because they were flowering (Figure 2 and 3).

Why are identifying errors so crucial?

The identification of errors and the correction of the errors are critical to science. This gives rise to the principle that science is self-correcting (Brown et al., 2018). Errors can be advantageous for the advancement of science. Therefore, it is important to have taken note of what errors occurred in this study as this will potentially help someone who wants to do a similar study in a different ecosystem, to know what to look out for.

Regarding data recording, there were some weeks when the data recording was delayed and done a few weeks after data collection; fortunately, no data was lost, but recording the species and filling in the phenology database could have been done better and could have been a less rushed process. Consequently, a major data cleaning process was required before analyses could occur.

Sutton and Austin (2015), state that whether one is doing a quantitative or qualitative study, one must be mindful of their own biases and not simply ignore them. For example, in the case of identifying and taking pictures in this study, a person could have gravitated toward taking a photo of flowering or fruiting species as these species would have been easier to spot. There was some bias in the study when it came to identifying the species that colonized the system postfire, especially concerning geophytes. Geophytes, for example, *Wachendorfia paniculata, Gladiolus wilsonii,* and *Albuca longifolia* were difficult to spot and identify as they are generally more noticeable only when they are flowering. Most geophytes are recognized by their flowers (Figures 2 and 3). As a result, this potentially caused an error in the data collected as these geophytes could have been missed if not flowering. Consequently, this has resulted in biases in the information used to describe this dune system postfire regeneration vegetation community.



Figure 2: Months of emergence of *Gladiolus wilsonii* and *Wachendorfia paniculata*.



Albuca longifolia, was observed on two days in the 8th month



A very practical way to solve the errors that occurred in this study is taking field notes. This is something that was rarely done and could have helped in putting the discussion parts together. Field notes allow a researcher to maintain and comment on observations they make, reminding the researcher of information that may be important during data analysis (Sutton and Austin, 2015). More field notes would have been very useful in a study such as this, with many plants being affected by many variables. For example, the first observation should have been noted when a species was dying out.

Conclusion

Coastal dunes systems are among the most dynamic and diverse ecosystems on Earth. They are highly specialized for the harsh environment and disturbance prone environments as they have the incredible ability to restore themselves. This study has provided evidence that these coastal dune systems are home to a unique and highly specialized flora. In this study, monitoring the postfire regeneration of these coastal dunes systems over time is key to their conservation. Observing the composition of regenerating species in the coastal dune can provide us with fundamental insights into the functioning of these ecosystems and may also provide us with whether these ecosystems will be able to keep delivering the ecosystem services they are known to provide in the future.

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Appendix A

Table 1: Species list including growth form and fire response (Postfire Regeneration Strategies) of plants that recovered in the first 12 months postfire on the coastal dune systems of Mandela University reserve and Noordhoek.

Species	Growth Form	Postfire Regeneration Strategies	Reference
Trachyandra divaricata	Herbaceous geophyte	FS	Field observations (Dug up) - Jongo
Colchicum eucomoides	Herbaceous geophyte	FS	Grobler, personal communication
Selago canescens	Woody dwarf shrub	FS	Grobler and Cowling 2021
Helichrysum teretifolium	Woody low shrub	FS	Grobler and Cowling 2021
Restio eleocharis	Herbaceous Evergreen hemis	FS	Field observations (Dug up) - Jongo
Rubia petiolaris	Herbaceous vine	FS	Field observations postfire - Jongo
Aizoon canariense	Herbaceous annual	FS	Field observations (Dug up) - Jongo
Felicia amoena	Herbaceous annual	FS	Field observations (Dug up) - Jongo
Jamesbrittenia microphylla	Woody dwarf shrub	FS	Grobler and Cowling 2021
Delosperma cooperi	Woody dwarf shrub	FS	Grobler and Cowling 2021
Tetragonia fruticosa	Woody lianes	FS	Grobler and Cowling 2021
Disphyma crassifolium	Woody dwarf shrub	FS	Grobler and Cowling 2021
Cyrtanthus loddigesianus	Herbaceous geophyte	FS	Grobler, personal communication
Arctopus echinatus	Herbaceous geophyte	FS	Grobler, personal communication
Cynanchum obtusifolium	Herbaceous vine	FS	Grobler, personal communication
Astephanus zeyheri	Herbaceous vine	FS	Grobler, personal communication
Cynanchum ellipticum	Herbaceous vine	FS	Grobler, personal communication
Trachyandra ciliata	Herbaceous geophyte	FS	Grobler, personal communication
Arctotheca prostrata	Herbaceous forb	FS	Grobler, personal communication
Ursinia anthemoides	Herbaceous Deciduous hemis	FS	Grobler, personal communication
Lactuca inerme	Herbaceous forb	FS	Grobler, personal communication
Osteospermum moniliferum	Woody tall shrub	FS	Grobler and Cowling 2021
Convolvulus sp.	Herbaceous vine	FS	Grobler, personal communication
Kedrostis nana	Herbaceous vine	FS	Grobler, personal communication
Ficinia lateralis	Herbaceous Evergreen hemis	FS	Grobler, personal communication
Schoenus sp.	hemis	FS	Grobler, personal communication
Euphorbia silenifolia	Herbaceous geophyte	FS	Grobler, personal communication
Adenocline pauciflora	Herbaceous forb	FS	Field observations (Dug up) - Jongo
Aspalathus sp.	Woody dwarf shrub	FS	Grobler and Cowling 2021
Indigofera glaucescens	Woody dwarf shrub	FS	Grobler and Cowling 2021
Indigofera verrucosa	Woody dwarf shrub	FS	Grobler and Cowling 2021
Otholobium sp. nov, "algoensis"	Woody dwarf shrub	FS	Grobler and Cowling 2021
Dipogon lignosus	Woody lianes	FS	Grobler and Cowling 2021
Aspalathus recurvispina	Woody dwarf shrub	FS	Grobler and Cowling 2021

Species	Growth Form	Postfire Regeneration Strategies	Reference
Lotononis pungens	Woody dwarf shrub	FS	Grobler and Cowling 2021
Otholobium sp.	Woody dwarf shrub	FS	Grobler and Cowling 2021
Albuca longifolia	Herbaceous geophyte	FS	Grobler, personal communication
Albuca cooperi	Herbaceous geophyte	FS	Grobler, personal communication
Empodium gloriosum	Herbaceous geophyte	FS	Grobler, personal communication
Gladiolus sp.	Herbaceous geophyte	FS	Grobler, personal communication
Gladiolus wilsonii	Herbaceous geophyte	FS	Grobler, personal communication
Romulea sp.	Herbaceous geophyte	FS	Grobler, personal communication
Chasmanthe aethiopica	Herbaceous geophyte	FS	Grobler, personal communication
Moraea australis	Herbaceous geophyte	FS	Grobler, personal communication
Romulea rosea	Herbaceous geophyte	FS	Grobler, personal communication
Salvia aurea	Woody low shrub	FS	Grobler and Cowling 2021
Stachys aethiopica	Herbaceous forb	FS	Grobler, personal communication
Linum africanum	Woody low shrub	FS	Grobler and Cowling 2021
Hermannia althaeifolia	Woody low shrub	FS	Grobler and Cowling 2021
Oxalis depressa	Herbaceous geophyte	FS	Field observations (Dug up) - Jongo
Ehrharta villosa	Herbaceous Deciduous	FS	Grobler, personal communication
	Herbaceous Deciduous	10	
Polypogon monspeliensis	hemis Herbaceous Deciduous	FS	Grobler, personal communication
Cymbopogon sp.	hemis	FS	Grobler, personal communication
Setaria sphacelata	Herbaceous Deciduous hemis	FS	Grobler, personal communication
Sporobolus africanus	Herbaceous Deciduous hemis	FS	Grobler, personal communication
Polygala ericaefolia	Woody dwarf shrub	FS	Grobler and Cowling 2021
Chaenostoma campanulatum	Herbaceous forb	FS	Field observations (Dug up) - Jongo
Dischisma ciliatum	Woody dwarf shrub	FS	Grobler and Cowling 2021
Dischisma capitata	Woody dwarf shrub	FS	Grobler and Cowling 2021
Solanum linnaeanum	Woody low shrub	FS	Grobler and Cowling 2021
Roepera maritima	Woody dwarf shrub	FS	Grobler and Cowling 2021
Tephrosia capemsis	Woody dwarf shrub	FS	Grobler and Cowling 2021
Indigofera sp. nov. 'sinusalgoae'	Woody dwarf shrub	FS	Field observations - Grobler
Indigofera tomentosa	Woody dwarf shrub	FS	Grobler and Cowling 2021
Lessertia stenoloba	Woody dwarf shrub	FS	Grobler and Cowling 2021
Pelargonium capitatum	Herbaceous forb	FS	Field observations - Grobler
Helichrysum rosum	Woody dwarf shrub	FS	Field observations - Grobler
Drosanthemum candens	Woody dwarf shrub	FS	Grobler and Cowling 2021
Cymbopogon marginatus	Herbaceous Deciduous hemis	FS	Grobler and Cowling 2021
Cynodon dactylon	Herbaceous Deciduous hemis	FS	Field observations - Grobler
Wachendorfia paniculata	Herbaceous geophyte	FS	Grobler and Cowling 2021
Tribolium hispidum	Herbaceous Deciduous	FS	Field observations - Grobler
	nomio	10	

Species	Growth Form	Postfire Regeneration Strategies	Reference
	Herbaceous Deciduous		
Ehrharta calycina	hemis Herbaceous Deciduous	FS	Field observations - Grobler
Ehrharta erecta	hemis	FS	Field observations - Grobler
Eragrostis curvula	hemis	FS	Field observations - Grobler
Ficinia bulbosa	Herbaceous Evergreen hemis	FS	Field observations - Grobler
Ficinia dunensis	Herbaceous Evergreen hemis	FS	Field observations - Grobler
Isolepis sp.	Herbaceous Evergreen hemis	FS	Field observations - Grobler
Kaalaria aananaia	Herbaceous Deciduous	50	Field about retions Crabler
Koeleria caperisis	Herbaceous Evergreen	<u>го</u>	Field observations - Grobler
Schoenus nigricans	hemis	FS	Field observations - Grobler
Solanum sisymbriifolium	Herbaceous forb	FS	Field observations - Grobler
Sonchus oleraceus	Herbaceous forb	FS	Field observations - Grobler
Themeda triandra	hemis	FS	Field observations - Grobler
Thesium triflorum	Woody lianes	FS	Grobler and Cowling 2021
Gazania rigens	Herbaceous forb	NS	Field observations postfire - Jongo
Gazania krebsiana	Herbaceous forb	NS	Field observations postfire - Jongo
Indigofera sulcata	Woody low shrub	NS	Grobler and Cowling 2021
Hebenstretia integrifolia	Herbaceous forb	NS	Grobler, personal communication
Mesembryanthemum aitonis	Herbaceous annual, succulent	NS	Field observations (Dug up) - Jongo
Carpobrotus deliciosus	Woody dwarf shrub	NS	Grobler and Cowling 2021
Felicia echinata	Woody low shrub	NS	Grobler and Cowling 2021
Felicia erigeroides	Woody low shrub	NS	Grobler and Cowling 2021
Senecio glutinosus	Woody low shrub	NS	Grobler, personal communication
Senecio ilicifolius	Woody low shrub	NS	Grobler and Cowling 2021
Sonchus sp.	Herbaceous forb	NS	Grobler, personal communication
Achyranthemum sordescens	Woody low shrub	NS	Grobler and Cowling 2021
Cotula discolor	Herbaceous forb	NS	Grobler, personal communication
Helichrysum cymosum	Woody dwarf shrub	NS	Grobler and Cowling 2021
Metalasia muricata	Woody tall shrub	NS	Grobler and Cowling 2021
Brassicaceae sp.	Herbaceous forb	NS	Grobler, personal communication
Erucastrum strigosum	Herbaceous annual	NS	Grobler, personal communication
Heliophila linearis	Herbaceous forb	NS	Grobler, personal communication
Petrorhagia prolifera	Herbaceous annual	NS	Grobler, personal communication
Crassula mesembryanthemoides	Succulent	NS	Grobler and Cowling 2021
Ficinia ramosissima	hemis	NS	Field observations (Dug up) - Jongo
Ricinus communis	Herbaceous annual	NS	Grobler, personal communication
Acacia cyclops	Woody tall shrub	NS	Grobler, personal communication
Medicago sp.	Herbaceous forb	NS	Grobler, personal communication
Melilotus sp.	Herbaceous forb	NS	Grobler, personal communication

Species	Growth Form	Postfire Regeneration Strategies	Reference
Chironia baccifera	Woody dwarf shrub	NS	Grobler and Cowling 2021
Sebaea micrantha	Herbaceous annual	NS	Grobler, personal communication
Pelargonium grossularioides	Herbaceous annual	NS	Field observations (Dug up) - Jongo
Pelargonium alchmilloides	Herbaceous forb	NS	Grobler, personal communication
Lobelia erinus	Herbaceous forb	NS	Grobler, personal communication
Bromus sp.	Herbaceous annual	NS	Grobler, personal communication
Lagurus ovatus	Herbaceous annual	NS	Grobler, personal communication
Muraltia satureioides	Woody dwarf shrub	NS	Grobler and Cowling 2021
Muraltia squarrosa	Woody low shrub	NS	Grobler and Cowling 2021
Anagallis arvensis	Herbaceous annual	NS	Grobler, personal communication
Phylica litoralis	Woody dwarf shrub	NS	Grobler and Cowling 2021
Phylica ericoides	Woody low shrub	NS	Grobler and Cowling 2021
Agathosma sp.	Woody low shrub	NS	Cowling et al., 2019; Grobler and Cowling 2021
Coleonema pulchellum	Woody low shrub	NS	Grobler and Cowling 2021
Nemesia affinis	Herbaceous annual	NS	Grobler, personal communication
Datura sp.	Herbaceous forb	NS	Grobler, personal communication
Physalis peruviana	Woody low shrub	NS	Grobler, personal communication
Withania somnifera	Herbaceous annual	NS	Grobler, personal communication
Passerina rigida	Woody low shrub	NS	Grobler and Cowling 2021
Fumaria muralis	Herbaceous annual	NS	Field observations - Grobler
Hibiscus trionum	Herbaceous annual	NS	Field observations - Grobler
Anthospermum aethiopicum	Woody low shrub	NS	Grobler and Cowling 2021
Aspalathus subtingens	Woody low shrub	NS	Grobler and Cowling 2021
Brassica tournefortii	Herbaceous annual	NS	Field observations - Grobler
Bromus japonica	Herbaceous annual	NS	Field observations - Grobler
Datura ferox	Herbaceous annual	NS	Field observations - Grobler
Helichrysum versicolor	Herbaceous annual	NS	Field observations - Grobler
Silene aethiopica	Herbaceous annual	NS	Field observations - Grobler
Solanum rigescens	Woody low shrub	NS	Grobler and Cowling 2021
Rhoicissus tridentata	Woody lianes	OS	Grobler and Cowling 2021
Asparagus asparagoides	Woody lianes	OS	Grobler and Cowling 2021
Asparagus capensis	Woody dwarf shrub	OS	Grobler and Cowling 2021
Searsia laevigata	Woody tall shrub	OS	Grobler and Cowling 2021
Lauridia tetragona	Woody low shrub	OS	Grobler and Cowling 2021
Euclea racemosa	Woody tall shrub	OS	Grobler and Cowling 2021
Rapanea gilliana	Woody low shrub	OS	Grobler and Cowling 2021
Olea exasperata	Woody tall shrub	OS	Grobler and Cowling 2021
Boophone disticha	Herbaceous geophyte	OS	Field observations postfire - Jongo
Searsia crenata	Woody tall shrub	OS	Grobler and Cowling 2021

		Postfire	
Species	Growth Form	Strategies	Reference
		J	Cowling et al., 2019; Grobler and
Searsia glauca	Woody tall shrub	OS	Cowling 2021
Searsia lucida	Woody tall shrub	OS	Grobler and Cowling 2021
Carissa bispinosa	Woody tall shrub	OS	Grobler and Cowling 2021
Cussonia thyrsiflora	Woody lianes	OS	Grobler and Cowling 2021
Asparagus suaveolens	Woody lianes	OS	Grobler and Cowling 2021
Asparagus aethiopicus	Woody lianes	OS	Grobler and Cowling 2021
Brachylaena discolor	Woody tall shrub	OS	Grobler and Cowling 2021
Putterlickia pyracantha	Woody tall shrub	OS	Grobler and Cowling 2021
Mystroxylon aethiopicum	Woody tall shrub	OS	Grobler and Cowling 2021
Maytenus procumbens	Woody tall shrub	OS	Grobler and Cowling 2021
Grewia occidentalis	Woody tall shrub	OS	Grobler and Cowling 2021
Cissampelos capensis	Woody lianes	OS	Grobler and Cowling 2021
Morella quercifolia	Woody low shrub	OS	Grobler and Cowling 2021
Melica racemosa	Herbaceous Deciduous hemis	OS	Field observations postfire - Jongo
	Herbaceous Deciduous		
Stipagrostis zeyheri barbata	hemis	OS	Field observations postfire - Jongo
Imperata cylindrica	Herbaceous Deciduous hemis	os	Field observations postfire - Jongo
	Herbaceous Deciduous		
Stenotaphrum secundatum	hemis	OS	Field observations postfire - Jongo
Clausena anisata	Woody tree	OS	Grobler and Cowling 2021
Dovyalis rotundifolia	Woody tall shrub	OS	Grobler and Cowling 2021
Scolopia zeyheri	Woody tall shrub	OS	Grobler and Cowling 2021
Colpoon compressum	Woody tall shrub	OS	Grobler and Cowling 2021
Rhoiacarpos capensis	Woody lianes	OS	Grobler and Cowling 2021
Sideroxylon inerme	Woody tall shrub	OS	Grobler and Cowling 2021
Solanum africanum	Woody lianes	OS	Grobler and Cowling 2021
Solanum retroflexum	Herbaceous annual	OS	Field observations postfire - Jongo
Scutia myrtina	Woody lianes	OS	Grobler and Cowling 2021

Appendix B:

Figure 1: Presence of plant species that recovered in the first 12 months postfire on the coastal dune systems of Mandela University reserve and Noordhoek.



Appendix C:

Figure 2: Flowering of plant species that recovered in the first 12 months postfire on the coastal dune systems of Mandela University reserve and Noordhoek

