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INVASIVE PLANT SPECIES IN LESOTHO'S RANGELANDS: SPECIES CHARACTERIZATION AND POTENTIAL CONTROL MEASURES

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ABSTRACT

Lesotho is experiencing rangeland degradation manifested by invasive plants including *Chrysochoma ciliata*, *Seriphium plumosum*, *Helichrysum splendidum*, *Felicia filifolia* and *Relhania dieterlenii*. This threatens the country's wool and mohair enterprise and the Lesotho Highland Water Project which contributes significantly to the economy. A literature review-based study using databases, journals, books, reports and general Google searches was undertaken to determine species characteristics responsible for invasion success.

Generally, invasive plants are alien species, but Lesotho invaders are native as they are traced back to the 1700s. New cropping systems, high fire incidence and overgrazing initiated the process of invasion. The invaders possess inherent characteristics such as high reproduction capacity associated with a long flowering period that ranges between 3-5 months. They are perennial, belong to the Asteraceae family and therefore have small seeds with adaptation structures that allow them to be carried long distances by wind. These invaders are able to withstand harsh environmental conditions. Some are allelopathic, have an aggressive root system that efficiently uses soil resources. As opposed to preferred rangeland plants, they are able to colonize bare ground. Additionally, *F. filifolia* and *R. dieterlenii* are fire tolerant while *H. splendidum* and *S. plumosum* have woolly coverings that limit water loss when temperatures are high. *S. plumosum* has the ability to shield other plants as it grows fast and produces volatile oils to guard against herbivory. *S. plumosum* and *H. splendidum* limit transpiration by reflecting sunlight and rolling leaves to the underside, respectively.

The literature suggests various control methods to curb these invasive plants. Based on the current study, I suggest using integrated weed control that should incorporate education and social aspects. Research should be engaged to map areas and stages of invasion, trace the history of the vegetation, determine and prevent new invasions. Lesotho also should give land resources a monetary value, which will draw attention to sustainable land management.

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1. INTRODUCTION

Lesotho has a land surface of roughly 3 million hectares of which about 60% are rangelands. Rangelands are important in the success of livestock keeping, as farmers seldom practice supplementary feeding. Livestock production contributes significantly to the livelihoods of rural communities through provision of meat, milk, draught power and transport (DRRM [Department of Range Resources Management] 2014). Livestock is a valuable property that reflects wealth and social well-being. It is an investment that is not readily available, but it can be converted into money which makes livestock rearing even more profitable than any other income generating enterprise for wool and mohair farmers. Consequently, farmers rear animals in very large numbers (ORASECOM [Orange-Senqu River Commission] 2014a). The rangelands of Lesotho are as a result overstocked and it is estimated that the current stocking has exceeded carrying capacities by 75 to 300% (Motsamai et al. 2002; DRRM 2014). This practice has led to overgrazing, which is characterized by selective removal of palatable plant species, leaving behind a modified habitat susceptible to degradation (Kakonge 2002).

Lesotho has experienced vast soil erosion (Rooyani & Badamchian 1986; Morris et al. 1996, Grundling et al. 2015) and it is one of the most eroded countries in the world (Calles & Kulander 1996). In addition, Lesotho is now facing a new type of land degradation caused by encroachment of invasive plant species facilitated by a number of factors including overgrazing and changing fire regimes (Motsamai et al. 2002). The problem has been intensified by climate change (DRRM 2014). Invasive bushes lower the quantity and quality of forage, interfere with grazing and poison animals (DiTomaso et al. 2010) and slow down animal weight gain (DeBeer 2009; DiTomaso 2000). They also affect the quality of wool and mohair which is a lucrative enterprise positively impacting farmers' livelihoods and which contributes up to 4.8% to the Gross Domestic Product (GDP) in Lesotho (ADBG [African Development Bank Group] 2013).

Lesotho prides itself on its high quality and abundant water, affectionately referred to as “white gold” for it generates income through the Lesotho Highland Water Project Treaty and exports water to neighboring South Africa (DRRM 2014). Rangelands are not only sources of water but their soils filter and purify it too. Rangeland degradation threatens this national resource and may jeopardize the country’s hydropower industry (Maile 2001). In order to sustain the Lesotho Highland Water Project and improve wool and mohair production, rangeland condition should be of priority. Lesotho’s water is not only beneficial to its own citizens as the highlands are the main source of water of the Senqu Rivers which drives the economies of Lesotho, South Africa, Botswana and Namibia (ORASECOM 2014a; ORASECOM 2014b). For example, the economic value of rangelands is well known in Lesotho. However, *Seriphium plumosum*, one of the native invasive plants, threatens sustainability of the Lesotho Highland Project as it prefers wetter habitats (Avenant 2015).

Some areas in Lesotho have deteriorated to a level of non-recovery due to overgrazing, fires and invasive plants (Pooley 2009). The driving forces for this deterioration are rangeland fires, overgrazing and invasion by invasive plants. Bush encroachment in southern Africa has been evident from the 19th century and was caused by interaction between fires (Germond 1967), drought, increased atmospheric carbon dioxide concentration and climate change and increased rainfall (O’Connor et al. 2014).

The objective of this study was to investigate the characteristics and possible control of the five main invasive plant species found on Lesotho’s rangelands, *Chrysochoma ciliata*, *Seriphium* *plumosum, Helichrysum splendidum, Felicia filifolia* and *Relhania dieterlenii,* by answering the following questions:

1. What characterizes their life cycle, especially with regard to reproduction?
2. What characteristics make them invasive?
3. What potential measures can be used to control them and at which stages of the lifecycle are they most susceptible to control methods?
4. What future research is needed to facilitate their control?

2. BACKGROUND

2.1 History of bush encroachment in Lesotho

There is a lack of data on historical vegetation changes in Lesotho. However, there exist records on major vegetation changes and driving forces recorded by travelers and European missionaries that lived in Lesotho during the colonial period (Singh 2000, Bremer 1976, Dieterlen 1914a). The history of rangeland management and environmental condition can be traced from the 1700s. During this era, there lived the first inhabitants of Lesotho, formerly Basutoland, the San people (Bushmen). The Bushmen were hunter-gatherers who depended on hunting, feeding on plant roots and leaves. Their effects on the environment would have been minimal because they kept moving from one area to another (Singh 2000).

According to Singh (2000) and Germond (1967), the 1800s marked the colonial period in Lesotho. During this period, its occupants succeeded in maintaining a subtle balance between cultivation and grazing. They adhered to very strict norms and policies in favor of the environment and observed three types of spare grazing land (*maboella)* which was set aside and was characterized by animal exclusion and rangeland resting. The first type of *maboella* stated that it was illegal to kill a living tree. Only dead branches and trees killed by extreme weather were utilized. The second type involved grasses and reeds which were exclusively used for hatching and construction of wind shields. The last type of *maboella* was unutilized spare rangeland which was used only in winter to avoid degradation by prolonged periods of grazing. However, the arrival of Europeans undermined the existing values and introduced new farming, range management and agricultural techniques which initiated land degradation. The conflict between these activities was made worse by the increased demand for wheat, which was highly marketable, and the introduction of other new crops. More land was transformed into cropland and animals were moved to marginal lands. The people of Lesotho then started to forget about their policy of sparing grazing land. The first afforestation attempt was around 1876 when eucalyptus was introduced into Lesotho. The success of this project is not documented but currently in Lesotho lands occupied by eucalyptus are mostly eroded and other plants in their vicinity have disappeared.

The interaction of climate and human activities in the 1800s resulted in the distinct vegetation types for the lowlands, valley flats and highlands of Lesotho observed in the early 1900s. The lowlands were covered by grassland with open savanna woodlands and riverside willow thickets. There were dispersed patches of woodlands, especially on scarp slopes and hollows in the hills, dominated by the species *Olea capensis*, *Cussonia spicata*, *Podocarpus latifolias, Eulea ramose* and *Qcotea bullata* (MacVean 1977).

MacVean (1977) indicates that the valley flats of Lesotho consisted of tussock grass swamplands with reed and sedges (*Cyperus* sp.), which formed natural water spreading systems over the flood plains. These vegetation types extended to 200 m a.s.l. or so, and then were succeeded by montane scrub woodland dominated by *Leucosidea sereea* and *Budlea salviifolia* with patches of meadow in the moister places, giving way to grassland on the ridges. *Leucosidea* at times would continue with more stunted scrub of *Passerina*, *Cliffortia*, *Phillipia* and *Athanasia,* especially on the north slopes and shallow rocky soils. There were also reeds and peat bogs that collected and distributed water to the rivers in a non-erosive manner (Jacot-Guillarmond 1962). In the valleys, there could also be riverside willow thickets and *Aloe capensis* (Germond 1967, MacVean 1977).

Alpine vegetation, occurring above 2900 m *a.s.l.* consisted of spring bogs, wet herb and sedge meadows, *Merxmuellera* (*Danthonia*) tussock grassland, *Festuca* and *Pentaschistis* heaths, open grassland. *Helichrysum*, *Chrysocoma*, *Relhania*, and *Felicia* species (now invasive) were also recorded during this time. Alpine vegetation may have changed a little up to 1977 (MacVean 1977). However selective grazing and rangeland fires in subsequent years reduced it (Jacot-Guillarmond 1962; O'Connor et al. 2014).

There were high incidences of fires and high utilization of timber which converted the natural woody vegetation into grassland which amalgamated with subalpine and alpine grassland in the higher mountains in the late 1800s. This era was also marked by considerable felling of timber (up to 20m tall) on the hilltops. The surviving timber suffered the extremely low temperatures at the end of the century (MacVean 1977). There was increased felling of timber also because of an outbreak of rinderpest from 1897 to 1899 (Phoofolo 2003) that killed livestock in large numbers and resulted in shortage of animal dung, which was another source of energy (MacVean 1977).

A significant increase in invasive plants was first realized and documented in this period in the late 1900s and early 2000s. Increased incidences of rangeland fires and heavy rainfall was experienced in mid 1970s. The interaction of rainfall, fires and increased animal numbers, especially cattle which were at their peak numbers, weakened the grasses. This was made worse by the fact that it followed drought (O'Connor et al. 2014). Extreme drought started and was recorded in 1933, the dust bowl, which may have been responsible for seed dispersal, and subsequently other droughts in 1968 (O'Connor et al. 2014), 1983 and 1990 (Masih et al. 2014). It was during this period that *Chrysocoma ciliata* (Van Zinderan Bakker & Werger 1974; O'Conner et al. 2014) and *Felicia filifolia* (ORASECOM 2014a) were identified as threatening the biodiversity of Lesotho. In 1938 *Chrysocoma ciliata* occupied 10% of the country's rangelands (Killick 1963) and increased to 16% by 1998 (Marake et al. 1998). This could be attributed partly to droughts experienced in 1968, 1983 1990, 2002, 2007 and 2011 (Masih et al. 2014).

Invasive plant species are plants that are not native to the area under consideration and introduction has a likelihood of causing economic (Pimentel et al. 2002; Kolar and Lodge 2001) or environmental harm, or to be harmful to human health (Huxel 1999; Brooks et al. 2004; Borland et al. 2009). Native species are those that occur in an area without introduction and can be historically traced to the area (Masters & Shelley 2001). Native plants can also become invasive (Simberloff 2010; Thacker et al. 2008) under some circumstances (Ray &McCormick-Ray (2004). Invasive plants, whether native or nonnative, have similar effects (Borland et al. 2009). Agriculture, aquaculture and transportation are attributed to both accidental and intentional spread of invasive plant species (Kolar & Lodge 2001). Poor rangeland management characterized by overgrazing and frequent fires can also cause invasive behavior of some native plants (DRRM 2014).

Invasive plant species have become a threat to the natural biodiversity and ecosystem functions (Kolar & Lodge 2001; Robinson et al. 2014). They change vegetation dynamics (Barney 2016) and reduce the ability of an ecosystem to recover (DiTomaso et al. 2010). The other effect of invasive species is an increase in the mortality of native species. This implies that they possess a powerful force in natural selection (Callaway et al. 2005). This is also evidenced by the study of Vilá & Weinar (2004) in which they studied the competitive ability of invasive plants against native ones. They concluded that invasive plants are often more competitive. The effects of invasive plant species are also not limited to displacement of native plants but are also able to change genetic make-up as hypothesized from the high potential for interbreeding (Huxel 1999). Allelopathy is another contributing factor in invasiveness. Many invasive plants have been associated with allelopathy, the release of exudates that interfere with the growth of other plants (Callaway & Ridenour 2004; Walker et al. 2003). Invasive plants may cause contamination of water bodies (McCormick et al. 2009).

The presence of invasive plants on rangelands can result in production of poor quality forage, interferes with grazing, and can even add poisons, causing livestock losses (Wells & Stirton 1882; Westbrooks 1998). Hence, invasive plants can reduce the value of land and reduce wildlife food and habitat (DiTomaso et al. 2010). Invasive plants that add more biomass to the rangelands can furthermore increase fire intensity (Brooks et al. 2004; Chamier et al. 2012).

Control of invasive plants is a global concern and costs governments a great deal of money. In the US between 137 (Kolar &Lodge 2001) and 800 billion US$ (Pimentel et al. 2004) are spent on control of these plants per annum. In comparison, Lesotho spends USD$ 7 500 000 per annum on land reclamation activities (Ishii 2015), of which more than half goes into control of invasive plants in favor of grass (Lesotho Meteorology Services 2013).

Knowledge about mechanisms and characteristics that facilitate the process of invasion is imperative for land management decisions (Bosdorf et al. 2005; Jose et al 2013; Acharya 2014). According to Borland et al. (2009), invasive plants are generally opportunistic and have aggressive characteristics that dominate in the ecosystem. Furthermore, they have effective reproduction and dispersal, many are capable of vegetative reproduction through rhizomes, tiny roots and stem fragments, and seeds remain viable in the soil for many years. These plants often store energy in the extensive root systems and can therefore re-sprout after cutting. They can also outcompete other plants through higher growth rates by shading them.

Climate change is identified as one of the factors contributing to aggressiveness of invasive plants (Birch 2000). For instance, in the study conducted by Truscott et al. (2006), heavy rains resulting from climate change have contributed to the spread and long-distance colonization of *Mimulus guttatus*. There is a high likelihood that it will spread fast along rivers in the near future due to high-flow rainfall events. In the context of Lesotho, invasive plants escalate the rate of soil erosion, thereby contaminating water bodies which are mainly on the rangelands (ORASECOM 2009).

2.2 Morphological descriptions and adaptations of invasive plants found in Lesotho's rangelands

2.1.1 *Chrysocoma ciliata*

Chrysocoma ciliata, previously known as *Chrysocoma tenuifolia* and *Chrysocoma coma-aurea* L (Kobisi 2005), is a shrublet belonging to the family Asteraceae (Tsoanyane 2014). It derives its name from Greek, *Krusos* meaning gold and *kome* meaning hair or lock. The name also comes from Latin, *coma* meaning head hair and *aureos* meaning yellow or golden (Fig. 1A). *C. ciliata* is commonly known as golden heads, bitter bush, golden cow cud (English), bitterbos (Afrikaans) (Adcocks 1971; Tsoanyane 2014) and Sehalahala (Sesotho) (Kobisi 2005). It is slender stemmed and has downy pale-green needle-like leaves and a perennial root. There are flowers on almost every branch, no ray florets, and a white calyx remains when seeds are distributed. These flowers are produced from June to July while seeds ripen in autumn. Pollination is mainly by bees (Millar 1969; Adcocks 1971; van Wyk et al. 2002; Tsoanyane 2014; Flann 2016). Bitter bush is also a main attraction for birds which aid in the dispersal of seeds (Trendler & Hes 2000).

According to Squires & Trollope (1979), Cowling et al (1997) and the Global Fire Monitoring Centre (GDNR 2004), *Chrysocoma ciliata* derives its invasiveness from its allelopathic properties. Chemical analysis of *Chrysocoma ciliata* indicates that it contains monoterpenes and sesquiterpenes (Cowling et al. 1997) that are known to suppress germination and reduce germination speed, seedling growth, chlorophyll content and respiratory activity of other plant species (Abdegaleil & Hashinaga 2007; Roux 2001; Singh et al. 2002). It spreads faster by its roots than by seeds, which allows it to colonize bare ground effectively (Wells et al. 1983). It is fast-growing and is therefore capable of outcompeting grasses (Tsoanyane 2014). It propagates quickly by its creeping root that is capable of extending 2-3 feet every year (Millar 1969).

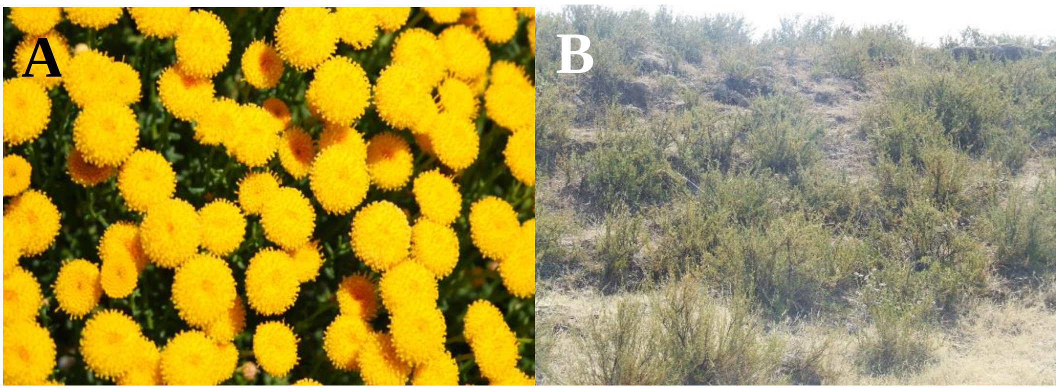

Figure 1. Two invasive species in Lesotho's rangelands: A) *Chrysocoma ciliata* bearing seeds in large numbers, indicating its high reproductive capacity (photo: D. Chuah, 7 February 2012); B) *Felicia filifolia* replacing grass through high germination rates on rangeland in Pokane, Quthing (photo: M. Hae, 1 September 2014)

2.1.2 *Felicia filifolia*

Felicia filifolia, previously *Aster fillifolius,* is a member of the Asteraceae family. It derives its name from Latin name *Felix*, which means cheerful, in reference to its bright flowers, and *filifolia*, which means fern-like. It is a twiggy shrub (Fig. 1B) that grows moderately fast, is well branched and grows to 1 meter high (Harvey 1894). Its foliage is made up of tufted bunches of needle-like leaves that are clustered in clumps at the end of branch tips. It bears large numbers of daisy-like attractive flowers that have a unique aroma (van Wyk 2000) from October to December. These flowers occur in different colors such as white, purple or mauve. Seed heads are fluffy and creamy in color. It is commonly known as Sehalahala-se-seholo (Sesotho), draaibos (Afrikaans) (Viljoen 2004; Moffett 2010).

Felicia filifolia has a high reproductive capacity and reproduces both by seeds and root division. It grows moderately fast and has a low water requirement. It is also frost hardy and resprouts if damaged by frost (Viljoen 2004). Climate change contributes to its success as its population can increase after dry and hot spells when populations of most other plants would decline (Brand et al 2011). *Felicia filifolia* is relatively tolerant to droughts and high temperatures (Du Toit et al. 2014).

2.1.3 *Helichrysum splendidum*

Helichrysum splendidum (Fig. 2A), a synonym for *Gnaphalium splendidum*, is a member of the Asteraceae family and is commonly known as Cape gold (English), Geelsewejaarjie (Afrikaans), Phefo-ea-loti or Toane-moru (Sesotho). It is a fast-growing shrub that forms large colonies and can grow up to 1.5 m high and 1 m wide to form a knoll (van de Walt 2003; van Wyk et al. 2002; Schiller et al. 2008). The leaves are gray in color (Snell 1978), woolly (van de Walt 2003), approximately 1-3 cm wide, linear-oblong to linear lanceolate in shape, and have a characteristic aromatic smell (Hyde et al. 2016). *H. splendidum* flowers have a sweet scent and are bright yellow in color (Schiller and Schiller 2008). The flowers are also long-lasting (van de Walt 2003).

According to van de Walt (2003), *Helichrysum splendidum* is adapted to harsh climatic conditions as it is frost hardy and has a low water requirement. The woolly covering on leaves and stems reduces water loss so it can thrive even in periods of drought. The leaves are rolled to the base to make them even narrower and hence reduce transpiration. *H. splendidum* is adapted to a wide range of environments such as mountain tops, gullies, streams and croplands.

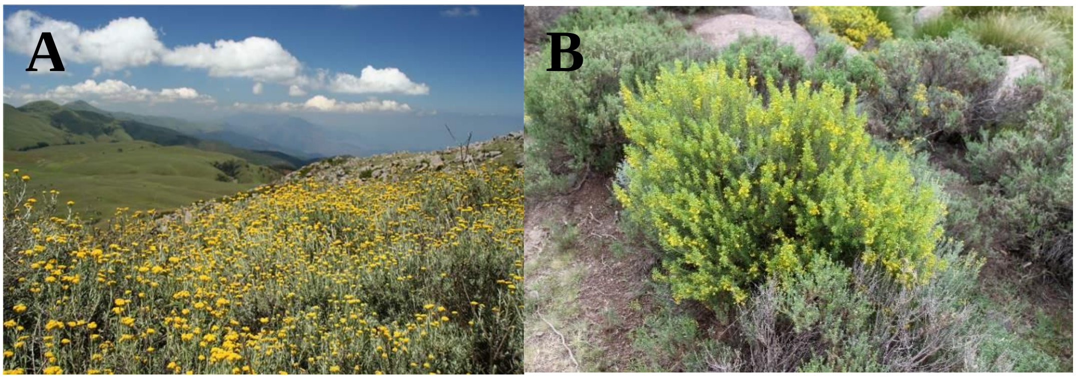

Figure 2. Two invasive species in Lesotho's rangelands: A) *Helichrysum splendidum* spreading fast on a rangeland by first forming monocultures (photo: Fact Sheets, 10 April 2015), and B) *Relhania dieterlenii* which effectively becomes the dominant plant species because of its high germination rates (photo: A. Yakovlev 17 March 2010)

2.1.4 Relhania dieterlenii

Relhania dieterlenii, a synonym of *Nestlera dieterlenii* and *Relhania acerosa* (Fig. 2B), is commonly known as rapeisi, mamenoana or Moholu-oa-lekhoaba (Sesotho) (Foden & Potter 2005; Moffett 2010) and is known as a shrub endemic to Lesotho (Bremmer 1976). It belongs to the Asteraceae family. It was first recorded in Lesotho by the Irish botanist Richard Relhan in Roma and Leribe (Dieterlen 1914). *R. dieterlenii* grows up to 1.6 m tall. It is large but moderately branched. Seedling branches have characteristic dense, curly, matted, soft and wooly hairs. The leaves are arranged in four distinct rows, bear tufts of hairs and are folded lengthwise with upper surfaces against each other. Flowers are flat-topped, determinate with central flowers opening first and continue with auxiliary buds with growth (Dieterlen 1914a; Foden & Potter 2005; Bremer 1976).

Relhania dieterlenii's invasive ability is associated with high seed production and high quantities of seeds deposited into the seedbank. It regenerates easily from seeds and outcompetes other plants in the ecosystem. *R. dieterlenii* can grow under diverse conditions including rock slabs, caves, mountain slopes, very high altitudes and any area which cannot sustain growth of other plants (de Villiers 2012). This species germination increases after fire events and produces sesquiterpenes (Cronquist 1980) that suppresses germination and growth of other plants by sesquiterpenes by causing developmental modifications (Abdegaleil & Hashinaga 2007).

2.1.5 Seriphium plumosum

Seriphium plumosum, which is synonymous with *Stoeb*e *vulgaris* and *Stoebe plumosa*, is also a member of the Asteraceae. It is commonly known as bankrupt bush (English), slangbos, vaalbossie, and Khoi-goed (Afrikaans). It is a shrub characterized by numerous branches gray in color (Badendorst 2004; Koekemoer 2004). The branches are thin, have a wiry appearance and are attached to the stem at right angles. The shoots are short and colored with wooly clustered leaves that are also gray in color (Fig. 3A). Leaves are small in size, form groups and are pressed to the stem to give a gritty look. Flowers are also borne in groups and are attached near the end of the main shoots, thus forming a spike-like inflorescence. Flowering occurs in in April to June and also in spring (Badendorst 2004; Snyman 2012).

Seriphium plumosum possesses allelopathic traits and is therefore able to suppress germination, growth and recruitment of grasses (Snyman 2010). It is also yields volatile oils as a protective measure against herbivory (Badendorst 2004). *S. plumosum* has small leaves covered by wooly hairs of a light color that reflect sunlight, which are adaptations to survive long, dry summers. Its seeds are dispersed by wind, water and animals (Fig. 3B) and the seeds can germinate even after fire events (Badendorst 2004; Koekemoer 2004).

Figure 3. *Seriphium plumosum* (A) shielding and dominating grass and other plants (photo: H. Snyman, 12 July 2011). Mechanical removal of seeds of *Seriphium plumosum* (B) can assist its dispersal (photo near Morija, M. Hae, 4 September 2013)

2.2 Plant characteristics that contribute to invasiveness

The process of plant invasion involves introduction, naturalization and invasion (Niemiera & von Holle 2009). It is necessary to have an in-depth knowledge of the attributes and traits of plants as well as ecological conditions that favor invasions (Rejmánek & Richardson 1996). This will make it possible to avoid future economic and environmental losses (Keane & Crawley 2002). High photosynthetic capacity and biomass accumulation, great plasticity, high reproductive capacity, efficient use of resources and combination of these adaptive traits contribute to invasiveness (Osumkoya et al. 2014; McDowell 2002). Effective seed dispersal also contributes to plant invasion success (Caño et al. 2008). Poor land management is often associated with invasion success. In order to control invasive plants, it is important to understand the plant characteristics and conditions that contribute to invasion success (Holzemueller & Jose 2009).

2.2.1 Effective resource uptake

For a plant species to become a prosperous invader, it has to capture the resources of water, light and/or nutrients efficiently (Holzemueller & Jose 2013). In most cases, sites that are species rich are associated with maximum utilization of these resources, making the environment unfavorable for establishment of invasive species (Hierro et al. 2005). Inversely, plants in less diverse areas do not utilize resources effectively and thereby create "empty niches" susceptible to invasions (MacDougall et al. 2009). Invasive plants can have the ability to utilize resources below the rooting zones of other plants in the community (Scharfy et al. 2009). However, competitive ability depends on the varied distribution of resources, stage of invasion, phenotypic manipulability and evolutionary adaptations which are superior in invaders (Gioria & Osborne 2014). For example, *Chrysocoma ciliata* and *Seriphium plumosum* two of the major invasive plant species in Lesotho, have extensive root systems that grow fast and are capable of utilizing soil nutrients below the rooting zones of other species (Millar 1969; Avenant 2015).

2.2.2 Rapid growth and reproduction

The process of invasion starts with dispersal, which means that a plant or its propagule has to be moved across geographic barriers. This is followed by successful establishment, growth and reproduction. Invasive plants are often high-volume seed producers (Holzemueller & Jose 2009) and have high growth rates (Allison &Vitousek 2004). MacDowell (2002) & Osunkoya et al. (2014) are of the view that this may be attributed to high rates of net photosynthesis and efficient resource consumption. As a result, these species tend to form dense monocultures that spread fast (Holzemueller & Jose 2009). *R. dieterlenii* is a good example in support of this as it gains its invasive ability through prolific production of seeds (de Villiers 2012). In addition to fast growth, invaders may have a long flowering time (Westbrooks 1998; Gallagher et al. 2014). Some successful invasions are associated with a short juvenile stage, small genome and low seed mass that can be dispersed by wind (Rejmánek, 1996). For example, the success of invasive plants found on Lesotho's rangeland can be attributed to the fact that they belong to the Asteraceae family (Raven et al. 1986; Bergh 2009) which has composite flowers that produce many smaller fluffy structures (Fig. 4A), each producing a single seed (Elpel 2015). The family has a specialized calyx called pappus (Fig. 4B) which adheres to the mature cypsela and forms a plume-like structure that aids in wind dispersal (Raven et al. 1986).

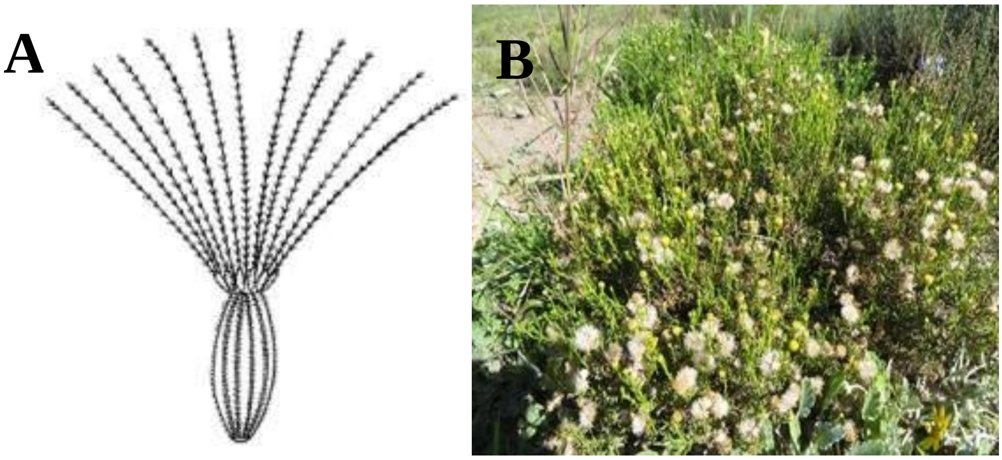

Figure 4. Typical structure of Asteraceae seeds (A) attached to the pappus responsible for long distance dispersal (source: Herman 2002). Detail of fluffy *Chrysocoma ciliata* seeds still attached to the mother plant. Even a gentle wind can blow seeds over long distances (photo: van der Berg 2015).

2.2.3 Empty niche hypothesis

The "empty niche" hypothesis has, a number of times, been used to conceptualize invasion success (Rai 2015, Hierro 2005). It states that a limited native species pool makes the ecosystem unsaturated and therefore invaders take advantage of spare resources, occupy unused niches and use then efficiently (Catford et al. 2009). Mack et al. 2000 suggest that if the recipient community has bare patches, it may surrender to incoming members. This hypothesis was confirmed by the study of Maron et al. 2004 in which they tested the dominance of the invasive plant *Centaurea solstitialis*. Their results revealed that *C. solstitialis* builds robust stands on grasslands due to their deep roots capable of using water deeper than native plants can access. Fire and overgrazing, which create empty niches, promote proliferation of invasive plants (Holzemueller & Jose 2009) by creation of bare ground. For example, degradation of Lesotho's rangelands by invasive species, especially *Felicia filifolia* and *Chrysocoma ciliata,* has been more prevalent following overgrazing, which creates bare ground (ORASECOM 2014a; Bennett et al. 2015).

2.2.4 Novel weapons theory

Plants with invasive ability are capable of altering the invaded location through production and release of allelo-chemicals, novel weapons (Callaway & Ridenour 2004; Weir et al. 2006) that impede the growth of other plants (Holzemueller & Jose 2009; MacDougal et al. 2009. Success of plant invasions based on the theory of novel weapons is evidenced by *S. plumosum* which releases volatile oils so that it is not browsed on (Badendorst 2004). Additionally, *H. splendidum* has been proven to have a burning effect on other plants (Snyman 2009), while *R. dieterlenii* and *C. ciliata* contain sesquiterpenes and monoterpenes (Squires &Trollope 1979; Cronquist 1980; Roux 2001) that suppress germination, seedling emergence and growth of neighboring plants (MacDougall et al. 2010). Modification of the above-ground environment can also occur by increased biomass that changes fire regimes (Holzemueller & Jose 2009).

2.2.5 Enemy escape

All plant species have natural enemies that moderate their populations. These include microbes, herbivores and other plants (Holzemueller & Jose 2009). Invasive plants are believed to gain dominance in the invaded areas because of lack of natural enemies, according to the "enemy release hypothesis" (Keane & Crawley 2002; Inderjit et al. 2005; MacDougall et al. 2009; Rai 2015). This theory was proposed by Callaway & Ridernour (2004) who indicate that non-native invasive plants leave behind specialized consumers. They therefore increase their competitive ability as less resources are allocated for consumer defense and more allocated for growth. Gioria & Osborne (2014) also emphasize the fact that resource competition is of high importance in invasion success. A clear example is *H. splendidum* whose fast growth in the area of introduction makes it possible to form large dense monocultures within a short period of time (van de Walt 2003). When other plants have been eliminated, invasional meltdown can occur. Invasional meltdown theory states that two or more introduced plants facilitate one another's establishment or aggravate the impact of other invasive species on native plants (von Holle 2011). For example, *C. ciliata* is often in co-existence with *R. dieterlenii* (Fig. 2B) and together the two have a more serious impact on native communities than either individually (Wright 2013).

2.2.6 Morphological and physiological characteristics

Understanding the anatomy and physiology of invasive plants is very important in the battle against them. These include seed size and mass, seed dispersal, seed production capacity, duration of juvenile period, photosynthetic capacity, transpiration, phenotypic elasticity, leaves, stem and root structure and their efficiency in utilizing resources (Rejmanék1996; Richards et al. 2006). The traits influence invaders' success in the new environment (Osumkoya et al. 2014; McDowell 2002). Morphological and physiological traits interact. For example, *H. splendidum* is characterized by a gray woolly covering and narrow leaves which are rolled to the underside when temperatures increase to reduce the rate of transpiration (de Walt 2003). Another example is that of *C. ciliata* and *S. plumosum* which have extensive root systems enabling them to access water from below the rooting zone and thereby increasing their ability to survive dry environmental conditions (Millar 1969: Avenant 2015).

Photosynthetic capacity, transpiration and phenotypic plasticity are some of the physiological traits that have been mentioned in plant invasion studies (McDowell 2002, Osunkoya et al. 2014). Photosynthetic capacity is affected by the ability of the invading pant to harvest light and carboxylation reactions which influence the rate of photosynthesis (Ali et al. 2015). The importance of photosynthetic capacity in plant invasion was confirmed by a study undertaken by McDowell (2002) where photosynthetic capacity and resource use efficiency were tested in two invasive *Rubus* species and two other non-invasive species; photosynthetic capacity was high and maintained for a longer period in invasive plants. Phenotypic plasticity is defined as the ability for a particular trait of an organism to respond to the environment and be able to preserve and increase fitness under unfavorable conditions (Richards et al.2006). The ability to succeed in varied conditions is a key to allowing incoming plants to spread across new zones (Matesanz et al. 2012). Phenotypic plasticity can be viewed as a safeguard from the natural selection of invaders, thereby allowing them to survive the establishment stage of invasion (Dyer 2007) and is linked to the success or failure of the introduced plant (Denovsky et al. 2012).

2.3 Influence of climate change on plant invasions

Plant invasions are the product of complex interactions between species traits, community interactions and environmental variations (Caño et al. 2007). Climate change can increase the risk of an invader expanding to new areas in different ways (Bradley et al. 2009, Birch 2000).

Extreme climatic conditions act as disturbances that kill neighboring plants and render other plants less resistant and by so doing increase resources available for invaders (Ziska & Dukes 2014). Climate change alters the distribution and spread of invaders (Runyon et al. 2012; Dukes &Mooney 1999). For example, Lortie & Cushman 2007, found that plant species richness decreased with increased wind erosion. Dukes & Mooney (1999) indicate that invaders are able to capitalize on their inherent physiological and life history traits to resist the effects of changing climatic condition. Additionally, phenotypic plasticity can provide adaptive response to varying environmental conditions (Rai 2015). Another study confirming the effects of climate change in promoting success of plants invasion is that of Dukes & Mooney (1999). In their experiments, they simulated warm conditions and their results showed that higher temperatures favored the invasive shrub *Atermisia tridentata*.

2.4 Control of invasive plants on rangelands

Controlling invasive plant infestations is expensive and unsuccessful in most cases (Pimentel 2002; Kolar & Lodge 2001). This is more problematic when dealing with long-lived plants with complex life-cycles and high seed dispersal rates (Pichancourt et al. 2012). In addition, often there are no guidelines or strategies for limiting dispersal (Davies et al. 2007). A successful invasive plant control programme is one that involves prevention, early detection and eradication as well as preventing new infestations (DiTomaso 2010; Rejmánek 2000). Pichancourt et al. (2012) suggested some practical and cost-effective tips for control of invasive plants with complex li-cycles and high dispersal rates which state that it is best to identify the stage of invasion and devise the most effective and cheaper control methods. Davies & Sheley (2007) advise that prevention and control of invasive plants should shift from being reactive but be informed by scientific research for them to be effective.

2.4.1 Elements of integrated control of invasive plants on rangelands

Integrated invasive plants management has been adopted from integrated pest management in agricultural crops (Masters & Shelley 2001). It involves a combination of biological, cultural, mechanical and chemical control of pests (Beck 2013, Sellers & Ferrell 2016). This concept has been introduced and applied in brush control program on rangeland management (DiTomaso et al. 2010). Integrated weed control should also include restriction of propagule movement and public awareness and ongoing public education (Masters & Shelley 2001). Integrated control of invasive plants necessitates cautious planning that incorporates a long-term approach involving prevention and education plans, as well as management strategies (DiTomaso et al. 2010). Integrated invasive plant management is developed and applied in a chronological manner to reduce the detrimental effects that bush encroachment has on preferred plants and relies more on the use of low-cost local and minimum use of herbicides (Brock 1988).

Biological control of invasive plants is an important part of integrated control of invasive plants. The main expectation is to control invasive plants without any injurious effects to other vegetation in the area (Müller-Schärer & Schaffner 2008). The goal is usually not to totally destroy the unwanted plant but to exert enough environmental stress to reduce its dominance (DiTomaso 2000). Biological control of invasive plants is characterized by the use of living organisms such as insects (Kok & Gassman 2002) and fungi (Buckingham 2002; Pemberton 2002) to limit reproductive capacity, density and effects, and release of a control agent is not without risks as the agent can also affect preferred plants (Sheley & Masters 2001). The biological agent should however have a narrow range of alternative hosts (Brock 1988).

Cultural methods also make up part of integrated brush control on rangelands (DiTomaso et al. 2010; Beck 2013). They involve proper grazing management to minimize the spread of invasive plants and to moderate grazing levels to reduce disturbances, prescribed burning, re-seeding and increased plant competition (DiTomaso et al. 2010). It is necessary that plants used in revegetation are competitive to resist invasion (ORASECOM 2014b). Intensive grazing can also be employed to counteract inherent dietary preferences by livestock. It is also necessary to maintain a healthy rangeland with multiple species to increase their resilience (Elmqvist et al. 2003). Equally important in integrated management of invasive species are mechanical control methods which involve hand pulling (Müller-Schärer & Schaffner 2008), hoeing, tilling, mowing, grubbing, chaining and bulldozing (DiTomaso 2000). Mechanical methods are immediate and positive but for them to be effective, knowledge about regrowth characteristics of invasive species is of high importance to inform choice of machinery and tools and timing of intervention (Wiedmann 2016).

The other method considered primary in integrated control of rangeland invaders is chemical control (DiTomaso 2000). Chemicals often give excellent results, especially when used according to manufacturer's instructions. These chemicals exist in ground, basal, pellet and liquid forms and can be either selective or non-selective (Simmons et al. 2007). The aim of chemical control in integrated methods is to use a minimum of herbicides and only when necessary. For successful chemical control, timing of application is very important (DiTomaso 2000). Use of spot treatment is recommended which targets the unwanted plant without any harmful effects to other plants (Mattrick 2016).

2.5 State and transition models

In recent years, state and transition models (STMs) have received a lot of attention in rangeland management (Bestelmeyer et al. 2003). STMs are based on the fact that a rangeland is an ever-changing ecosystem transitioning from one state to the other. They are pointers of resilience by ecological sites (Bestelmeyer et al. 2003. They indicate the critical thresholds (Bestelmeyer et al. 2009) and developed using the historical background of vegetation and herbarium samples (Morris et al. 2013). STMs give information on potential vegetation, plant species composition and plant community dynamics (Holmes & Millar 2010). Briske et al. (2005) suggest that STMs consist of reversible vegetation dynamics in which one state replaces another and incorporates changes brought about by fires, weather variability, management activities and grazing. A well-developed STM is characterized by a description of plant succession, control methods, dispersal agents and estimations which are used in the creation of the current distribution of invasive plants and indicate where to focus use of resources (Frid et al. 2013).

3. METHODS AND DATA SOURCES

Individual invasive species first records, morphological description and characteristics of their invasive ability were gathered from the following databases Global Checklist (Fann 2016) JSTOR (Dieterlen 1914a & b, Bolus, 1788), TROPICOS (Bremmer 1976) Plantzafrica (van de Walt 2003; Viljoen 2004; Tsoanyane 2014), Flora of Southern Africa, Flora of Zimbabwe (Hyde et al. 2016), Flora Capensis (Harvey 1894), Opera Britannica (Bremmer 1976) Department of Agriculture, forestry and fisheries of South Africa, which also includes Southern African Plant Atlas (SAPIA), (Adcocks 1971), National Botanical Garden of South Africa (Badendorst 2004), National Herbarium Pretoria South Africa (Koekemoer 2004). Journals, books, reports and travelers accounts were also used for species specific information on plant invasions and their possible control methods. A general literature review was done by navigating the Icelandic national web portal http://hvar.is/ (which provides access to Google Scholar, Google Books, Web of Science, Elsevier ScienceDirect, Springer Link, e-books on Life Sciences, HighWire and Directory of Open Access Journals (DOAJ)), Google search and other data base search as indicated.

A State and Transition model for plant invasion was developed, using records from previous works on vegetation (May 2000), maps which showed coverage by each species for the period from the early 1900s to early 2000s (Conservatoire et Jardin Botaniques & South African National Biodiversity Institute, 2012), fire history (ORASECOM 2014a, DRRM 2014, climatic conditions (e.g. precipitation, temperature), missionaries' reports and pictures (Singh 2000) and rangeland management history, as suggested by Bagchi et al. 2013). In some cases, coverage of invasive species was recorded in hectares and converted into the percent of a total area of the country (Motsamai et al. 2009; May 2000).

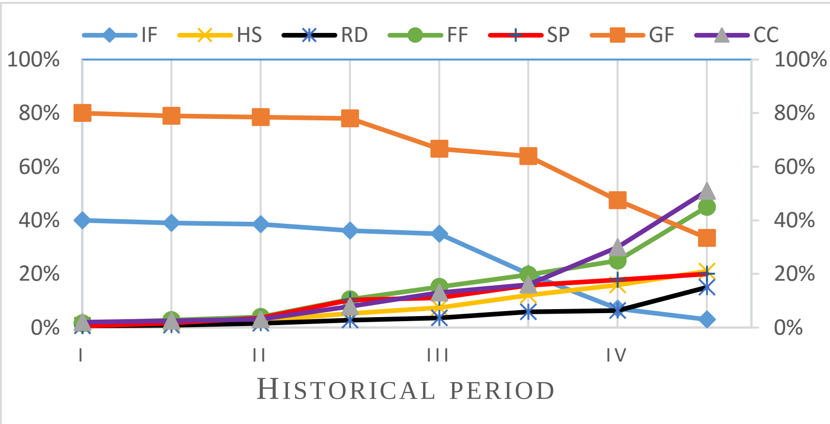

Figure 5. Species composition and abundance over time on Lesotho's rangelands in different historical periods (I=1700s, II=1800s, III=1900s and IV=2000s). IF=Indigenous forests, GF=grasses and forbs HS=*Helichrysum splendidum*, RD=*Relhania dieterlenii*, FF=*Felicia filifolia*, SP=*Seriphium plumosum*, CC=*Chrysocoma ciliata*. Reconstructed species abundance based on: May 2000, MacVean 1977, Singh 2000, O'Connor et al. 2014, Van Zinderan Bakker & Werger 1974, Masih et al. 2014, Marake et al. 1998, Killick 1963, Overseas Geological Surveys 1963, National Environmental Secretariat 2009, ORASECOM 2014, Klimanov & Sirin 1997, Bremer 1976, Jacot-Guillarmond 1962, Killick 1963, Bainbridge et al. 1991, Harvey 1894 and Phoofolo 2003.

4. RESULTS AND DISCUSSION

4.1 Historical changes in Lesotho's vegetation

The history of Lesotho's vegetation changes in relation to the invasive plant species found on rangelands and drivers of degradation is presented in Figure 5, while drivers of degradation and the associated invasion hypotheses are presented in Table 1. During the period from 1700 to 1750, the main vegetation types were woodlands and grasslands and there were fewer disturbances to the land than in recent years, as compared to subsequent years. This state of environment was sustained until 1850. Some of the problematic invasive plants today were recorded in that era in a few areas of the country, which means they might be native to Lesotho.

This differs, however, from the definition of Niemiera & von Holle (2009) that an invasive plant is the one that is alien or non-native. The results of the current study indicate that not only alien plants are invasive but native ones too, if conducive conditions are created (Simberloff 2010).

Table 1. Simulated history of invasion, vegetation types and associated drivers of degradation

Historical period			
1700s	1800s	1900s	2000s
Vegetation types • natural forests (high) • grasslands • some invaders(low) Drivers of degradation • minimum effect from uprooting by gatherers • few rangeland fires Management activities • no rangeland management in place. • inhabitants are hunters/gatherers moving from one place to another Invasion Theory • species richness hypothesis	Vegetation types • natural forests(high) • grasslands • invader(low) Drivers of degradation • new farming systems by missionaries • few forest fires Management activities Early 1800s • rotational grazing and maboella • utilization of only dead trees or tree branches • illegal to kill a tree • reed used only for construction Late 1800s • felling of timber • rinderpest outbreak Invasion Theory • species richness hypothesis • empty niche hypothesis	Vegetation types natural forests(low) grasslands (low) invaders (High) Drivers of degradation • frequent drought after which invader population increases while grasses are weakened • heavy rainfall • strong winds • overgrazing • exotic tree species • increased fire events • dust bowl which might be responsible for seed dispersal Invasion theory • empty niche • species richness (low) • novel weapons • invasional meltdown	Vegetation types • natural forests (almost nonexistent) • grasslands (low) • invaders (high) Drivers of degradation • frequent droughts • heavy rainfall • overgrazing • increased fire events • strong winds Invasion theory • empty niche • novel weapon • invasional meltdown as invaders are increasing at a high speed and are mostly found in coexistence with each other • species richness

Constructed from: May 2000: MacVean 1977: Singh 2000: O'Connor et al. 2014: Van Zinderan Bakker & Werger 1974: Masih et al. 2014: Marake et al. 1998: Killick 1963: National Environmental Secretariat 2009: ORASECOM 2014a: Klimanov & Sirin 1997: Bremer 1976: Jacot-Guillarmond 1962: Killick 1963: Harvey 1894: Phoofolo 2003.

The early 1900s marked the beginning of severe soil erosion, loss of woodland and grasses and taking over by invasive plants (MacVean 1977; Singh 2000). This could be attributed to the rinderpest outbreak between 1897 and 1899 (Phoofolo 2003) during which high numbers of animals died and there was a lack of dung for fuel. As result the demand for timber increased. In the 1900s the frequency of drought which followed high rainfall was experienced. Of high significance in plant invasion was the dust bowl which occurred in 1933 and might have been responsible for seed dispersal across the country. In this period, the effects of climate change started to be manifested and invasive species increased at an alarming rate. Climate change, poor rangeland management, and high animal numbers are blamed for the weakening of grasses and indigenous trees while invaders were spreading. From the 2000s most of the country's land had reached degradation beyond repair.

4.2 Earliest historical record, reproductive mode and seed dispersal agents

The earliest records, life cycle, reproductive mode and seed dispersal agents of some invaders found in Lesotho's rangelands are presented in Table 2. Their ability to invade and eliminate other plants in the ecosystem is related to their fast reproduction, which is both vegetative and by seeds. Most invaders are successful as they are large seed producers and have long flowering period (Holzemueller et al. 2005). The success of these invaders could also be attributed to their small seed mass and adaptation features that allow seeds to be dispersed to greater distances by wind than other plants, a typical characteristic of *Asteraceae* (Raven et al. 1986). The species *S. plumosum* is the only one that is dispersed by an additional agent, water, thereby even further increasing its chances of domination. The fact that *C. ciliata, H. splendidum, R. dieterlenii, F. filifolia*, and *S. plumosum* are all perennials may be the reason for their successful establishment.

Table 2. Earliest historical record, life cycle, reproductive mode (V: vegetative, S: by seeds), reproduction, seed dispersal agents (W: wind, H: water, A: animals), duration of flowering and reference.

Species name	Earliest record	Life cycle	Reproduction		Seed dispersal			Duration of flowering	Reference
			V	S	W	H	A		
C. ciliata	1894	perennial	x	x	x	-	-	4 months	12,11,1,1
H. splendidum	1832	perennial	x	x	x	-	-	3 months	10a,2,3
R. dieterlenii	1884	perennial	x	x	x	-	-	3 months	10b,4,8,9
F. filifolia	1788	perennial	x	x	x	-	-	3 months	12,10a,6
S. plumosum	1894	perennial	x	x	x	x	-	5 months	7,13,14

Prepared with reference to 1=Tsoanyane 2014: 2=van de Walt 2003: 3=de Villiers 2012: 4=Bremer 1976:5=Millar 1969: 6= Viljoen 2004: 7= Koekemoer 2004: 8= Bergh 2009: 9= Modigo-Mponga 2004: 10a =Dieterlen 1914a: 10b =Dieterlenii:11=Squires & Trollope:12=Harvey 1894: 13= Badenhorst 2004:14 Harvey 1894

4.3 Factors that contribute to invasive success of plants found in Lesotho's rangelands

Factors that contribute to the invasive ability of *C. ciliata, H. splendidum, R. dieterlenii, F. filifolia, and S. plumosum* are presented in Table 3. These species are successful invaders as they possess high reproductive and allelopathic abilities (except *F. filifolia*) through which they release allelo-chemicals that render the environment not conducive for the neighboring plants. This phenomenon qualifies as the use of novel "weapons," as suggested by (Callaway & Ridenour 2004). They are all perennials and can therefore reproduce fast vegetatively by cloning, hence their success in invasion, as suggested by supported by Cadotte et al. (2006).

In addition, all five species are xerophytic, well adapted to a wide range of climatic and soil conditions and have the ability to colonize bare ground. This means that when conditions become unfavorable they still thrive at the expense of grasses and thereby gain dominance. *C. ciliata*, *splendidum* and *S. plumosum* have extensive root systems which are extended both to below the root zone of other plants and to the sides to access water and nutrients out of reach of other plants. All these invasive species have small leaf areas to limit transpiration, and for *F. filifolia* and *R. dieterlenii* it is the only drought adaptation trait to survive hot dry conditions. *S. plumosum* has a bonus in attributes related to its xerophytic ability. It has leaves that roll to the underside to reduce the exposed leaf area. As indicated by Hierro et al. (2005) many invasive plant species are successful because they are aggressive and efficient resource users.

H. splendidum and *S. plumosum* have wooly coverings on both stems and leaves, contributing even more to reduction of water loss. In addition, *S. plumosum* has a light color that reflects sunlight, also contributing to low transpiration rates. *R. dieterlenii* success as an invader lies in the fact that it is a reseeder. The results of the current study confirm the findings of Rejmanék1996 and Richards et al. (2006) that the success of invasive species can be attributed to possession of morphological and physiological properties that allow them to resist extreme climatic conditions and access resources that are beyond reach by preferred plants and become dominant.

Table 3.: Summary of factors that contribute to invasive success of plants found in Lesotho's rangelands: *Chrysocoma ciliata* (CC), *Felicia filifolia* (FF), *Relhania dieterlenii* (RD), *Helichrysum splendidum* (HS), *Seriphium plumosum* (SP).

What favors its invasiveness	CC	FF	RD	HS	SP	Reference
Profuse reproduction	x	x	x	x	x	1,2,8,12,13,15,16
Allelopathic/vulnerary	x	-	x	x	x	3,10,11,17
Aggressive root system	x	-	-	x	x	3,4,9,18
Xerophytic	x	x	x	x	x	5,8,12,13,20
Ability to colonize bare ground	x	x	x	x	x	6,8,12,22,
Frost hardy	x	x	x	x	x	19,8,12,13
Leaves rolled underside	-	-	-	x		8
Small leaf area	x	x	x	x	x	4,8,12
Wooly hair on leaves/stems	-	-	-	x	x	8,15
Re-seeder	-	x	x	-	-	21,22
Adaptation of wide range of climatic conditions	x	x	x	-	x	4,12,13
Tolerance to fire (adults)	x	x	-	-	-	1,14
Fast growing canopy/shielding	-	-	-	-	x	15
Ability to reflect sunlight	-	-	-	-	x	15
Release volatile oils for protection against animals	-	-	-	-	x	15

References:1=Squires &Trollope 1979: 2=Roux 2001: 3=Millar 1969: 4=Tsoanyane 2014: 5=Trollope 1978: 6= Wells et al. 1983: 7= Cowling et al. 1997:8= van de Walt 2003:9= Trendler&Hes 2000: 10= Schiller &Schiller 2008:11= Cronquist 1980:12= de Villiers 2012:13= Viljoen 2004: 14=du Toit et al. 2014: 15= Badendorst 2004: 16=Koekemoer 2004: 17= Snyman 2009: 18=Avenant 2015: 19 = Cheeke 1989: 20=Bergh 2009 RD 21 = Modigo-Mponga 2004, 22=0RASECOM 2014a

4.4 Possible control methods that could be adopted for invasive plants on Lesotho's rangelands

Different control methods that have proven successful in the control of different invasive plants on Lesotho's rangelands are presented in Table 4. At the seedling stage *C. ciliata* is susceptible to fire and at the adult stage reseeding bare ground and livestock exclusion are the remedy to their dominance. There are concerns, however, regarding the use of fire to control *C. ciliata* as often it is found in association with *R. dieterlenii* whose seed germination increases after fire events (de Villiers 2012). If mechanical methods are employed, the adult plant should be uprooted to completely remove the root. This is important as *C. ciliata* spreads more by the root than by seeds. Although there are no records of herbicide control of *C. ciliata*, it may be more effective in targeting the root system, especially with systemic herbicides.

Table 4. Recorded and tried control methods that could be used for control of invasive plants on Lesotho's rangelands

Species	Growth stage	Possible control methods	Reference
C. ciliata	seedling	Fire	1
	adult	Reseeding bare ground	2
		Livestock exclusion	2
		Rangeland resting	3
		Uprooting	2
H. splendidum	adult	*Mechanical uprooting	4
		Use of herbicides	4
		Fire	4
R. dieterlenii	seedling	*Fire	5
	adult	*Mechanical uprooting,	4
		Chemicals	4
F. filifolia	adult	Uprooting	2
		Chemical control	2
		Rangeland re-seeding	2
		Rangeland resting	2
S. plumosum	seedling	N fertilizer	6
		sodium chloride	6
		Fire	7
		Mechanical uprooting	9
	adult	Soil applied herbicides	6

*=based on related species: 1=Trollope 1975:2=ORASECOM 2014: 3=Trollope 1986:4=van Wilgen 2001: 5=de Villiers 2012:6=Snyman 2012: 7=Snyman 2011: 8=Snyman 2012:9=Avenant 2015

There are only three control methods recorded for *H. splendidum*, uprooting, fire and herbicides. Uprooting is the easiest and more economical and involves hand pulling or use of simple tools. However, uprooting should be done when the soil is wet to ensure total removal of the root, otherwise the plants will re-sprout. *H. splendidum* is prone to fire and can be eliminated by herbicides. Likewise, *R. dieterlenii* can be controlled by use of fire, uprooting to completely remove the root and use of herbicides.

There are several methods tested for the control of *S. plumosum*, including use of N fertilizer and sodium chloride which are less detrimental to the environment at seedling stage. These are to be overdosed in order to have high depth rates. Fire and mechanical rooting are also effective at the seedling stage. At the adult stage, *S. plumosum* is very difficult to control. Only herbicides, which have to be spot applied, have proven to be effective. *S. plumosum* infects mainly wetter areas like springs, rivers and streams and this is a real change for countries such as Lesotho whose economy depends on water resources. For all the invasive plants (Table 4.4) it is wise not to wait for the plant to bear seeds as interfering with the seed bearing plant will only help distribute the seeds even more.

Uprooting, re-seeding, and rangeland resting are the safest control methods identified for the successful control of *F. filifolia.* Where uprooting is considered, it should target removal of the root and therefore the right tools should be used. Chemical control is more effective as it results in higher death rates. Reseeding and rangeland resting are also suggested (Table 4.3). This may help to reverse the effect of the empty niche.

The current study concludes that integrated weed management is the best way to control invasive plants on rangelands; it incorporates all methods of control. It wise to consider expenses related to each and every control method included. For example, to reduce expenses related to re-seeding the possibility of a rich seedbank should be considered first as some areas are able to recover without reseeding. On the other hand, chemicals can be spot applied to reduce detrimental environmental effects the plant possesses. It is also vital to know the traits that the plant possesses prior to its control. For instance, fire is suggested as the other method to control some of the invasive plants. If it used on lands that were previously occupied by *R. dieterlenii*, this will increase its germination rate from even old seedbanks. On the other hand, if in the control of *C. ciliata* only the aerial part is removed and not its taproot, it will resprout and become even more aggressive.

4.5 State and Transition model for Lesotho's rangelands

The State and Transition model representing vegetation dynamics for Lesotho's rangelands is presented in Figure 6. State 1 represents sites with optimum productivity comprised of historically-dominant grasses and indigenous forests. Wetlands consist of peat bogs and reeds that collect and distribute water in a non-erosive manner. Some of the current native invader plants are present in insignificant populations. There is abundant clean water and animal production is profitable.

In state 2, historically dominant grasses and indigenous forests are still present but the invasive plants have invaded rangelands. The driving forces (1a) include overgrazing due to high livestock numbers and frequent rangeland fires. The land is likely not to recover and thereby progresses (1n) to state 3 if there are no remedial activities employed. It is comparatively cheaper and less labor intensive to reverse this state by brush control followed by rangeland rest (1b). Reseeding may not be necessary as the land could recover from the seedbank. State 2 represents the critical threshold beyond which rangeland is expensive to improve and the effects of drivers of land degradation are more detrimental.

State 3 represents a grassland dominated by invader plants. The population of invasive plants has increased tremendously and has become more aggressive due to persistent overgrazing, rangeland fires and ineffective brush control methods (2a). There are still remnants of dominant grasses in the interspaces but are nearing elimination. This state could be reversed by continued pressure on invaders through use of more efficient brush control methods and re-seeding to increase population of desired rangeland plants. However, the cost and complexity of brush control is higher than in states 1 and 2.

State 4 represents an almost irreversible stage of invasion. Historically-dominant grasses and indigenous forests are absent and invaders have taken over (invasional meltdown). Soil erosion is rampant and resources are lost out of the ecosystem. Fire regimes have changed due to a new type and increased fuel characteristics. The chances of reverting the land to state (3b) are slim.

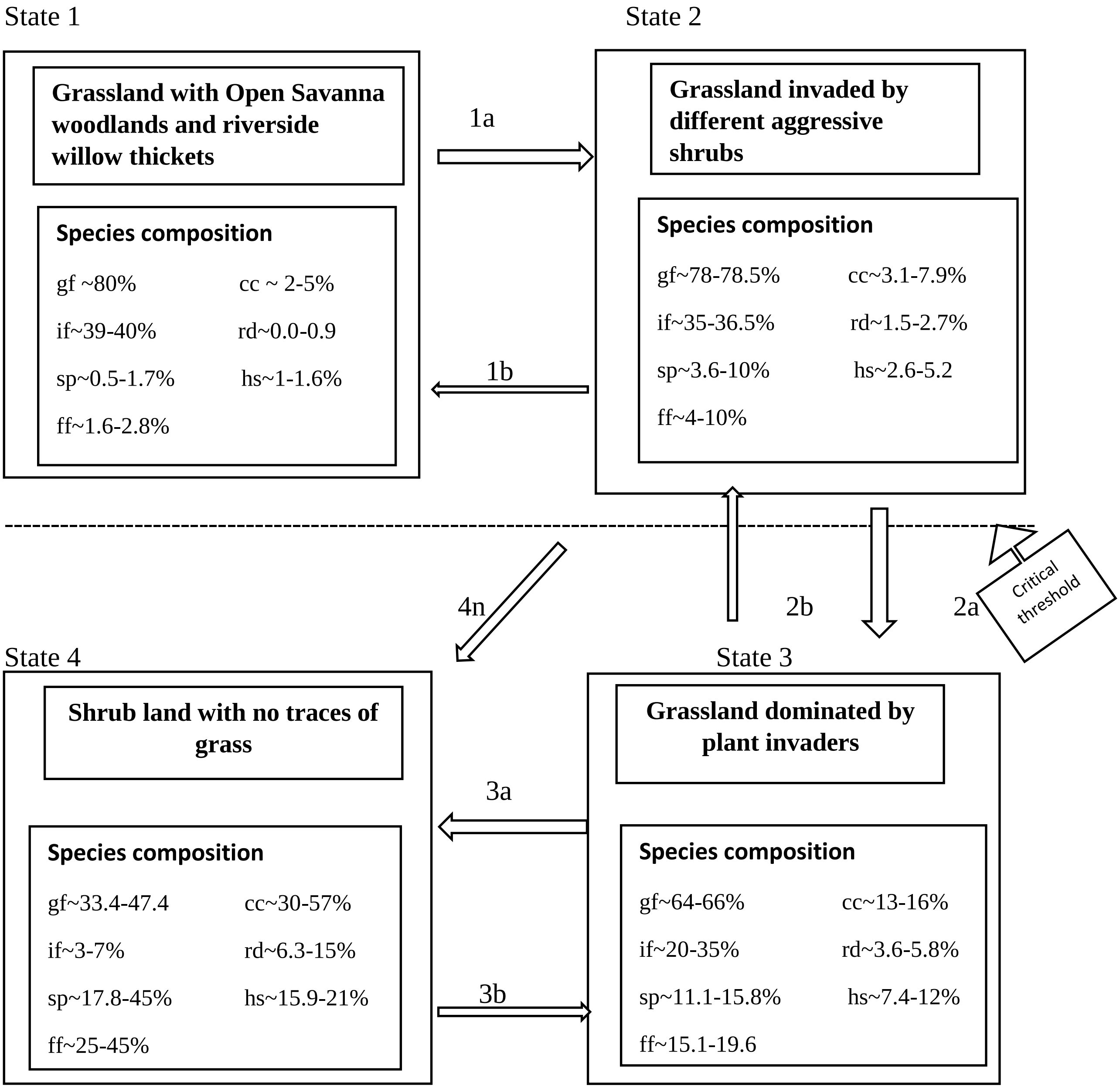

Figure 6. A conceptual state and transition model S1=S4 = states: State 3a = drivers of degradation overgrazing and rangeland fires: 3b low and less expensive management activities of re-seeding and brush control to reverse land degradation: 1n=lack of management activities result in rapid degradation to state 4 : 2a = persistent overgrazing, and rangeland fires: 2b=continued re-seeding and brush control may reverse back to state 2 but it is now moderately labor-intensive and expensive: 3a=more persistent overgrazing and rangeland fires : 3b management activities which are now even more labor intensive and expensive may reverse land back to state 3. Transition from state 4 to 1 is impossible: gf=grasses and forbs: if= indigenous forests: sp=*Seriphium plumosum*, ff=*Felicia filifolia*, cc=*Chrysocoma ciliate*, rd=*Relhania dieterlenii*, hs=*Helichrysum splendidum*

CONCLUSIONS AND RECOMMENDATIONS

Overgrazing and rangeland fires are major contributors to plant invasions; however, the problem might have started as far back as the arrival of European missionaries who undermined the way Lesotho's inhabitants managed the environment and who introduced cash crops. Introduction of cash crops confined livestock to smaller grazing areas as farming land increased in the 1800s, especially with the arrival of missionaries and the outbreak of rinderpest that led to a shortage of dung for energy and the subsequent felling of trees in large numbers. The problem spiraled even more in the 1900s with climate change and the famous dust bowl which might have contributed to massive seed dispersal over greater distances.

The effects of this historical events are experienced more in this era (2000s) and Lesotho's rangeland has now reached invasional meltdown. Additionally, Lesotho does not prioritize land management issues, which may be attributed to the fact that its monetary value is not obvious, as for other natural resources. Future research should therefore include monitoring of vegetation changes as a way to preserve species, retain genetic diversity and protect rangelands against invasion. Preserving vegetation should be given monetary value by relating it to culture, recreation, education, tourism and major economic players such as wool and mohair production, hydropower production and water sales to other parts of Southern Africa. By so doing, rangeland management and re-vegetation activities may be given more attention than now.

There are no formal records on vegetation dynamics as existing records are fragmented and not well documented, making research into vegetation dynamics a challenge. This can be done by production of maps which are management tool, for informed range management. Maps could be produced by simulation to also trace back vegetation changes which is cheaper and faster. Maps should include species names, their geographical range or spread (Sharma et al. 2005) and stage of invasion. Newly produced records on vegetation changes should also include future invasion risk, species specific control measures, stages of invasion and prediction of future invasion risk, and development of laws and protocols governing rangeland management. This will help scientists and rangeland managers on where to focus more and the estimation of future invasions. Inventories will be baselines that inform on plant species richness by identifying where invasions will occur, what they are, and whether they really pose any threat. Knowing the current spread of invaders will assist in forecasting future spread and inform management (Trueman et al. 2014).

The current study also concludes that unlike most areas of the world where invaders are alien, those found in Lesotho's rangelands are native as the historical records trace them as far back as the 1700s. The fact that these invader plants might be native is the reason why Lesotho was caught off guard as the invasion reached its peak. Additionally, invader plants possess morphological and physiological traits which are absent in other rangeland plants. These traits are responsible for resistance to climate change and control methods.

There is no current research that is specifically focusing on invasive plants and the ongoing rehabilitation programs are not based on scientific findings. Research activities should also include development of protocols for inventory and monitoring of invaders and their spread over time. It would also be beneficial to understand what contributes to making an environment vulnerable in order to deter new infestations either by new or known invaders (Jasiuk 2000, Shelley & Masters 2001). Social studies should include all categories of the society and the results be made public. The public can also be involved by reporting citing of invasive plants.

With reference to the findings of the current study, it is recommended that land management issues be prioritized and laws and policies enforced to retain the current biodiversity reserves before extinction. There should be research directed specifically to vegetation changes and recording of data preserved for future use. The current study included some of the problematic plants, but not all. It is therefore recommended that future research focus also on morphological and physiological traits that make invasion a success. Control methods should be based on the traits of the plant under consideration, consider all elements of integrated control and be cost-effective. Scientists and land managers should work together with policymakers to attempt to assess the monetary value of land and the losses associated with land degradation due to the presence of invasive plants and their impacts on the economy (for example: effects on water exports, wool and mohair enterprise and hydropower generation). This may raise the alarm at the relevant agencies involved and lead to action on the part of policy-makers.

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