Plant diversity and morphology in seasonally snow-abundant niches of the Drakensberg Alpine Centre, Lesotho.

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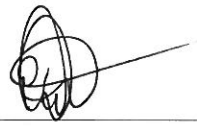
A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfillment of the requirements for the degree of Masters in Science

Johannesburg, 2015

DECLARATION

I hereby declare that this is my personal work. The articles are the results of my original work and writing; and I received guidance and assistance from my supervisors to a reasonable extent. The thesis is submitted for the fulfillment of the degree of Masters in Science at the University of the Witwatersrand, Johannesburg and I attest that it has not been submitted before for any other degree or examination at any other University.



28 day of October 2015 in Johannesburg

Abstract

Mountains are one of the most important and yet environmentally sensitive habitats in the world, they act as reservoirs of species, and have frequently served as refugia for organisms during periods of climate change and provided subsequent sources for speciation. As temperatures increase due to global climate change, species are shifting to higher altitudes to escape the effects of warming at lower altitudes. The spatial distribution and diversity of alpine vegetation is strongly influenced by environmental factors such as snow cover, solar radiation, soil moisture, humidity, and air/ground temperature. Snow cover is one of the most important factors controlling ground level microclimate and alpine plant growth. My study was undertaken near Kotisephola Pass at ca. 3300 m.a.s.l. in eastern Lesotho. Three zones were identified namely, upper, middle and lower zones at the site, as a result of vegetation differences that were observed along a 30 m transect from the rock scarp to the tussock grasses. The environmental variables of temperature, soil moisture, solar radiation, snow depth and humidity were measured over a period of 17 months using i-Buttons, Hobo and Tinytag data loggers, probes, solar radiation and temperature data loggers. Vegetation sampling was undertaken to determine aerial cover, and species composition, richness and diversity during the summer growing season of January and February 2013. The study site portrays strong fine-scale botanical micro-zonation owing to ground level microclimatic differentiation as a consequence of topographic (i.e rock scarp) shading and snow capture. Temperatures were >5 °C warmer in the upper zone from July – September 2012 due to the deep (1 m) snow cover which lasted for two months longer than in the middle zone, and only lasted for 36 hours in the lower zone. Accordingly, the upper zone had the lowest solar radiation throughout the data collection period due to the continuous snow cover and shading from the rock scarp. Three botanical zones were identified as characterised by different *Helichrysum* species. The upper zone (21 species) was more species rich than the the middle (19) and lower (18) zones. The vegetation is dominated by grasses which cover >35% of the study site, whilst herbs and shrubs cover only ca. 6% with an average of 12.3% bare ground. The strong zonation in plant species composition is a response to the fine spatial-scale changes in the environment, resulting from snow cover acting in ameliorating the harsh

alpine conditions in winter. More detailed research on a larger scale is still required to fully comprehend phenology and morphology of the plants at the study region.

Dedication

I would like to dedicate this thesis to my brother Ntandazo Cingo who has always believed in me, he unfortunately passed on before I could accomplish this milestone. This work is also dedicated to my entire family particularly my parents Thokozile Florencia Cingo and Mzikayise Tyeloncedo Cingo.

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1.1.1 What are alpine regions?

Alpine regions are ecosystems at or above the tree-line ecotone, commonly characterised by the absence of trees near and at the summit of high mountains (Figure1.1; Beniston, 2003). Although alpine regions occur on mountains, they are not defined by elevation as they occur at different altitudes in various regions of the world (Bliss, 1971; Carbutt & Edwards, 2001; Dirnböck *et al*., 2003; Körner & Paulsen, 2004). However, they tend to be above 3000 m for example in the European Alps they are above 3.300 m, while in the Australian Alps at Razorback Mountain and in the west of Indian Himalayas it can be as low as 1710 m, and in the east of the Indian Himalayas the alpine region is at 3800 m (Kala & Ratajc, 2012; Körner, 2007; Wahren, 2001).

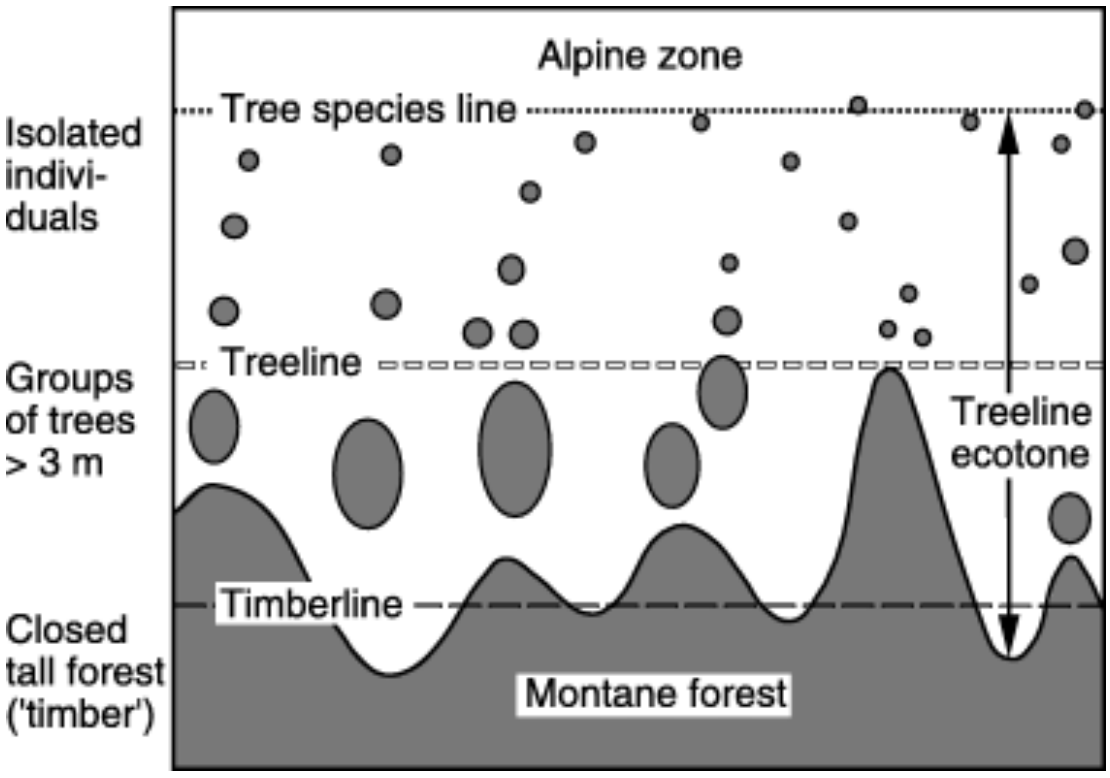

Figure 1.1 Schematic representation of the high altitude treeline ecotone: Timberline, Treeline, Tree species line and Alpine zone. Source: Korner & Pausen 2004, Figure 1.

For an area to be recognised as alpine, there are several factors to be considered, such as climatic conditions (temperature, solar radiation, precipitation in the form of rainfall, snow and wind) and edaphic factors including soil type and nutrient availability (Carbutt & Edwards, 2001). Climatic conditions and edaphic factors determine which plants survive at high altitudes, as temperatures tend to be at extremes and there are frequent frost occurrences in areas that are not covered by snow during winter. In addition, snow bank areas have deep snow cover which reduces sunlight penetration for several months; most plants therefore do not survive in these conditions (Marloth 1900; Nautiyal, 2001). Alpine regions house species that are often only found in constrained environments, and are thus restricted to mountain summits (Spehn & Körner, 2005).

This study was conducted in Lesotho, which forms part of the Drakensberg Alpine Centre (DAC). The DAC is recognised as a centre of diversity and endemism and has been identified as one of the biodiversity hot spots in southern Africa (Cowling & Hilton-Taylor 1977; Van Wyk & Smith 2001; Carbutt & Edwards, 2003; Carbutt & Edwards, 2006). The term "alpine" was given to the summit vegetation of the Drakensberg (2 865 – 3 353 m.a.s.l.), which extends from the Eastern Cape to KwaZulu-Natal and into the Lesotho highlands (Figure 1.2) (Marloth 1900; Killick 1963; Edwards 1967; Acocks 1988; Carbutt & Edwards 2001). Alpine regions act as reservoirs of species, and have frequently served as refugia for organisms during periods of climate change and provided subsequent sources for speciation (Comes & Kadereit 2003; Schönswetter *et al*. 2005; Holderegger & Thiel-Egenter 2009; Wesener *et al*. 2011). The Drakensberg is thought to have served as a refugium for Cape elements during periods of climate change (Carbutt & Edwards 2004). It has frequently also served as a 'stepping stone' for species migrating from the Cape Fold Mountains northwards (Galley & Linder, 2006) and also southwards from the tropical mountains of the afromontane archipelago of Africa (White, 1981).

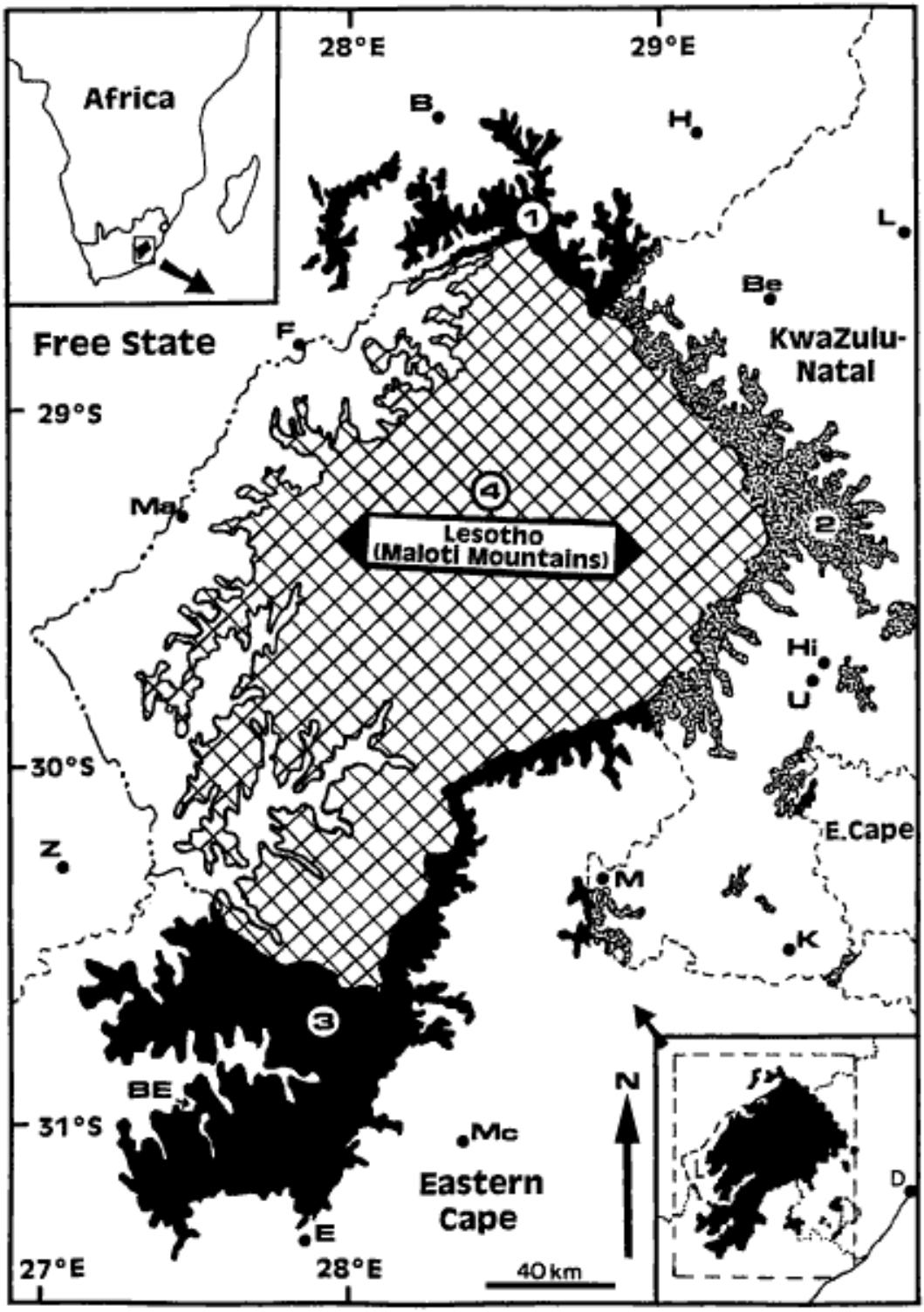

Figure 1.2 Drakensberg Alpine Region (DAR) comprising (1) Eastern Free State, (2) KwaZulu-Natal Drakensberg, (3) Eastern Cape Drakensberg and Witterberg and (4) Lesotho, Source: Cartbutt & Edwards (2001), Figure 3.

1.2 The Drakensberg Alpine Centre – altitudinal zones and geology

1.2.1 Altitudinal zones

In the central (Cathedral Peak) region of the DAC, Killick (1963) identified and described three vegetational belts corresponding to, namely: a montane zone from 1280 to 1829 m.a.s.l., a subalpine zone from 1829 – 2865 m.a.s.l. and alpine zones from 2865 to 3353 m. a. s. l. (Figure 1.3), these vegetation belts have now been more wildly recognized (Theurillat & Guisan 2001; Despland *et al*., 2012). Each altitudinal zone or 'vegetation belt' is characterised by a distinct vegetation: *Protea* savannas characterise the north-facing slopes of the montane zone, while afromontane forest may be found on south-facing slopes, and in sheltered gorges. In the Drakensberg Alpine Centre (DAC) of southern Africa, the alpine zone is generally recognised as above 2800 m (Figure 1.3). The sub-alpine zone is characterised fynbos and *Themeda-Festuca* grassland, while the alpine zone is characterised by *Erica* and *Helichrysum* species (Figure 1.3).

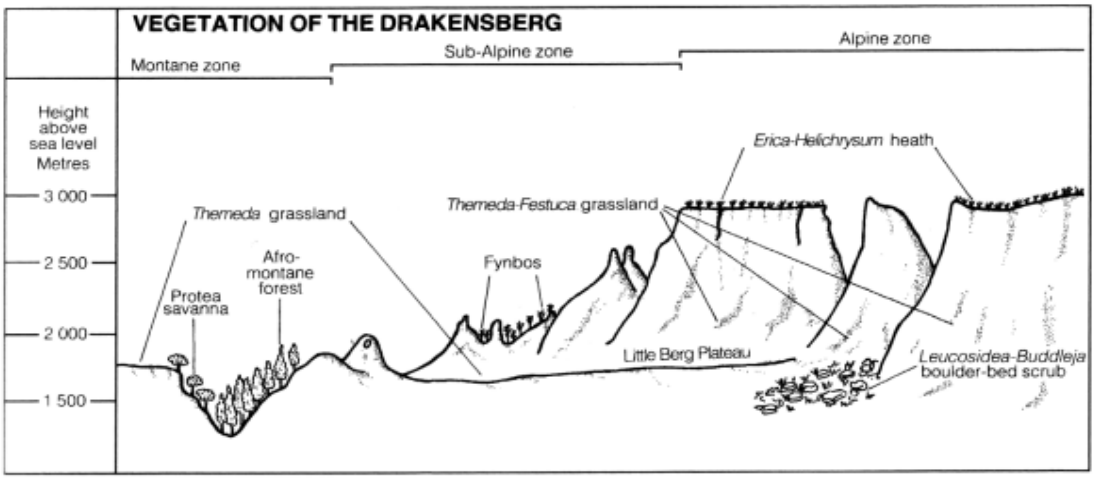

Figure 1.3 Vegetation belts of the Drakensberg with their chief plant communities at different elevations, Source: **http://www.uib.no/org/EECRG**

1.2.2 Geology

Five rock layers characterize the geology of the Drakensberg: Upper Beaufort rocks, Molteno Beds (Molteno Formation) at the base, followed by the Red beds of the Elliot Formation, then the Cave Sandstone of the Clarens Formation and uppermost, the basalt (Drakensberg Formation) (Figure 1.4). Soil covering the Clarens Formation (Stormberg Group, Karoo Supergroup) is fairly shallow and is in the form of

decomposing layers (Mucina *et al*. 2006). The alpine region consists mostly of basaltic lava, which welled up during past volcanic activity, resulting from the breakup of Gondwana between 187 and 155 Ma, and is therefore characterised by black soil (Haskins & Bell, 1995; Moore & Blenkinsop, 2006; Mucina *et al*. 2006).

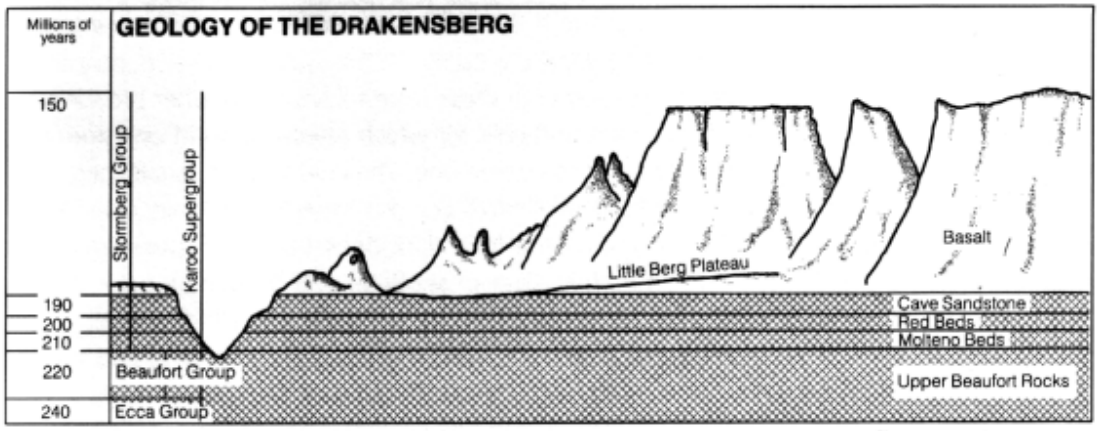

Figure 1.4 Geology of the Drakensberg with five rock layers and Veers in which they developed (Pickles 1985).

Basaltic salts of the Basalt formation consist of lava flows of 1400 m thickness; these salts contain minerals, which have contributed to the formation of clay, chlorite and zeolites (Haskins & Bell, 1995; Moore & Blenkinsop, 2006). Basalt soils are generally coarse grained, but also contain silt, clay and organic components. In some areas basalt soils have high organic matter content from decaying grass roots, and therefore play a significant role in retaining high water capacity of the soil at mountain summits (Mucina *et al*. 2006).

1.3 Environmental variables in alpine regions

1.3.1 Snow in the alpine regions and climate change implications

Snow depth and longevity are directly affected by climate change, as the increase in temperatures decreases snow depth, subsequently shortening snow longevity (Inouye, 2008). Future projections suggest that snowfall days and continuous snow cover may decline in the future as a result of increase in temperatures (Baptist *et al*., 2009; Rammig *et al*., 2010). Decrease in snow cover will expose species that are currently buffered by

the snow against extreme temperatures during winter and result in increased risk of frost damage and desiccation (Bannister *et al*., 2005). Snow persistence also directly influences soil moisture, air and soil temperature, frost, solar radiation, exposure to wind and available soil nutrients (Wahren, 2001; Spehn & Körner, 2005; Jonas *et al*., 2008).

Snow distribution is usually uneven in alpine environments as a result of the prevailing wind direction(s) and topography, e.g., rocks, depressions, mountain spurs or hillsides all influence the distribution of snow (Ferrari, 1995; Scott *et al*., 1993; Wahren, 2001). Snow blows from windward slopes onto less exposed slopes where it persists in sheltered slopes for several months during winter into spring late September/ October; (Oberbauer & Billings, 1981; Scott *et al*., 1993; Wahren, 2001).

Snow provides water continuously to the snow bed area for several months; as a result plants occurring in the heavy snow bed remain in moist soil for most of the year (Kudo, 1991; Kudo & Ito 1992; Wahren, 2001; Körner, 2007; Hacker *et al*., 2011). Mountains are an important source of water, globally contributing over 50% of water to rivers. Water is stored in the form of ice or snow for months to decades, however increase in temperatures has resulted in snow and ice melting more rapidly (Beniston, 2003; Sicart et al., 2008). The mountain hydrological cycle has been enhanced as a result of rising temperatures, and some regions with decreased snowfall will receive precipitation in the form of rainfall (Beniston, 2003). In addition to increased temperature, higher solar radiation and longer melting periods have been reported to be contributing to the melting of glaciers (Huss *et al*., 2009). The decline in snow cover has negative impacts on water supply and thus on global economies, for example, the Australian economy, where 30% of its water is from the Snowy Mountains (Sánchez-Bayo & Green, 2013). The snowline is increasing in altitude and glaciers are retreating in many mountain regions as a result of climate change, e.g. the European Alps have lost about 30 – 40% of their snowed surface area and volume, the Southern Alps of New Zealand have lost 25% in the last 100 years, and Mt. Kenya and Mt. Kilimanjaro have lost over 60% in the last century (Beniston, 2003).

The timing of snowfall, snowmelt and depth of the snow plays a significant role in the existence of plants by determining their growing season, for example, late snowmelt results in a late and short growing season (Kudo, 1991; Kudo & Ito, 1992;

Walsh & Butler, 1994; Totland & Alatalo, 2002; Inouye, 2008; Baptist *et al.,* 2009; Sánchez-Bayo & Green, 2013). Plants remain dormant in winter when covered by snow and resume growth after the snowmelt. This has negative effects on flowering, seed production and dispersal due to the short time available before the next snowfall (Kudo, 1991; Walsh & Butler, 1994). Plants covered by shallow snow complete their growing cycle earlier as they emerge and mature earlier; while plants in the deep snow habitats have only a short period to complete their growth cycle, as a result not all plants complete their vegetation annual growth every year (Billings & Bliss, 1959).

Snow also directly affects soil temperatures, particularly in winter as it insulates the soil and moderates temperatures at ± 0 °C. Soils are subjected to freeze-thaw cycles when there is less snow cover, as there is no insulation from the snow, and temperatures fall well below 0 °C, especially at night (Freppaz *et al*., 2007). This has implications for plant growth and species' persistence.

Habitat micro-zonation in the alpine regions has been observed as a result of snow depth and melt-rate (Billings & Bliss, 1959). In the Australian mountains, plants on the north-western slopes emerge earlier and have a longer vegetation growth cycle compared to those in deep snow banks on southeast slopes, which have a short vegetation cycle. Due to these differences in the vegetation cycles, the habitats tend to be different depending on the depth and longevity of the snow cover period (Billings & Bliss, 1959; Totland & Alatalo, 2002; Bannister *et al.,* 2005; Rammig *et al*., 2010; Camac *et al*., 2013). Nonetheless, areas with late snowmelt tend to have higher vegetation cover with higher species richness as they are cushioned by the snow cover from extreme weather conditions such as harsh winds, frost, and extremely low temperatures, and consequently have higher minimum temperatures compared to snow-free areas (Totland & Alatalo, 2002).

1.4 Alpine vegetation

1.4.1 Species diversity & composition

As noted previously, summit vegetation in the DAC is classified as 'alpine' at >2800 m.a.s.l. (Figure 1.2; Killick 1978, 1994; van Wyk & Smith 2001). Alpine

vegetation consists of climax heath (mainly species in the genus *Helichrysum*), dwarf shrubs, wetland plants, and tussock grasses (Killick, 1994; Ferrari & Rossi 1995). The summit vegetation is thus dominated by four life forms: dwarf shrubs, grasses and sedges forming dense clumps, rosette plants with leaves usually attached to the ground, and cushion plants (Körner, 2007). These growth forms are a result of adaptation to severe temperatures, as the leaves of these plants and their compact form tend to trap solar heat and can withstand strong solar radiation (Kudo & Ito, 1992; Körner, 2007). Some alpine plants are restricted to the semi-permanent snow patches; this could have negative implications for these plants with increases in temperature due to on going climate change (Green & Pickering, 2009). Alpine vegetation distribution is also subject to edaphic factors such as soil nutrients, soil acidity, pH, and soil moisture (Kudo & Ito 1992).

Plants growing in alpine regions often exhibit xeromorphic features that enable their survival in extreme temperatures (i.e. well below freezing), prolonged frost periods that may last up to six months, and extreme windy conditions that result in desiccation (Kimball & Salisbury, 1974; Rutherford & Westfall 1986; Scott *et al*., 1993). Most alpine plants are evergreen and some have grey woolly leaves (van Wyk and Smith 2001) due to a thick covering of long trichomes. Plants growing in the alpine snow beds, particularly cushion plants, are protected from desiccation, frost and wind (Kudo, 1991; Körner, 2007). Alpine plants are predominantly herbaceous and able to tolerate the short growing season. The alpine regions contain relatively few plant species due to species richness declining with elevation (Bliss, 1971; Wahren, 2001; Körner, 2007). Important families in the alpine regions include the Asteraceae (the daisy family) and Poaceae (grasses; Körner, 2007).

Episodic frost events can damage plant tissue, particularly during the growing season and when plant parts are not fully developed and therefore not yet frost resistant; these events can be expected in the changing unpredictable alpine climate (Hacker *et al*., 2011; Martin *et al*., 2010). Alpine plant species survive summer frost by preventing the formation of ice nucleation; only mature leaves can tolerate freezing while growing plant parts are unable to survive as plant tissue is damaged. Alpine plants are the most adapted to freezing due to their compact growth form (Martin *et al*., 2010; Haker *et al*., 2011).

1.4.2 Species shift to higher altitudes

As temperatures increase in alpine areas due to global climate change, species have responded by shifting to higher altitudes, and therefore the tree line has consequently also expanded to higher altitudes (Bannister *et al*., 2005; Rammig *et al*., 2010; Spehn & Körner, 2005; Wilson *et al*., 2005). Increase in temperature is already affecting ecosystems in the alpine regions, e.g. in the European Alps where some plants' physiology, phenology and distribution have been directly affected by climate change (Moen & Lagerström, 2008; Thuiller *et al*., 2005). Alpine plant species can either respond to increased temperatures by adapting to the changes in the environmental variables by changing their morphology and physiology, or by migration to higher altitudes or other micro-habitats where conditions are more favourable for these species (Cannone *et al*., 2007; Parolo & Rossi, 2008). Species that are already at their environmental limit (i.e. only survive at high altitudes) could be extremely restricted and may therefore be at risk of local extinction, as habitats suitable for alpine species are restricted and fragmented (Grabherr *et al*., 1995; Pauli *et al*., 1996; Bannister *et al*., 2005; Thuiller *et al*., 2008). Investigating the identity of alpine plants, morphology and their physiology may therefore provide valuable information on their likely extinction and inform conservation strategies, as well as elucidate strategies for species' survival at high altitudes – i.e. needed for altitudinal succession. Species with low dispersal abilities may be at the greatest risk of extinction as the rate of warming is threatening to "outpace" migration capabilities of some species (Thuiller *et al*., 2008). The dispersal mode of a species (e.g. wind, animal, gravity) as well as the weight and size of the seed or fruit (dispersal unit) will influence distance and rate of dispersal (Givnish, 2010).

There is evidence from palaeo-ecological studies and from several observations of species shift to higher altitudes as a response to climate change in the European Alps (Thuiller *et al*., 2008). Increases in vegetation cover are also evident in the European Alps as a result of species shift from lower altitudinal belts at an average of 6.1 m per decade (Cannone *et al*., 2007; Moen & Lagerström, 2008; Thuiller *et al*., 2008). Furthermore, changes in vegetation pattern in the European Alps were observed over a period of 63 years with an increase in species richness, turnover and change from fragmented vegetation to continuous vegetation cover (Cannone *et al*., 2007; Moen &

Lagerström, 2008; Pauli *et al*., 1996). A study conducted on 66 of Europe's mountain summits found that the average number of species on a summit increased by 8% from 34.9 to 37.7 between 2001 and 2008 (Gottfried *et al*., 2012). An increase in population density and species richness has been observed in the Alps above 3000 m during the past 100 years and 28 species have migrated to higher altitudes in the central Alps (Thuiller *et al*., 2005; Parolo & Rossi, 2008; Grabherr, 2009).

To date, no studies have been done on the effect of snow cover on plant species richness, phenology and environmental variables such as temperature, solar radiation, soil moisture in relation to plants in the DAC and the implications of global climate change and decreasing snow cover for the region are therefore not known. This study therefore aims to investigate alpine plant species composition and diversity (amongst other aspects) in a seasonally snow-covered region of the DAC and a study site was selected where winter snow packs up against a rock scarp and persists on the south-facing slope below it. This study site was chosen because of the steep south-facing slope adjacent to a rock-scarp, which collects snow for several months. Due to the steep slope, the vegetation along the slope varies creating micro-zones— some plant species only occur in the upper zone (a few metres from the rock scarp) and are covered by snow for several months in winter; compared to the lower zones that are not under snow for prolonged periods. The plant species composition therefore varies along the slope and the plants experience different environmental factors such as temperature, solar radiation, soil moisture and humidity, accordingly. This study explores the differences in the environmental factors affecting the plants along this slope as well as changes in species composition. There was a visible difference in vegetation along the 30 metre slope, and therefore the slope was divided into three zones namely; upper, middle and lower zones.

1.5 Study site

This study was undertaken in the Drakensberg Alpine Centre in Lesotho near Kotisephola Mountain, also known as 'Black Mountain' (Figure 1.6), located at 29° 30.863 S; 29° 13.145 E at 3325 m.a.s.l. (Figure 1.5). The study site therefore is within the alpine belt, which extends from 2740 to 3480 m a.s.l. in the Sani Pass area (Killick 1978), with the highest peak in southern Africa, Thabana Ntlenyana at 3482 m a.s.l. about 8 km

from the study site. The site is on the south-facing aspect of a rock scarp along a ridge running east to west, the summit of which lies at 3325 m.a.s.l. The rock scarp provides long-lasting shade to the south-east facing slope below it and snow accumulates against it at a height exceeding 1 m above ground and lasts for several months during winter near its base. The snow, in turn, provides continuous moisture during spring for the uppermost part of the study site (Figure 1.5A). The ridge selected was one of several in the region where snow accumulated on the protected south-facing slopes, however snow appeared to be more persistent below this ridge, which was one of the longest in the surrounding area.

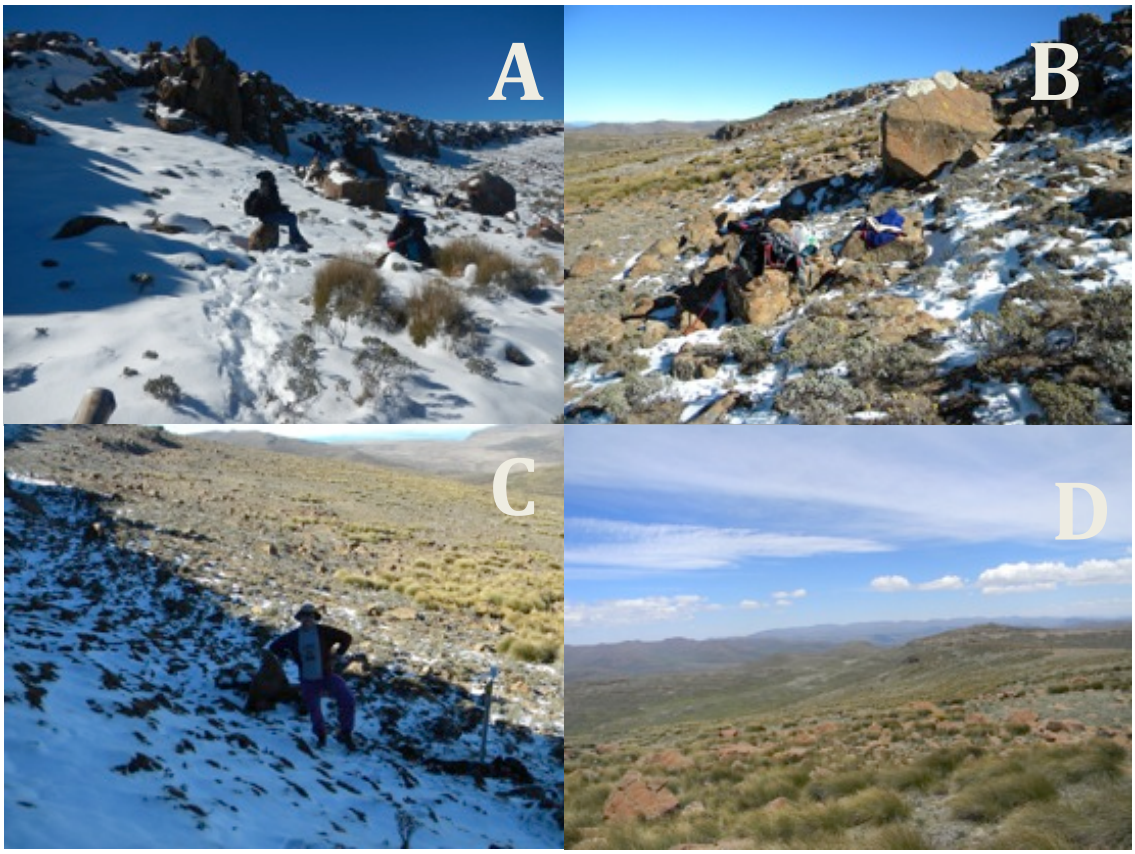

Figure 1.5 Study site landscape: A) Part of the rock scarp with the slope below it covered in snow; B) Rocks scattered on the surface of the study site with *Helichrysum* shrublets; C) Snow and shade at the behind the rock scarp; D) The tussock grass, *Merxmuellera drakensbergensis,* dominates the landscape towards the base of the slope and beyond.

Micro-zonation of the vegetation was evident down the slope below the rock scarp and so the study site was divided accordingly into three zones (Figure 1.7): (1) an upper zone adjacent to the rock scarp with the most shade, deep winter snow packs and

dominated by *Helichrysum witbergense*, which is restricted to this zone, (2) a middle zone, a transition zone between the upper and the lower zones with increasing sunlight and less persistent winter snow cover with the dominant species of *H. trilineatum,* and (3) a lower zone with short-term winter snow cover and exposed to sunlight for a longer time period dominated by *Helichrysum praecurrens, Dracoscirpoides falsa* and *H. albo-brunneum* (Figure 1.6). Beyond this lower zone, the slope vegetation was predominantly the tall tussock grass *Merxmuellera drakensbergensis*, where snow did not persist for long and diversity appeared to be very low. Snow also did not persist on the north-facing slopes of the ridges, which were much warmer and drier and appeared much less diverse than the southern slopes.

Figure 1.6 The study site: near Kotisephola Mountain Pass in the Lesotho highlands of the Drakensberg near Sani Pass

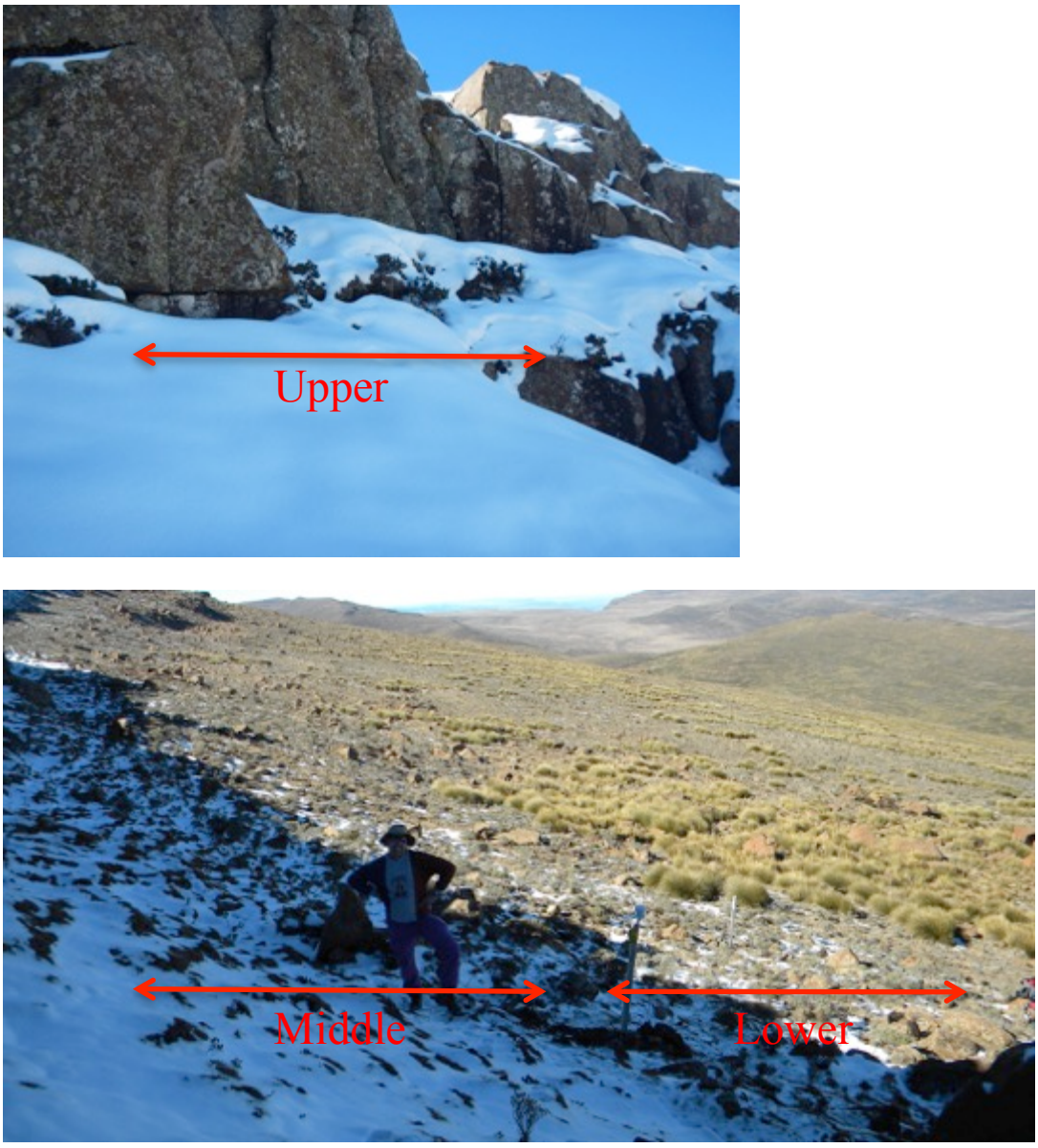

Figure 1.7 Study site with three zones namely: Upper, Middle and Lower zones created by the snow banks and shade from the rock scarp characterised by different dominant plant species.

1.6 Aims and Objectives

The aims of this study were to investigate the plant species composition and diversity (alpha and beta) in a seasonally snow-covered area along a south-facing slope at the base of a rock scarp on a high altitude ridge in the DAC. The study investigates and compares

the habitats, morphology and ecophysiology of selected alpine plant species in the cline adjacent to the rock scarp observed at the selected study site.

The objectives associated with these aims are as follows:

1. To determine the composition and diversity of plant species present in the winter snow patches in a preselected site in the Drakensberg alpine region, and the percentage surface covering (litter, gravel, rock, vegetation, and snow).
    a. *What is the plant species composition at the selected site?*
    b. *What is the alpha and beta diversity in the selected site? i.e. How does it compare across the gradient below the rock scarp?*
    c. *Does the percentage surface covering differ across the cline in the observed zones?*
    d. *Is there any correlation between species turnover and environmental variables?*
2. To study the microhabitats created by the snow against the scarp face in terms of (a) temperature, (b) soil moisture content, (c) solar radiation, (d) snow depth, (e) soil and substrate features, and (f) soil nutrients.
    a. *Is there any correlation between the microhabitats and the occurrence of specific plants?*
    b. *How do the microhabitats compare across the zones?*
    c. *Is the observed zonation in the vegetation created by the microhabitats?*
3. To determine the modes of plant persistence under the winter snow using the Raunkiaer system.
    a. *Are the plants predominantly geophytes (terrestrial cryptophytes: with underground storage organs, e.g. bulbs), hemicryptophytes (graminoids), chamaephytes (buds above the ground (up to 25 cm) – cushion plants), or therophytes (annuals that only survive the unfavourable season in the form of seeds)?*
4. To study and characterise the morphology and phenology (flowering period) of four selected plant species that persist within the winter snow patches.
    a. *How do morphological features of the selected plants differ across the zones?*

b. *What are the morphological features that enable the selected plant species to grow in the alpine zone and under the snow patches?*

5. To explore in discussion, the implications of climate change on the biodiversity of the alpine region of the DAC, taking into consideration that this is a very localised study of a seasonally snow-covered slope.

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CHAPTER 2 – Environmental impacts of snow cover on a high altitude south facing slope in the Drakensberg Alpine Centre (DAC)

Abstract

Snow cover is one of the most important factors controlling ground level microclimate and alpine plant growth. Snow depth and longevity have significant impacts on environmental factors such as solar radiation, air and soil temperature, soil moisture, soil texture and soil nutrients. This study was undertaken on a south facing slope near Kotisephola Pass at ca. 3300 m.a.s.l. in eastern Lesotho. The environmental variables of temperature, soil moisture, solar radiation and snow depth were measured over a period of 17 months (May 2012 – September 2013) using i-Buttons, Hobo and Tinytag data loggers, probes, solar radiation and temperature data loggers. Soil samples were collected and various physical and chemical parameters determined. Three zones were studied: the upper, middle and lower zones, each zone was 10 m long extending from the rock scarp, and characterised by different vegetation composition. Air temperatures at 20 cm above ground were >5 °C warmer in the upper zone during winter months (July – September 2012) due to the deep (1 m or more) snow cover which lasted for two months longer than in the middle zone, whereas in the lower zone snow cover only exceeded 15 cm depth above ground for 36 hours and 20 cm depth for 33 hours. Accordingly, the upper zone had the lowest solar radiation throughout the data collection period due to the continuous snow cover and shading from the rock scarp. The lower zone had the highest soil nutrients, most likely due to nutrients leaching downslope with snowmelt and rainfall. The years 2012 and 2013 had very different snow cover (depth and longevity) as the year 2012 had several snowfall occurences with snow patches lasting from weeks to months while 2013 had several light snowfalls with snow patches melting within a few days. Snow distribution across the zones controls the microclimate of the zones which in turn controls the biodiversity ocurring in these zones. Snow distribution and longevity plays an important role in habitat structure. Snow occurrence is one of the environmental factors that is negatively influenced by climate change as increased temperatures reduce snowfall events and increase snowmelt rate.

2.1 Introduction

2.1.1 Snow in Alpine environments

Snow distribution is usually uneven in alpine environments as a result of wind and topography — i.e., rocks, depressions or shrubs, mountain spurs or hillsides (Wahren *et al.,* 2001). In the southern hemisphere, particularly in the Australian Alps, snow persists on sheltered southeast-facing slopes for several months in winter until spring (September/ October); snow is also blown from windward slopes onto less exposed slopes (Oberbauer & Billings, 1981; Wahren *et al.,* 2001). Areas with late snowmelt are usually areas with less sun on southerly exposed slopes in the southern hemisphere - i.e. in the Drakensberg Mountains (Mulder & Grab 2009). The slopes with less snow are predominantly northwest facing slopes in the European Alps; they have higher solar radiation as they receive sunlight for longer hours of the day (Huss *et al.,* 2009). Plants on the north-western slopes in the Medicine Snowy Mountains, United States, emerge earlier and have a longer vegetation cycle compared to plants in deep snow banks, which have a shorter growth cycle (Billings & Bliss, 1959). In addition, species that occur on windward slopes are exposed to extreme temperatures and solar radiation (Bannister *et al.,* 2005; Billings & Bliss, 1959; Rammig *et al*., 2010; Totland & Alatalo, 2002; Wahren *et al,*. 2001).

The timing of snowfall, snowmelt and snow depth plays a significant role in the persistence of plants by determining their growing season, composition and phenology, for example, late snowmelt results in a later and shorter growing season (Kudo & Ito, 1992; Inouye, 2008). Snowfalls in the Drakensberg occur on average eight times per annum from May to September, with the highest snow cover between June and August (Mulder & Grab 2009). Areas with late snowmelt tend to have higher vegetation cover with greater species richness as they are cushioned by snow from extreme weather conditions such as harsh winds, frost, and extremely low temperatures, and consequently have higher minimum temperatures compared to snow-free areas in winter (Totland & Alatalo, 2002).

Snow persistence directly influences soil temperature, soil moisture, air temperature, frost occurrence and intensity, solar radiation, exposure to wind and soil nutrients (Wahren, 2001; Spehn & Körner, 2005; Jonas *et al.,* 2008). Snow cover provides

insulation to the soil, keeping soil temperatures between –2 °C and 0 °C, depending on snow depth, while early snowmelt may expose soil to extremely low temperatures at night and higher temperatures during the day more likely leading to soil freezing (Freppaz *et al*., 2007; Baptist *et al*. 2009). Areas with persisting snow cover have relatively higher soil moisture compared to slopes with no snow cover, depending on the local precipitation regime, as they continuously receive water from the melting snow cover and insulation from strong winds. Long-term snow cover directly influences the release of nitrogen and the decomposition of organic matter from the grasses and leaves from the dwarf shrublets, as it controls the length of the growing season and decomposition depends on the growing season. Nitrogen release depends on decomposition and mineralisation, which in turn depends on the growing cycle as decomposition occurs after snowmelt when plants are shedding old leaves (Baptist *et al*., 2009). Nitrogen release from snow occurs during snowmelt, and reduced snow cover has a weak effect on decomposition, thus late snow covered areas have higher litter cover than early snowmelt areas, resulting in a large impact on nutrient cycling over a long period of time (Hiltbrunner *et al*., 2005; Baptist et al., 2009; Martinsen *et al*., 2012).

Micro-zonation of species and communities in alpine regions has been observed as a result of uneven distribution of snow (Billings & Bliss 1959; Keller *et al*., 2005; Kudo *et al*., 2010). The micro-zonation results from differences in snow cover over a gradient; some habitats are cushioned by snow from extreme temperatures, whereas adjacent habitats on windward slopes have little to no snow cover (Keller *et al*., 2005). The differences in snow cover in these microhabitats affects plant diversity, as some plant species survive under snow while others survive in habitats with no snow. Similarly, some plant species have a high frost tolerance and therefore can survive extremely cold temperatures not covered by the snow, while other species have a low frost tolerance and therefore need to be 'cushioned' by snow during winter (Keller *et al*., 2005).

In addition to the effects of the presence or lack of snow on air temperature, there are differences in soil temperature between those habitats covered by snow versus those with no snow cover. Included are differences in water retention, as some habitats covered by snow have higher soil moisture content given that water is retained in the form of snow and is released slowly during snowmelt, however, this depends on the amount of snow

accumulation. Other habitats covered by snow are deprived of soil moisture as water from snowmelt is lost downslope (Billings & Bliss, 1959). The soil on the windward slopes is usually frozen during winter, whereas the snow covered slopes have soil temperatures ranging between −1 and +1 °C. Thus, the vegetation in the snow covered and uncovered areas is different (Billings & Bliss, 1959; Keller *et al*., 2005).

The study site is near Kotisephola Mountain Pass in the DAC, Lesotho, where there is clear micro-zonation down a slope created by a south facing rock scarp face, against which snow builds up during winter, in some years lasting for several months. The snow gradually thins down the slope, resulting in temperatures varying significantly between the zone adjacent to the rock scarp and the zone further away from the scarp. This then affects the plants growing in this area, as some plants may only be able to survive under prolonged snow, whilst others have adapted to extremely cold temperatures.

2.1.2 Aims and Objectives

The aims and objectives of this study are to investigate the microhabitats created by the varying depths and persistence of snow against the south facing rock scarp face and further down slope away from the scarp face in terms of (a) temperature, (b) soil moisture content, (c) solar radiation, (d) snow depth, (e) soil and substrate features, and (f) soil nutrients. The following questions are addressed:

a. *How does snow depth and persistence influence the environmental parameters on a south-facing slope in this alpine habitat of the DAC?*
b. *How do the microhabitats compare across the zones?*

2.1.3 Methods and Materials

Data were recorded for several environmental variables to assess their influence on the vegetation variation across the three micro-zones recognised (viz. upper, middle and lower) below the rock scarp at the study site near Kotisephola Pass in Lesotho, and located within the DAC. The variables measured included: air and soil temperature, humidity, solar radiation, soil moisture, soil texture and nutrients, snow depth and longevity. These variables were measured across all three zones and compared between the zones. Temperatures (in °C) were recorded hourly for ten months (May – September)

in 2012 and 2013 using iButtons and Tinytag data loggers. However, temperatures in the upper zone were measured for one month longer (i.e. including October) in 2012 due to the presence of snow to a depth of over 1 m until early October, resulting in the data loggers not being retrievable at an earlier date. Monthly absolute minimum and mean temperatures were derived from the hourly means.

Three iButtons were attached to a wooden rod inserted into the ground adjacent to selected study plant species and four iButtons were attached on the plant species (*Helichrysum trilineatum* and *H. witbergense*) at 5, 10 and 20 cm above ground, and within the plants' canopy.

Six Maxim iButton temperature loggers were attached to the south side of the rock scarp to measure air temperature and humidity on the rock wall (at heights of 5, 10, 20, 40, 60, 80 and 100 cm from the ground), and two were placed under the mat-forming dwarf shrublet *Helichrysum milfordiae* against the scarp wall for 16 months to measure temperature difference between the rock surface covered by the plant and the exposed rock surface.

Snow depth and longevity were inferred from temperature recordings by the Tinytag data loggers from all three zones, which were measured from 2 – 100 cm above ground from May – October of 2012 and 2013. Snow presence was indicated by temperatures ranging between –1 °C and 1 °C. Little or no variation in temperature may also indicate snow presence when temperatures remain at ± 0 °C for several hours or longer.

Soil moisture was measured over 16 months from May 2012 to September 2013, using 10HS soil moisture smart sensor-S-SMD-M005 with the H21-002 HOBO micro station inserted into the ground in all three zones at three depths below ground level, viz. 5 cm, 10 cm and 20 cm. The probes were set up to record at an hourly interval. Air temperature ($\pm$1.5 m above ground) was also measured using a Tinytag temperature data logger that was protected by a ventilated plastic radiation shield. Soil temperature was also measured at 5 cm below ground in all three zones for 16 months from May 2012 to September 2013. The data loggers were wrapped with insulating tape for protection against water damage and hidden under rocks as a precaution against theft from local shepherds.

Solar radiation was measured hourly for 12 months using radiation sensors inserted in the ground in the three zones; the radiation sensor in the upper zone was adjacent to the rock scarp and was therefore under snow during winter and also in shade for most of the day, whilst in the middle and lower zones the radiation sensors were relatively unshaded and received maximum daily sunlight. The sensors were set up to record data hourly.

Nine soil samples (three from each zone) were collected from each of the three zones at c. 0–15 cm depth. The soil samples were sent to The Soil Fertility and Analytical Services Section of the KwaZulu-Natal Department of Agriculture and Environmental Affairs at Cedara for analysis of total C (%), total N (%), pH (KCl), sample density (g/ml), total cations (cmol/L), available P (mg/l), exchangeable K (mg/l), exchangeable Ca (mg/l), total Zn (mg/l), total Mn (mg/l), total Cu (mg/l), exchangeable acidity (cmolc/l) and soil texture.

2.1.4 Statistical analyses

All data from 2012 and 2013 were compared and tested for significant differences between the two years using Graph Pad Prism 6. In addition, significance of differences was tested across the three zones within each year for the period of measurement. Significant differences of snow, soil moisture and temperatures were also tested within the zones at different depths and heights using one-way ANOVAs. A paired t-test was used to compare soil moisture at 5 and 10 cm depths below ground over 17 months. An unpaired t-test was used to compare soil moisture between 2012 and 2013 at both 5 and 10 cm below ground. All the soil characteristics were compared statistically between the three zones using one-way ANOVAs. Fisher's Least Significant Difference (LSD) test was used to highlight significant variations across the zones; LSD was used due to the low replication of samples. Fine silt, coarse and fine silt, clay, carbon and nitrogen were arcsine transformed prior to analyses. Pivot Table in an Excel spreadsheet was used for sorting the data into years, months, weeks, days and hours and most graphs were done on the Pivot Table. Pearson's correlations were determined between P, K, Zn, Mn, Ca and N; these nutrients were chosen because they were significantly different across the zones.

2.2 Results

2.2.1 Snow depth

Snow occurrence, depth and longevity differed over the two years of study, with considerable snow falling at and drifting into the upper zone of the slope and persisting over the winter and spring months of 2012 compared to 2013, when there was minimal snow. The first snowfall occurred in May of both years, however, by the end of June 2012 snow depth was 50 cm above ground whereas in June 2013, the snow had melted from all three zones (Figure 2.1). Snow depth and longevity were inferred from temperature records measured over five winter months (May – October) in 2012. The upper zone during this period had significantly higher snow depth of >1 m (Figures 2.4 & 2.5) compared to the middle and lower zones with $\leq$ 0.2 m ($F_{2, 13701} = 16.01$, $P < 0.0001$) (Figures 2.2 & 2.3). Snow lasted for four months in the upper zone whereas it ablated within four weeks in the middle zone and ablated within 3 days in the lower zone. Snow started melting in the upper zone over the period 17 – 25 October 2012 when it rapidly decreased from 100 to 50 cm (Figures 2.3, 2.4 & 2.5). Ground temperature records in the lower zone did not indicate presence of snow cover from May to mid-July and from late July to October 2012 (Figure 2.1).

Snow also ablated (vaporised, melted and eroded due to wind) from the scarp wall (Figure 2.2); this may be due to heating from heat storage of the wall, but could also be due to abrasive action of air flow as the wall offers a barrier to air flow. Snow melted gradually from 100 to 50 cm in eight days (17 – 24 October 2012); as soon as the snow reached a depth of 50 cm, all the loggers in the upper zone were exposed as a result of the snow ablating from the rock scarp (Figure 2.3). The melting ablation of the snow away from the rock scarp explains the sudden temperature variation in the upper zone after the snow melted to 50 cm and then 10 cm above ground and/or below that height (Figure 2.2 & 2.3). Some parts of the upper zone very likely remained under snow after the date the loggers indicated as the last day of snowmelt, which means there is no record of the date the snow melted completely from the upper zone in 2012.

Figure 2.1 Daily minimum air temperatures in the upper zone at 20, 50 and 100 cm height above ground in 2012 and 2013 during the winter and spring months (May – November and May – September respectively). Interpreting these results shows continuous snow cover from 24 June to 16 October in 2012 but not in 2013 when snow cover was probably only for short, intermittent periods.

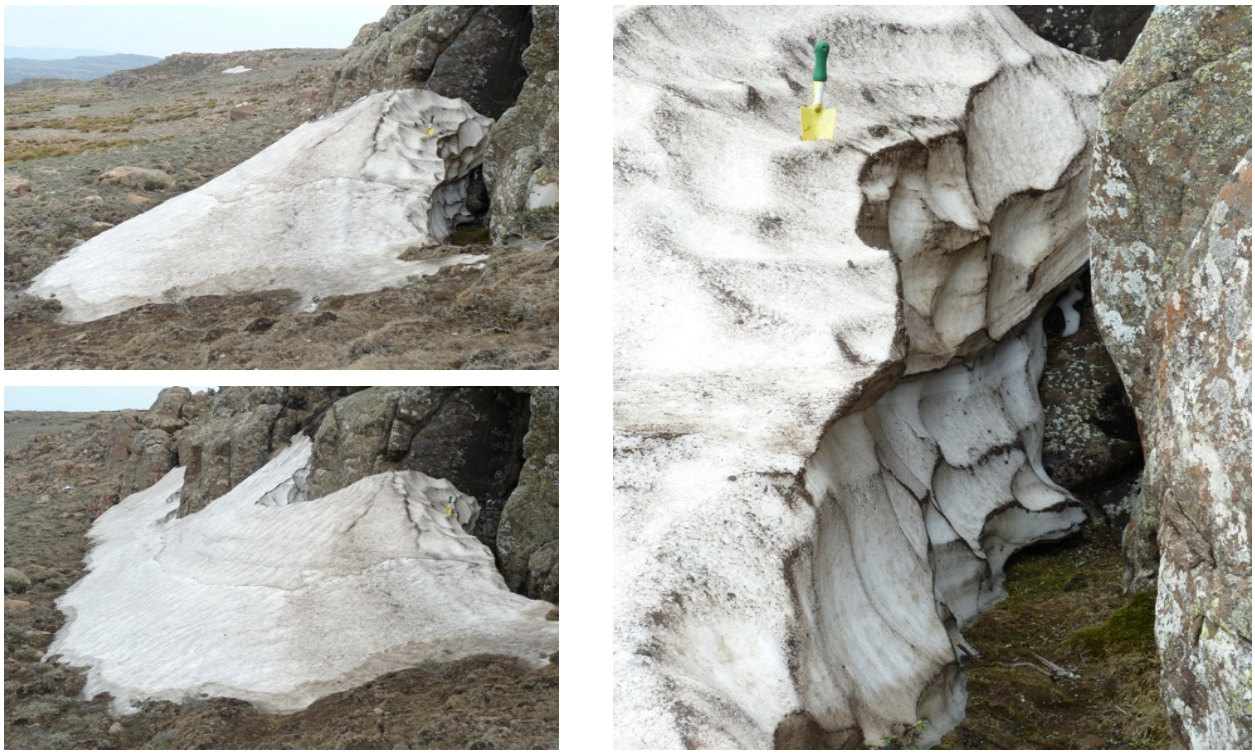


Figure 2.2 Snow melting away from the scarp wall as a result of increased temperature of the rock wall, September 2012.

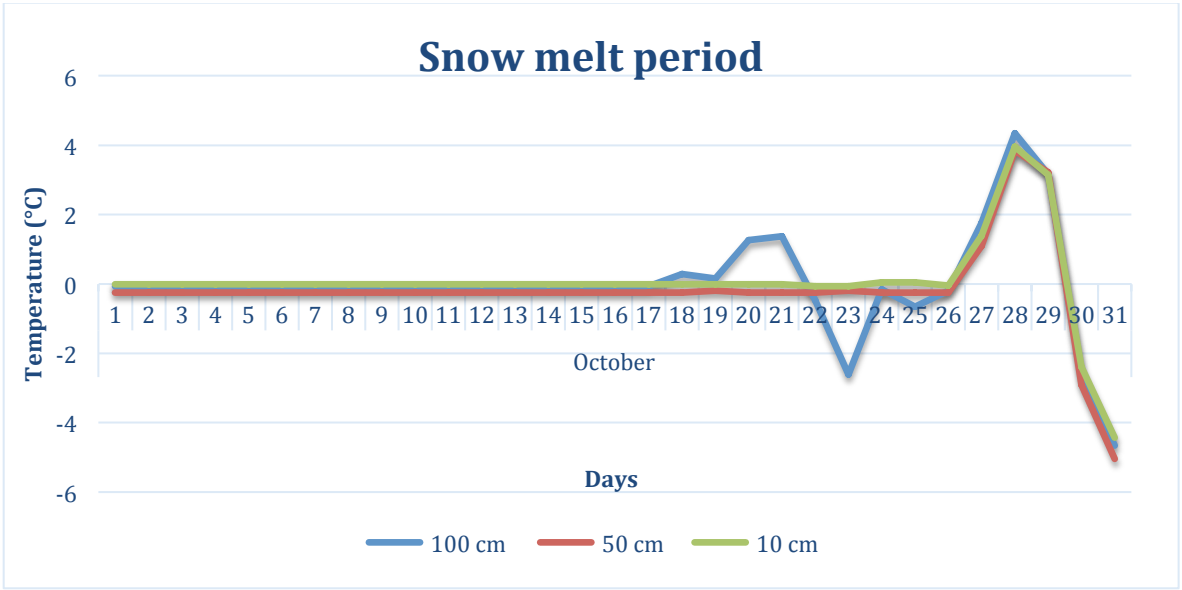


Figure 2.3 Snowmelt period as inferred from temperature changes during October 2012 in the upper zone at three depths above ground (100, 50 and 10 cm) at the study site (3325 m.a.s.l.) near Kotisephola Pass, Lesotho. Snow had melted down to 100 cm above ground on 17 October, and then to 50 and 10 cm on 26 October.

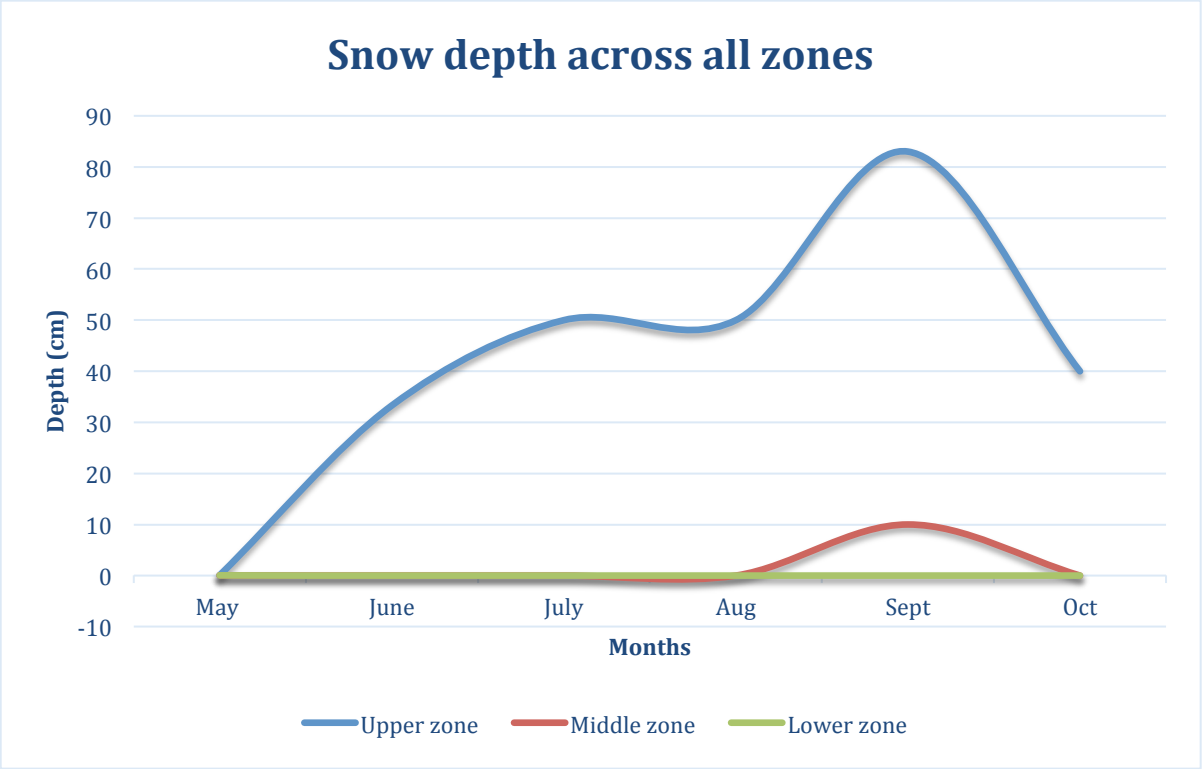


Figure 2.4 Mean snow depth across the three zones (upper, middle and lower) from May –

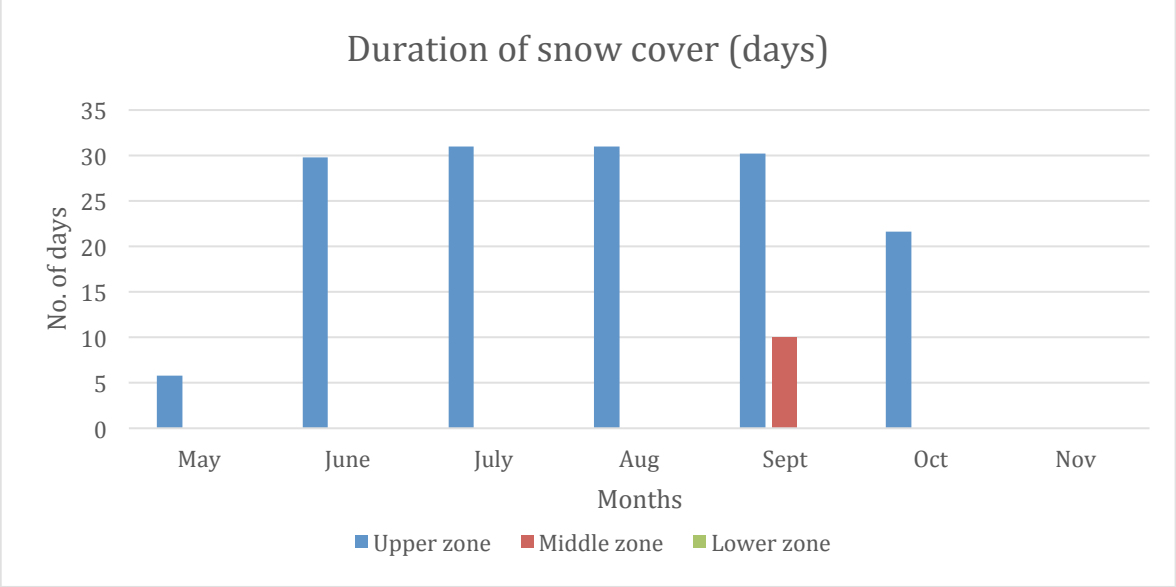


Figure 2.5 Mean number of days of snow cover over 5 months (May – November 2012) across the upper, middle and lower zones at the study site (inferred from temperature measurements at various depths over the same period)

2.2.2 Temperature

Air temperatures differed significantly across the three zones and at different heights above ground level within the zones during the winter to spring (May – October) of 2012. Absolute minimum temperatures were highest in the upper zone (–5.0 ± 1.6 °C) compared to the middle (–10.0 ± 1.4) and lower zones (–10.5 ± 1.5), differing by ca. 5 °C. Mean daily minimum temperatures in the upper zone were below 0 °C (–0.8 ± 0.5) during this period. The lowest temperatures were recorded in the lower zone — reaching an absolute minimum of –16 °C in August 2012 (within the canopy level of the plant). The lowest recorded temperature in the middle zone was –14.5 °C in June and the lowest in the upper zone was –11.5 °C in June. The absolute maximum temperature (35 °C) was recorded at 5 cm above ground in the middle zone in October 2012 at 10h00 in the morning (Figures 2.6 & 2.7). Mean temperatures were lowest at 5 cm above ground in the lower zone at –14 °C in August at 22h00 (Figure 2.6).

Temperatures differed significantly across all three zones at 5 cm above ground ($F_{2, 10892}$= 88.4, P <0.0001) from May – October 2012 (Figure 2.7). Temperatures reached an absolute minimum of –11.5 °C in the lower zone in mid-May, thereafter dropping to –15 °C at the beginning of June 2012 with daily maximum temperatures reaching –1.4 °C. Temperatures further dropped to a minimum of –16 °C in early August, thereafter increasing and remaining above 0 °C until October 2012. There was a rapid drop of temperatures at the beginning of September due to another snow fall; however by mid-September temperatures increased once again, reaching a recorded maximum of 35 °C. Temperatures varied in the lower zone by ± 10 °C each day in September, dropping sharply (to –8 °C) every night after 20h00 and rising up to 35 °C after 8h00 in the middle zone. In the upper zone, temperatures fluctuated hourly from 17 October until November 2012, indicating the gradual snowmelt from 100 cm to 50 cm above ground by 26 October 2012 (Figure 2.3).

There was minimal temperature variation in the upper zone (as shown by the low standard errors) due to the prolonged snow cover, which effectively buffered against significant temperature changes in the winter months of 2012, (mean± S.E. at 5cm: –1.1 ± 0.0 °C; 10 cm: –0.9 ± 0.0 °C; 20 cm: –0.9 ± 0.0 °C, canopy: –0.9 ± 0.0 °C).

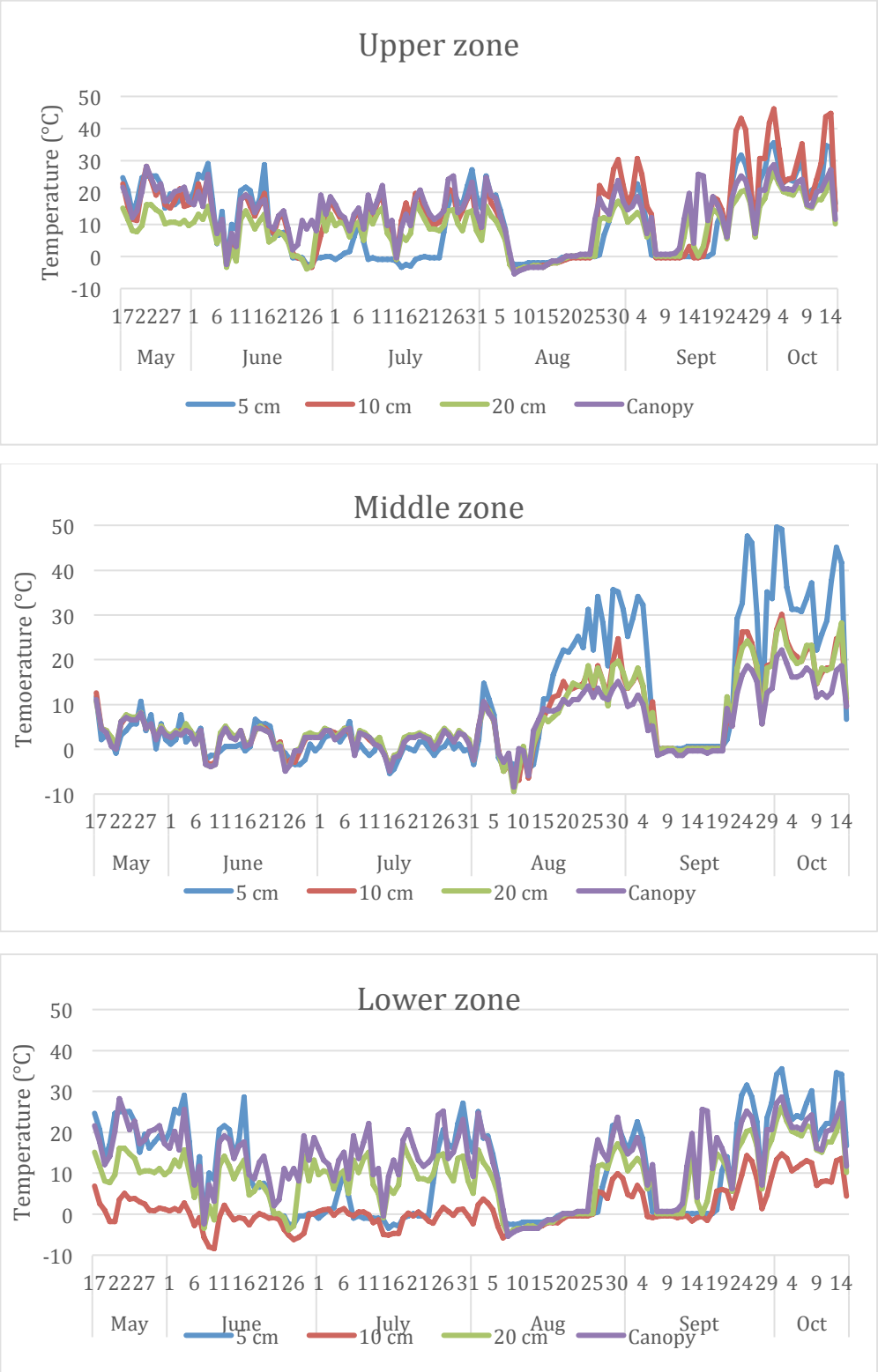
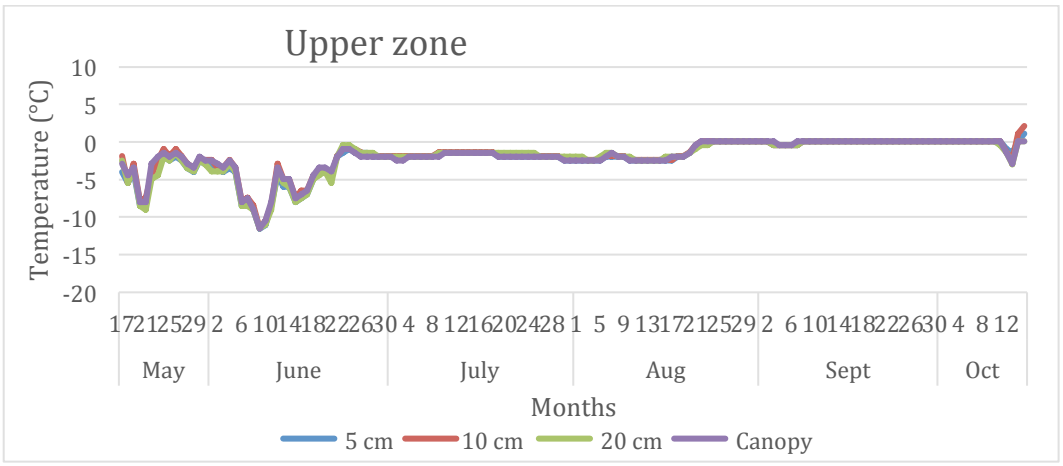
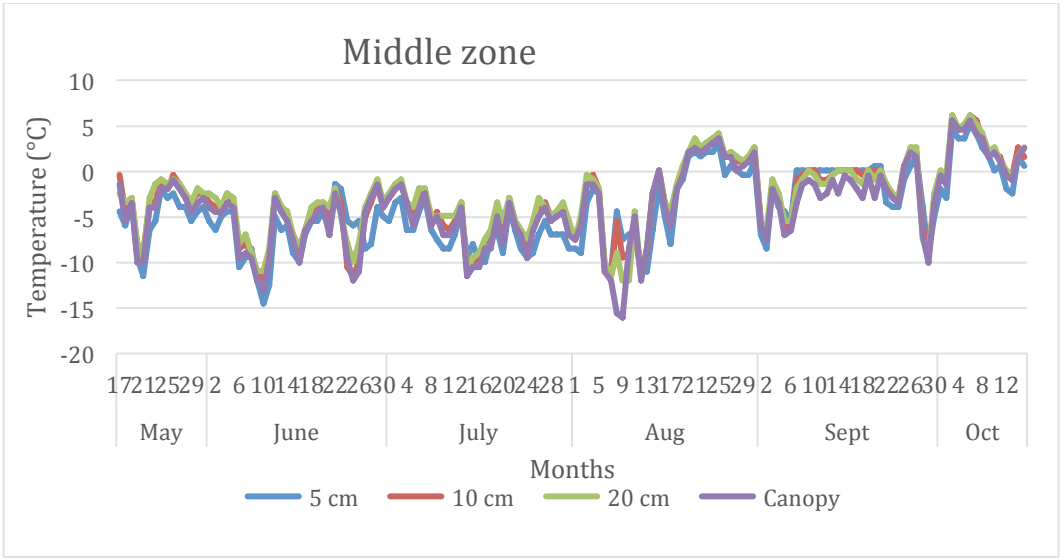


Figure 2.6 Daily maximum air temperature (ºC), at heights of 5, 10 and 20 cm above ground and within the canopy, for plants in the three zones below the rock scarp from May to October 2012.


Upper zone
Temperature (°C)
10
5
0
-5
-10
-15
-20
17 21 25 29 2 6 10 14 18 22 26 30 4 8 12 16 20 24 28 1 5 9 13 17 21 25 29 2 6 10 14 18 22 26 30 4 8 12
May
June
July
Aug
Sept
Oct
Months
5 cm
10 cm
20 cm
Canopy


Middle zone
Temperature (°C)
10
5
0
-5
-10
-15
-20
17 21 25 29 2 6 10 14 18 22 26 30 4 8 12 16 20 24 28 1 5 9 13 17 21 25 29 2 6 10 14 18 22 26 30 4 8 12
May
June
July
Aug
Sept
Oct
Months
5 cm
10 cm
20 cm
Canopy

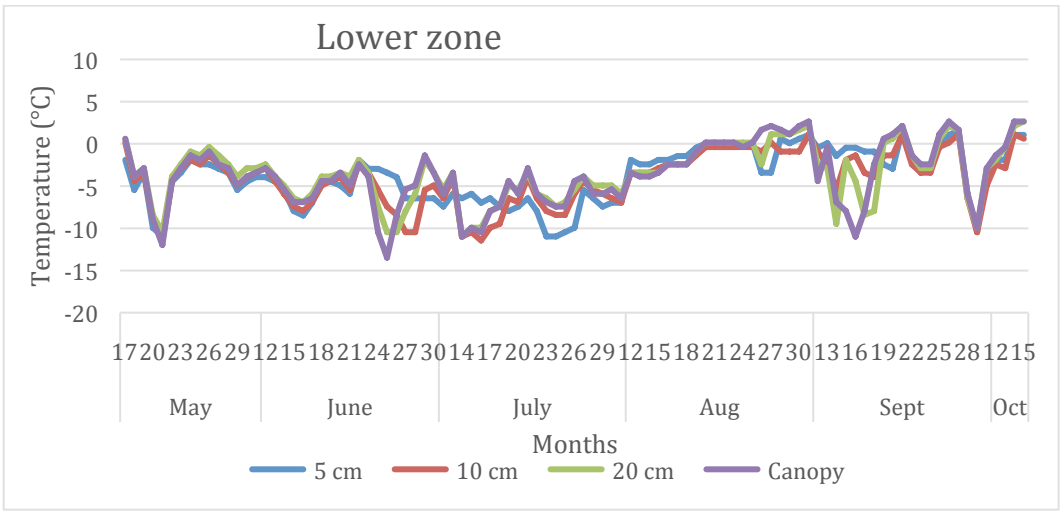


Figure 2.7 Daily minimum air temperature comparison across the three zones (Upper, Middle and lower): at 5, 10 and 20 cm above ground and within the plant canopy from May to October 2012.

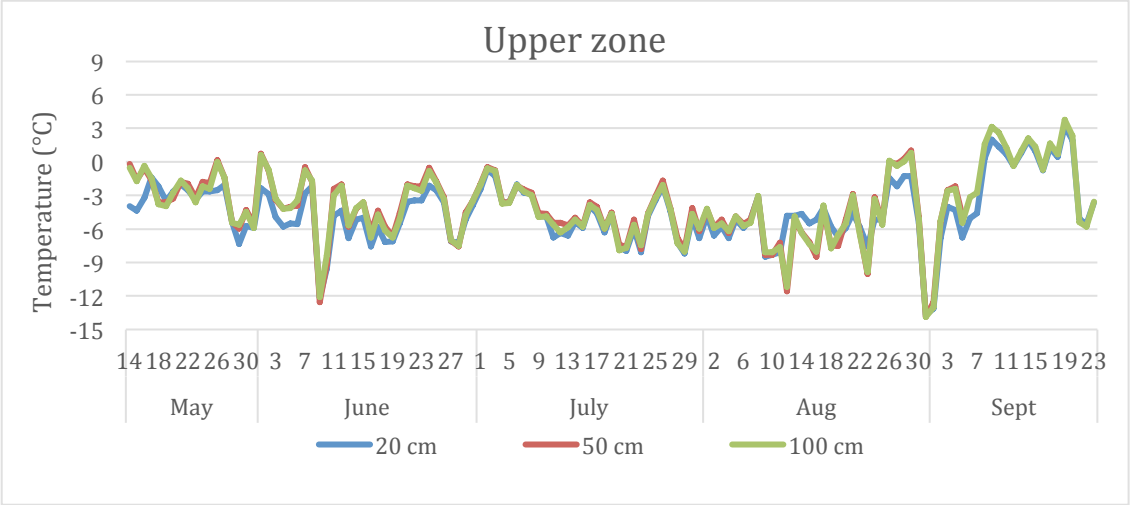


Figure 2.8 Daily minimum air temperature recorded by Tinytag data loggers across all three zones (Upper, Middle and Lower) at 20, 50 and 100 cm above ground from May – September 2013.

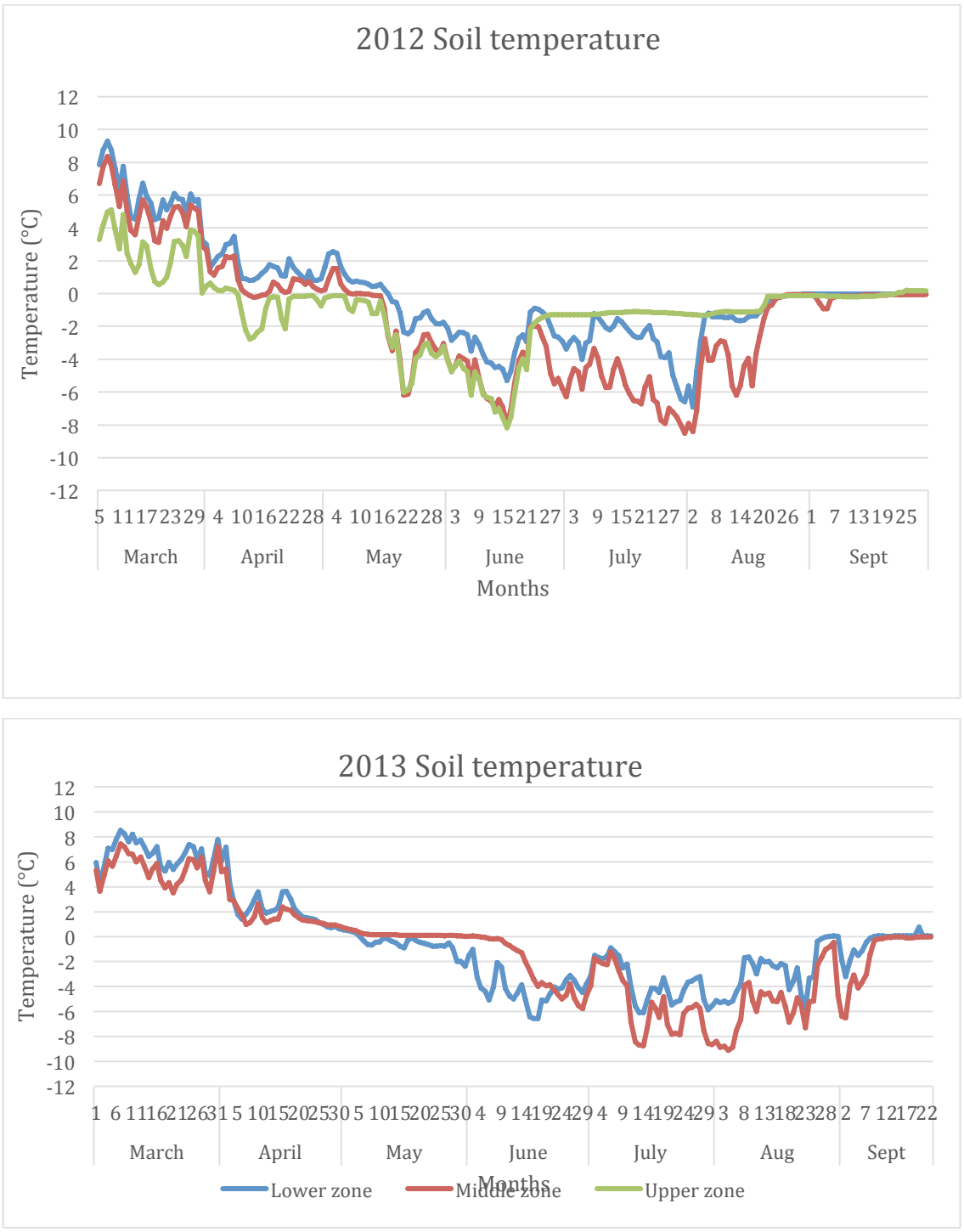


Figure 2.9 Mean daily minimum soil temperatures across the three zones (upper, middle and lower) at 5 cm below ground from March – September 2012 and 2013. The upper zone data logger malfunctioned in 2013.

Furthermore, there was a slight variation in temperature during the 2012 winter period in the middle zone (5 cm: 0.6 ± 0.1 °C; 10 cm: 0.8 ± 0.1 °C; 20 cm: 1.0 ± 0.1 °C; canopy: 0.2 ± 0.1 °C) and also in the lower zone (5 cm: 0.8 ± 0.1; 10 cm: 1.5 ± 1.4; 20 cm: 1.0 ± 0.1; canopy: 1.9 ± 0.1) as shown by higher standard errors relative to the upper zone. In contrast to 2012, temperatures were highly variable over the winter period of 2013 due to minimal snow cover. The highest temperature reached in the upper zone was 11.8 °C at 100 cm above ground at 14h00 on 9 September 2013 (Figure 2.8), and the minimum temperature in this zone reached −13.9 °C at 100 cm above ground at 6h00 on 31 August 2013 (Figure 2.8). The middle zone was the warmest zone with the maximum temperature reaching 23.8°C at 20 cm above ground at 12h00 on 17 August 2012 (Figure 2. 10), while minimum temperatures were – 14.3 °C recorded at 5 am on 31 August 2013 (Figure 2.8). The lower zone was the coldest zone during winter of 2013 with temperatures reaching a minimum of −14.5 °C at 70 cm above ground and −14.3 °C at 100 cm above ground on 31 August 2013 at 7h00, and an absolute maximum of 35 °C on 13 October at 12h00 (Figure 2.8).

For a suitable comparison between the years 2012 and 2013, maximum and minimum temperatures until 23 September are used since data loggers malfunctioned in 2013 after 23 September and therefore did not record until October. The year 2012 had the lowest temperatures with the absolute minimum reaching −16 °C, whereas the absolute minimum temperature reached during the winter of 2013 was −14.7 °C. The year 2012 had higher absolute maximum temperatures compared to the year 2013 in the upper and lower zones. The absolute maximum temperature recorded in the year 2012 was 29 °C on 23 September 2012 at 12h00 and 20 °C was reached on 18 September 2013 at 12h00 in the middle zone. The lower zone reached an absolute maximum of 22 °C at 12h00 on 23 September, higher by 1 °C to the 21 °C absolute maximum recorded in 2013 on 18 September 2013 at 11h00. The upper zone reached an absolute maximum temperature of 5 °C in June at the canopy of the plant in 2012 and in 2013 an absolute maximum of 12 °C on 18 September at 14h00.

2.2.3 Solar radiation

Solar radiation (W/m^2) measured at ground level over the period May to October 2012 in the upper (11.1 ± 0.9 W/m^2), middle (61.4 ± 3.12 W/m^2) and the lower (49.0 ± 2.7 W/m^2) zones was significantly different across all zones ($F_{2, 11831}$=139.7; $P < 0.0001$). It was progressively higher and slightly more variable down the slope. The solar radiation sensor in the upper zone was placed adjacent to the scarp wall on the ground and therefore received very little sunlight due to the shadow from the rocks and deep snow cover. In contrast, in the middle and lower zones, sensors were placed on unshaded ground, and they received sunlight for longer hours, and the snow melted earlier in these zones than in the upper zone. From mid-May to late June all three zones received solar radiation above 0.6 W/m^2 for a minimum of 11 hours (Figure 2.10). Sensors in all zones measured 0.6 W/m^2 solar radiation from July to August 2012, presumably due to the depth of snow covering them. Solar radiation in the upper zone remained at 0.6 W/m^2 from July – October 2012 (Figure 2.10). As expected, there was a significant difference (P <0.001) in the solar radiation received between the upper and middle zone (mean absolute difference of 87.7 W/m^3), and also between the upper and lower zones (mean absolute difference of 91.99, P <0.001) from August to October 2012 (Figure 2.10). The upper zone solar radiation reached an average daily maximum of 696.9 W/m^2 at midday due to total snow clearance and hence full exposure to sunlight except for the shading from the rock scarp, which explains why it is still a lower amount compared to the middle and lower zones (Figure 2.10).

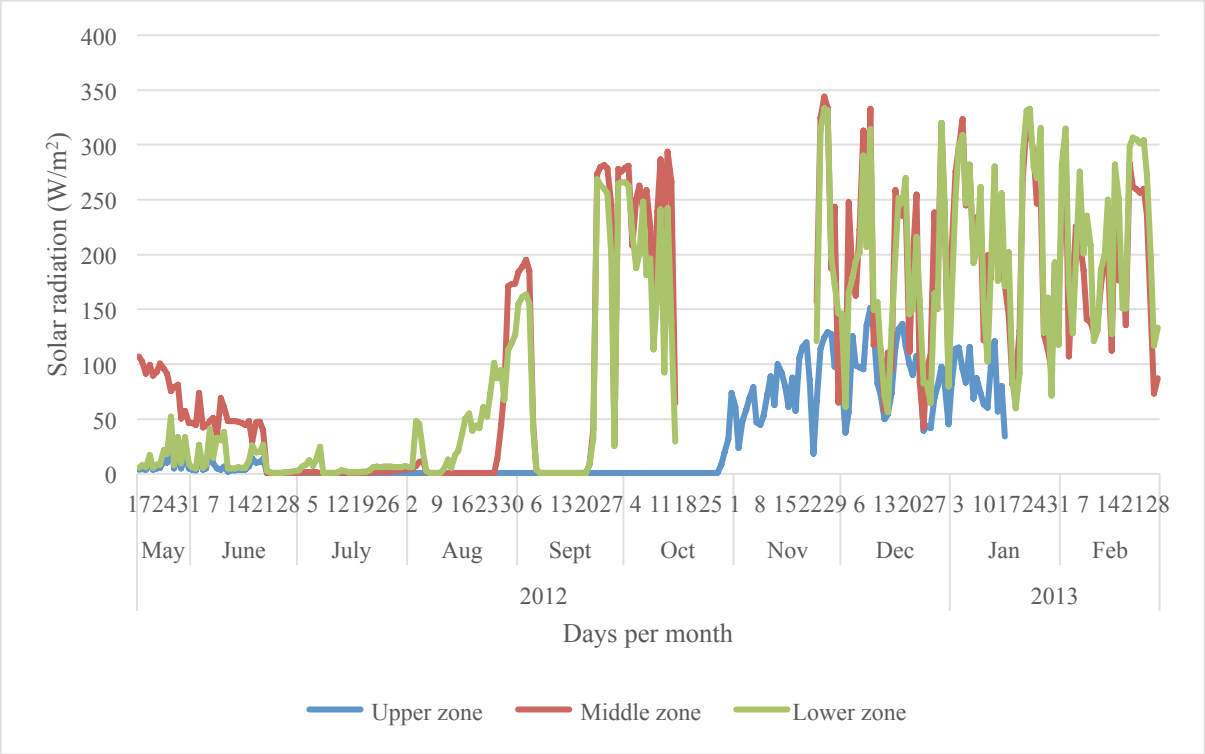


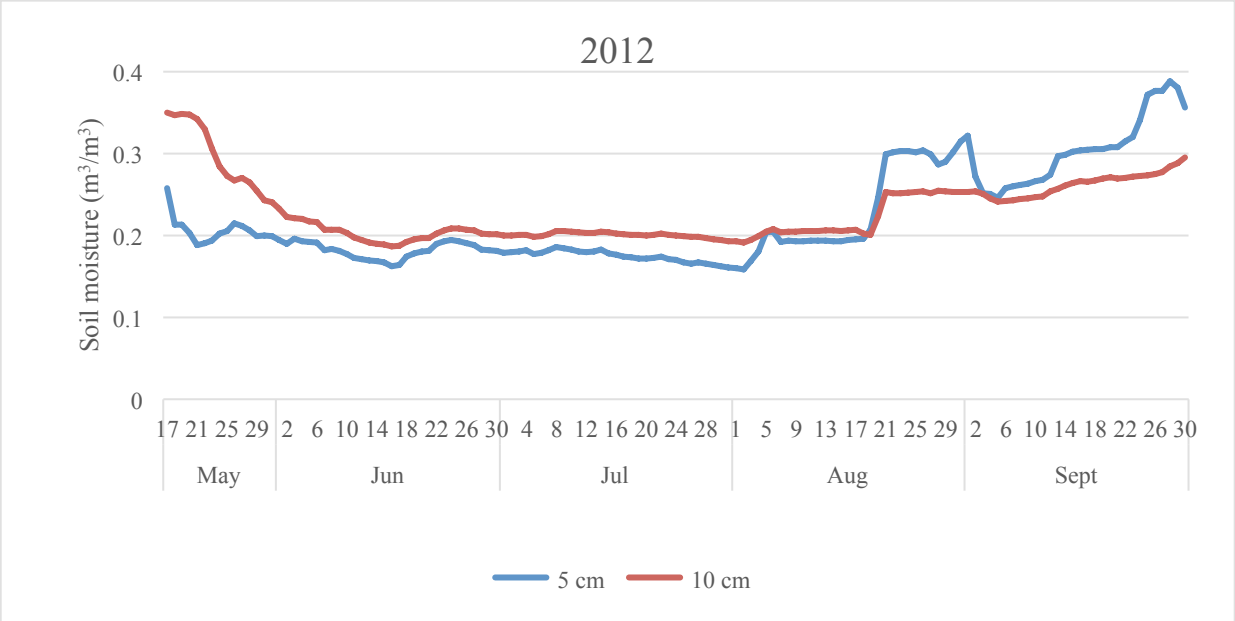
Figure 2.10 Mean daily solar radiation received per month in the upper, middle and lower zones from May 2012 – Feb 2013 at ground level on the southeast-facing slope of the study site near Kotisephola Mountain Lesotho

Solar radiation decreased in the middle zone from 80 W/m² to 0.6 W/m² from mid-May to mid-July 2012 (Figure 2.10) due to the presence of snow. Solar radiation then increased sharply in the middle zone to a daily average of 286.8 W/m² in October 2012 and in the lower zone it also reached 241.1 W/m² in October (Figure 2.10). The lower zone received a maximum of 8 hours of solar radiation every day from 27 June to 07 July, which then increased from 8 to 11 hours per day from July to October 2012 (Figure 2.10). Solar radiation in August 2012 in the lower zone was 362 W/m² on average at midday; and in October the lower zone received an average of 726.6 W/m² at midday. Highest hourly mean solar radiation was recorded in the middle zone at 942.4 W/m² in October at midday (Figure 2.10).

2.2.4 Soil moisture content

The study site was covered by snow continuously from May to October with several snowfall occurrences in 2012, while in the winter of 2013 there were far fewer snowfall occurrences and the snow cleared much more quickly. Results from the 2012 and 2013 soil moisture surveys showed that soil moisture was significantly lower during the winter of 2013 compared to 2012 this may be due to the differences in snow cover and rainfall before snowfall in the two years (Figure 2.11). Soil moisture was significantly different across all the zones (upper, middle and lower) and at different depths (5, 10, 15 cm). In year 2012, in the lower zone soil moisture content was significantly different ($F_{2, 13701}$= 2096, P<0.0001) between depths. Soil moisture in the lower zone was highest at 15 cm depth below ground (0.3± 0.001m^3/m^3) followed by 10 cm (0.3 ± 0.001 m^3/m^3) and lowest at 5 cm below ground (0.199 ± 0.001). Similarly soil moisture in the upper zone was significantly different at 5 cm ($F_{2, 10896}$ = 33.72, P<0.001; 0.2 ± 0.001 m^3/m^3) from the 10 cm (0.2 ± 0.001 m^3/m^3) and 15 cm (0.2 ± 0.001 m^3/m^3) levels below ground, while soil moisture at levels 10 cm and 15 cm below ground were not significantly different from each other. Soil moisture content across the three zones was significantly different ($F_{2, 10896}$ = 711.9, P < 0.001). The upper zone (0.2 ± 0.001 m^3/m^3) had the lowest soil moisture content due to the slope inclination of ca. 30° as water and snow leach down the slope, it gradually increased in the middle zone (0.2 ± 0.001 m^3/m^3), and was highest in the lower zone (0.3 ± 0.001 m^3/m^3).

Soil moisture decreased in the upper zone between May and June 2012 from 0.27 to 0.2 m^3/m^3, it then increased steadily from mid-June to mid-September up to 0.36 m^3/m^3 (Figure 2.12). Soil moisture was highest in all zones during September and October 2012, ranging from 0.3 – 0.3 m^3/m^3 during the snowmelt period (Figure 2.12). The higher soil moisture in the lower zone was most likely due to the water runoff from the upper zone. Soil moisture content increased with increasing depth below ground, there was higher soil moisture content at 15 cm below ground compared to 10 and 5 cm below ground in the lower zone, while in the upper zone there were no significant differences among the depths below ground, presumably due to freezing of the ground (Figure 2.12).



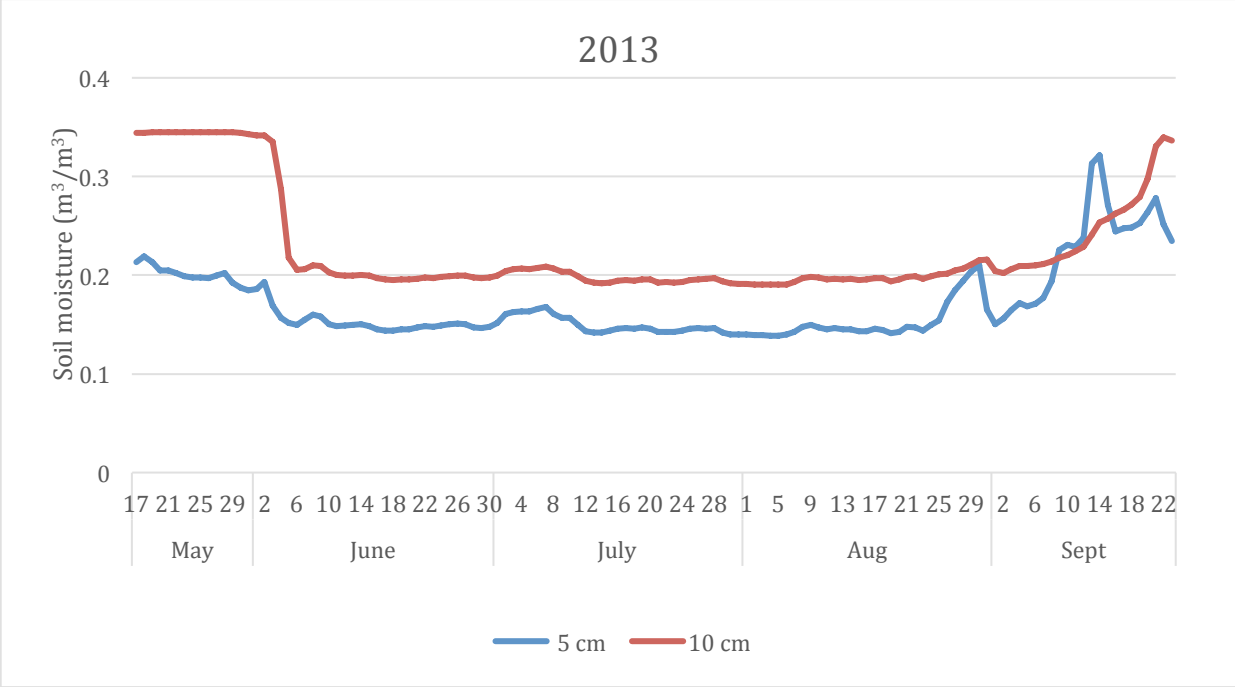


Figure 2.11 Soil moisture content (m^3/m^3) in the middle zone at 5 and 10 cm below ground during the winter months (May to September) in 2012 and 2013, unfortunately data loggers in the upper and lower zones were faulty in 2013.

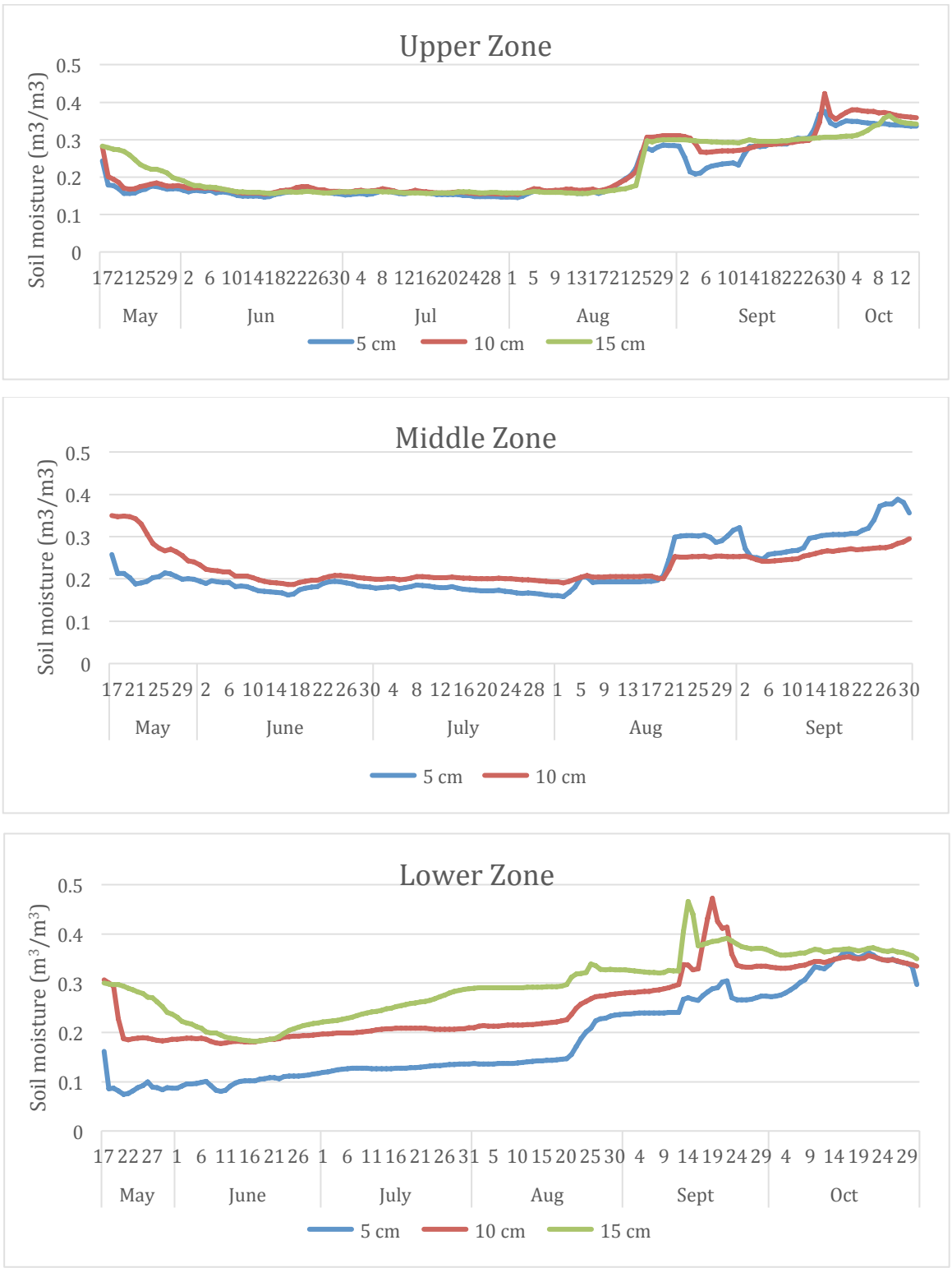


Figure 2.12 Soil moisture content across the three zones (Upper, Middle and Lower) at 5, 10, and 15 cm below ground from May to October 2012. The middle zone does not have the 15 cm figures as unfortunately the data loggers failed

Table 2.1 Summary of (mean ± S.E.) soil moisture (m^3/m^3) in the upper, middle and lower zones at 5, 10 and 15 cm below ground from May – October 2012.

	Upper zone			Middle zone		Lower zone		
May	0.1 ± 0.01	0.2 ± 0.002	0.28 ± 0.001	0.21 ± 0.001	0.29 ± 0.002	0.19 ± 0.0001	0.19 ± 0.001	0.24 ± 0.002
June	0.1 ± 0.003	0.19 ± 0.002	0.20 ± 0.001	0.18 ± 0.0004	0.20 ± 0.0004	0.16 ± 0.0003	0.17 ± 0.0002	0.16 ± 0.0003
July	0.13 ± 0.002	0.20 ± 0.002	0.25 ± 0.001	0.17 ± 0.0003	0.20 ± 0.0001	0.15 ± 0.0002	0.16 ± 0.0001	0.16 ± 0.0006
Aug	0.16 ± 0.001	0.23 ± 0.001	0.30 ± 0.001	0.23 ± 0.002	0.22 ± 0.001	0.19 ± 0.002	0.20 ± 0.002	0.19 ± 0.002
Sept	0.26 ± 0.001	0.33 ± 0.002	0.4 ± 0.001	0.30 ± 0.002	0.26 ± 0.001	0.28 ± 0.002	0.30 ± 0.001	0.30 ± 0.002
Oct	0.32 ± 0.001	0.34 ± 0.003	0.4 ± 0.0001	0.35 ± 0.0002	0.33 ± 0.001	0.34 ± 0.0004	0.37 ± 0.001	0.33 ± 0.001

2.2.5 Soil physical and chemical features

The lower zone generally had higher nutrient concentrations compared to the middle and lower zones (Table 2.2), probably due to the leaching of nutrients down-slope from the upper and middle zones and/or the decomposition of grass occurring in the lower zone (Table 2.2). The study site had a low carbon concentration ($F_{2,6}$= 0.18, P = 0.84, Table 2.2) compared to the nitrogen concentration ($F_{2,6}$ = 57, P= 0.0001; Figure 2.13 B) across all three zones (Table 2.2). The upper zone had the lowest concentrations (mg/L) of both carbon (0.3± 0.11 mg/L) and nitrogen (0.2 ± 0.01 mg/L) compared to the middle (carbon: 4.7 ± 0.42; nitrogen: 0.4 ± 0.02 mg/L) and lower zones (carbon: 5.2 ± 0.16; nitrogen: 0.4 ± 0.001 mg/L). This might reflect the lower rate of deposition of organic materials (due to less plant death/less plant matter present as most plants are ground covers/mats) and/or the lower rate of decomposition in the upper zone, or might simply be a function of greater leaching from the top of the slope.

Soil texture was very similar across the three zones, but the lower zone contained slightly more coarse sand and silt relative to the other zones, while clay content did not differ (Table 2.2). The upper zone had a slightly higher pH (4.8 ± 0.04) compared to the middle zone (4.8 ± 0.06) with only 0.03 difference, while the lower zone had the lowest pH (4.5 ± 0.05) with 0.3 difference compared to the upper zones representing a 10 times bigger margin of difference. Acid saturation, sample density and exchangeable acidity were not significantly different across the three zones (Table 2.2).

Table 2.2 Comparisons of the soil physical and chemical features between the three zones (mean ± standard error). Statistical comparisons by one-way ANOVA, D.F. = 2.6. Values with the same superscript letters within rows are not significantly different between the zones (Fishers LSD, $p<0.05$).

pH (KCI)	4.82 ± 0.04^{a}	4.79 ± 0.06^{a}	4.49 ± 0.05^{b}	13.3	0.0062
Acid saturation (mg/L)	0.10 ± 0.00^{a}	0.10 ± 0.01^{a}	0.21 ± 0.04^{a}	3.781	0.0866
Sample density (g/mL)	1.05 ± 0.06^{a}	0.98 ± 0.11^{a}	0.92 ± 0.01^{a}	0.78	0.5013
Exch. Acidity (cmol/L)	0.11 ± 0.01^{b}	0.14 ± 0.02^{ab}	0.40 ± 0.14^{a}	4.02	0.0782
Available P (mg/L)	2.07 ± 0.96^{b}	0.98 ± 0.11^{b}	9.67 ± 0.67^{a}	48.55	0.0002
Exchangeable K (mg/L)	61.33 ± 7.27^{c}	106.7 ± 6.69^{b}	208.7 ± 15.60^{a}	50	0.0002
Exchangeable Ca (mg/L)	1660 ± 79.68^{a}	1729 ± 74.30^{a}	1471 ± 216.40^{a}	0.91	0.451
Total Zn (mg/L)	0.50 ± 0.00^{b}	0.73 ± 0.22^{ab}	1.63 ± 0.41^{a}	5.1	0.0515
Total Mn (mg/L)	4.33 ± 0.67^{a}	5.00 ± 1.00^{a}	7.33 ± 1.20^{a}	2.577	0.1557
Total Cu (mg/L)	6.9 ± 0.12^{a}	5.57 ± 0.32^{b}	4.0 ± 0.12^{c}	49.5	0.0002
Total N (%)	0.24 ± 0.01^{b}	0.42 ± 0.02^{a}	0.44 ± 0.02^{a}	47.08	0.0002
Total C (%)	2.72 ± 0.11^{b}	4.67 ± 0.42^{a}	5.22 ± 0.16^{a}	24.01	0.0014
Fine silt (%)	12.67 ± 0.33^{a}	10.00 ± 1.00^{b}	13.67 ± 0.67^{a}	6.93	0.0275
Clay (%)	17.00 ± 2.08^{a}	13.67 ± 0.88^{a}	16.33 ± 0.67^{a}	1.68	0.265
Coarse silt & sand (%)	70.33 ± 2.40^{ab}	76.33 ± 1.76^{a}	70.00 ± 1.16^{b}	3.73	0.088

Furthermore Ca, Zn and Mn were also not significantly different across the zones. Acid saturation and exchangeable acidity increased down the slope, while sample density decreased downslope. P, N, Zn, Mn and K also increased down the slope while Cu and C decreased downslope (Table 2.2). The lower zone is therefore higher in nutrients compared to the middle and upper zones. P, K, Cu, N and C are significantly different

across the zones. There were positive correlations between P – K (r = 0.88), N – K (r = 0.70) and N – P (r = 0.41) while Cu – N (r = -0.88) and Cu – K (r = -0.91) were negatively correlated.

2.3 Discussion

2.3.1 Effects of snow and shading on air temperature

There is a clear micro-zonation at the study site as observed from the vegetation pattern. As previously stated in the introductory chapter, the micro-zonation is likely due to the micro-climate created by the rock scarp, which causes heavy snow drifts to bank up and also causes deep shading at the top of the slope with gradual lighter snow cover and less shading effect down the slope. Snowmelts earlier with increasing distance from the rock scarp face which accounts significantly for the observed micro-zonation. Timing of snowmelt has been found to be crucial to plant growth (Jonas *et al.,* 2008), as plant growth starts late with late snowmelt, and early with early snowmelt, thus affecting the vegetation growth period (Rammig *et al.,* 2010). However, whilst early snowmelt may result in early plant growth, a longer growth and vegetation cycle and perhaps higher productivity, early snowmelt also exposes plants to extremely low temperatures which may further result in frost damage and desiccation (Rammig *et al.,* 2010). Varying environmental conditions will ultimately affect the plant species composition down the slope, resulting in the micro-zonation observed (this is further discussed in Chapter 3).

There was very little temperature variation in the upper zone when it was covered by snow for several months during winter (Figure 2.7), thus protecting the plants from low temperatures. The two years (2012 and 2013) of data collection for this research were very different in terms of temperatures, snow depth and longevity and therefore allowed for a comparison (Figure 2.14) of environmental variables under snow and with less snow. The first snowfall for both years (2012 and 2013) occurred in May, and the snow lasted until late October in 2012 as a result of several snowfall occurrences, whereas in the winter of 2013 snow had melted completely by the end of June and there were up to four subsequent light snow occurrences with minimal snow accumulation on the ground of up to 10 cm depth until 1 June and 2 cm depth until 22 June. There was therefore considerably less snow during the winter and spring months of 2013 and the

plants were exposed to extremely low temperatures, whereas they remained under snow with temperatures ranging between −2 and 0 °C in the upper zone during the 2012 winter. Due to the lack of snow cover in 2013 and perhaps less severe cold fronts, air temperatures were higher than in the winter of 2012 when the study site was covered by snow.

A study by Sánchez-Bayo & Green (2013) in the Snowy Mountains of the Australian Alps showed that temperature is the main factor for snow cover longevity and snow depth; warm temperatures in spring result in early snow thaw (Nicholls, 2005), which in turn results in short snow cover periods. Reduced snow cover has negative implications on for alpine plant species and communities that 'normally' remain under snow for several months of the year (Green & Pickering, 2009; Billings & Bliss, 1959).

2.3.1.1 Air and soil temperature

Alpine regions are known for their low temperatures that play a significant role in water retention due to low evaporation and water stored in the form of snow (Zierl & Bugmann, 2005). Increased temperatures in alpine regions affect snow accumulation and result in early snowmelt; and consequently result in increased length of frost-free periods (Sjursen *et al*., 2005; Zierl & Bugmann, 2005). Ground temperatures experienced at this study site were significantly higher during winter in the upper zone compared to the middle and lower zones, due to the rock scarp (adjacent to the upper zone), which collects large drifts of snow, and further shelters the zone from harsh winds. As previously stated, persistent snow buffered the upper zone from extreme temperatures while the lower zones were not covered by snow. Snow lasted much longer in 2012 compared to 2013, and as a result, the upper zone experienced higher minimum temperatures with little variation in 2012 compared to 2013 (Figure 2.9). Air and soil temperatures were significantly ($P<0.005$) higher in the upper zone compared to the middle and lower zones during the winter of 2012, as a result of the long-lasting snow cover.

Soil temperature is greatly influenced by snow cover because of the insulation it provides during winter (Bannister *et al*., 2005; Edwards *et al*., 2007; Sánchez-Bayo & Green, 2013). Soil under snow has higher temperatures compared to exposed soil, which

experience temperatures below freezing point. Soil temperature was measured at 5 cm below ground in the upper, middle and lower zones. Temperatures in the upper zone were moderate (i.e. between 0 and –2 °C) while it was covered by snow in 2012 (Figure 2.9). In contrast, temperatures in the middle and lower zones ranged between –2 and –9 °C (Figure 2.9) over the same period when there was no snow cover. The difference in temperatures between the middle and the lower zones compared with the upper zone was largely caused by the absence of snow cover from the middle and lower zones.

Soil temperature is of greater importance to plants than atmospheric temperature as it has a stronger influence on nutrient cycling and soil moisture availability (Wundram *et al.,* 2010). Soil temperature furthermore plays a major role in plant growth rates as plant growth only commences when soil temperatures are above freezing point (Wundram *et al*., 2010). Plant activity under snow depends on plant structure, viz. trees have a high freezing tolerance of –40 °C or less, while some winter annuals, perennial herbs and woody plants are able to photosynthesize in winter or immediately after, and can tolerate –25 °C or less (Kappen, 1993). An increase in soil temperature increases the length of the growing season, and with high soil moisture availability, the plants' physiological activity also increases (Starr *et al*., 2008). Thus, low soil temperatures restrict nutrient and water cycling, which in turn restrict the physiological activities of the plants (Starr *et al*., 2004; Starr *et al*., 2008).

2.3.1.2 Solar radiation

Solar radiation levels are highest in alpine areas as there is less absorption and radiation transverses shorter distances through the atmosphere than in the lower altitudes (Blumthaler *et al.,* 1997; Blumthaler, 2012). While the study site was along a 30 m gradient from the rock scarp to the tussock grasses with no significant altitudinal differences, solar radiation was significantly different across the zones as a result of the micro-zonation created by the rock scarp and differences in snow cover and depth, as well as shading by the scarp itself. The upper zone received the lowest solar radiation compared to the middle and lower zones, due to the shading from the rock scarp that lasted for several hours of the day, and the snow covered this zone from May to September. The middle and lower zones, however, received continuous sunlight as they

were not under snow during winter and are only under shade for a few hours of each day. Areas that receive high solar radiation may lead to higher temperatures and therefore increase the rate of snowmelt (Wahren, 2001; Bannister *et al*., 2005; Huss *et al*., 2009). Thus, higher solar radiation in the middle and lower zones also played a significant role in early snowmelt and the rate at which snow melted. The upper zone only started receiving solar radiation above 0.6 W/m^2 (at ground level) towards the end of October in 2012 after the snow had melted.

2.3.1.3 Soil moisture content

Soil moisture availability depends on precipitation either in solid (hail, snow, graupel) or liquid (rainfall) form (Zierl & Bugmann, 2005; Sicart *et al*., 2008; Wipf & Rixen, 2010). Soil temperature plays a significant role in soil moisture availability, as extremely low soil temperature may cause the soil to freeze, thereby reducing soil moisture availability to plants (Hodkinson, 1999). In addition to atmospheric temperature and wind, soil temperature plays a significant role in melting the snow thereby increasing soil moisture. Snowmelt determines the release of water and nutrients from the snowpack (Hodkinson, 1999; Zierl & Bugmann, 2005; Wipf & Rixen, 2010). Thus, early snowmelt may cause early seasonal plant growth, short winters and long summers, which may lead to less available water in late summer and ultimately to possible drought (Jonas *et al*., 2008). Increased precipitation in the form of snow ensures longer water availability as the snowmelts gradually, and hence reduces water runoff (Hodkinson, 1999; Zierl & Bugmann, 2005; Sicart *et al*., 2008; Wipf & Rixen, 2010). Soil moisture was significantly higher in the upper zone compared to the middle and lower zones as a result of continuous water supply from the melting snow in the upper zone, and the zone is constantly under shade and sheltered from extreme winds and receives snow from the lower zones through snowdrift by winds. The lower zone had significantly ($P<0.05$) lower soil moisture content due to the early snowmelt, snowdrift and evaporation as a result of exposure to wind and solar radiation. Snowmelt in the upper zone increased soil moisture content from 0.206 m^3/m^3 to a maximum of 0.47 m^3/m^3 between August and September 2012 (Figure 2.11) as temperatures started increasing. The first year of data collection (2012) had a higher snowfall rate, due to several snowfall occurrences

compared to 2013, consequently soil moisture content was also higher compared to 2013 (Figure 2.11). Throughout the study period the soil moisture level hardly ever dropped below 0.10 m^3/m^3 (10% moisture content) in any of the zones, and was often much higher than that. Hence unlike most of southern Africa, this does not appear to be a water-limited system. Typically in the summer rainfall area of South Africa, surface soils dry out in the dry winter months (Mucina & Rutherford, 2006), but these specific alpine soils are not drying out in winter due to the rock scarp and the south facing slope. This area falls within the grassland biome (Mucina & Rutherford, 2006), but is very different from most of the other grasslands in terms of soil moisture availability, in both the grassland and savanna biomes.

2.3.2 Differences in soil physical and chemical features – possible effects of snow

Carbon and nitrogen were highest in the lower zone and lowest in the upper zone. Carbon (C) and nitrogen (N) were thus highest in the zone that had little to no snow cover during the study period. The nutrients were very likely leached down the slope from the upper to the lower zones during snowmelt (Baptist *et al.,* 2009). The lower zone has a greater mass of living organic matter (plant aerial cover), which could be due to the large tussock grasses that occur at the lower edge of this zone. Litter from these tussock grasses in the lower zone would also have contributed to the higher nutrient content in the lower zone compared to the upper and middle zones.

Nitrogen released during snowmelt is in two forms: nitrogen from snowmelt and nitrogen from mineralisation (Haselwandter *et al.,* 1983; DeLuca *et al.,* 1992). Nitrogen deposits are stored in the snowpack during winter and released during snowmelt in spring; due to the retention of N in the snow packs, its cycling is considered slow (Hiltbrunner *et al.,* 2005). Nutrient mineralisation processes in alpine regions are relatively inadequate for plant growth and slow due to temperatures ranging below freezing point in winter, and higher in non-frozen soils (Haselwandter *et al.,* 1983). The release of nitrogen (N) in the two years of this study (2012 and 2013) would have been different as snow cover was over 1m deep and lasted for more than six months in 2012 but only lasted for several weeks in 2013. Therefore the release from snowmelt would have been significantly higher in 2012 compared to 2013, as there was less snow cover

during the winter of 2013 as previously reported. Due to the significant differences in minimum temperatures between the years, N mineralisation would probably also have been significantly different as well. Significant variation would also be recorded across the zones, particularly in 2012, as the zones had significantly different temperatures.

The increase in temperatures due to climate change has a significant impact on freeze-thaw cycles and nutrient cycling, as it increases snowmelt and the nutrient cycling rate (Sjursen *et al*., 2005). Nutrient cycling is influenced by the freeze-thaw cycle, as in a winter with less snow or fast melting snow, the rapid snowmelt will erode the nutrients down the slope more quickly, resulting in higher soil nutrients accumulating in the lower zone (Haselwandter *et al*., 1983; Sjursen *et al*., 2005; Freppaz *et al*., 2007). This aspect of the study has not been thoroughly explored in the Drakensberg Alpine Centre and more data are needed to make any conclusive statements regarding mineralisation of nutrients in this region.

For this study, elements such as N, P, K, Cu and C were significantly different across the zones. The lower zone had the highest soil nutrient content due to leaching downslope, as indicated by a more acidic pH, and high organic matter from litter washed down from the upper zone to the lower zone. P, K, Zn, Mn and N were at higher concentrations downslope, while acid saturation and exchangeable acidity also higher downslope, suggesting water washing down from upper zones to the lower zones. The soil pH is also slightly higher downslope.

Microbial activity takes place when soil temperatures are above freezing (Schmidt & Lipson, 2003; Nemergut *et al*., 2005; Kielland *et al*., 2006). As the upper zone during winter is often insulated by snow, the soils are not frozen and significant microbial activity is likely to be occurring, whereas in the lower zones with less or no snow cover, the soils are frozen resulting in no microbial activity. Mineralization of N can occur during a transitional season (in late autumn), when soils are not frozen but plants are dormant; N is then released to be utilized by plants during snowmelt (Schmidt & Lipson, 2004; Kielland *et al*., 2006). The release of nutrients from litter occurs during and after snowmelt, but before plant growth (Schmidt & Lipson, 2004). Nutrients are therefore leached to the lower zones from the upper zone during snowmelt and precipitation, resulting in higher nutrients in the lower zones. There was very little interaction observed

between herbivores and plants at the study site, and therefore there is likely very little nutrient contribution from animals.

2.4 Conclusions

The rock scarp at the study site plays a significant role in collecting drifts of snow and providing shade for several hours of the day. The snow lasted for several months during the winter of 2012, and influenced soil and atmospheric temperatures, soil moisture, soil texture, and solar radiation received by the plants. Three distinct zones of vegetation were identified and the varying environmental factors experienced in these zones were measured and demonstrated. Snow is shown here to play a significant role in determining the environment, in which alpine plants survive, particularly areas which are covered by snow for several months in winter. One of the reasons is that snow cover/snowmelt is the main factor affecting the timing of the growing season. Steep environmental gradients were observed in this study due to the long lasting snow cover in the shaded upper zone. The uneven distribution of snow in this region due to topography and slope direction results in significant differences in environmental variables such as air and soil temperatures, solar radiation, soil moisture and soil texture and nutrients across the three zones recognised down the slope. This is the first study in the DAC in which detailed continuous environmental data have been collected to examine the effects of snow. A knowledge of the influence of snow cover on the environmental variables and thus on the plant species that occur in this region is imperative as it will inform our understanding of the role snow plays in the DAC. This study is the first of this kind in the DAC; to expand on it, the environmental variables addressed in this study could be measured at lower altitudes and on a north facing slope to allow for broader-based comparison.

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CHAPTER 3 - Plant species diversity and micro-zonation below a south facing rock-scarp in the Drakensberg Alpine Centre

Abstract

The Drakensberg Alpine Centre (DAC) is one of eight recognised biodiversity hotspots in southern Africa owing to its high endemism and rich flora. Species diversity and vegetation micro-zonation were studied at a site near Kotisephola Mountain at ca. 3300 m.a.s.l. in eastern Lesotho on a south facing slope below a rock-scarp where snow accumulates and persists through much of the cooler seasons. The aim of this study was to investigate the plant species composition and diversity in the snow patches during cooler seasons at a preselected high altitude site in the Drakensberg Alpine region. Three distinct vegetation zones were observed at the study site, which may be a function of shade and snow cover due to the rock-scarp. Of the three zones recognised at the site, the upper zone had the highest species richness, and the total number of species gradually decreased down-slope. Vegetation percentage cover was measured along ten transects of 30 m using 1 m^2 quadrats laid on alternate sides of the transect line. A total of 26 species was identified from the site. Graminoids (a sedge and grass species) had the highest percentage ground cover followed by rocks and then shrublets and herbaceous plants; mosses and lichens had the lowest percentage cover respectively. The dominant plant life forms were sedges, tussock grasses, dwarf shrublets, herbaceous plants with basal rosettes and cushion plants. The observed species diversity and abundance at the study site was strongly influenced by the environmental variables which changed downslope, such as temperature, which was highest in the upper zone when the site was under snow; solar radiation, which was highest in the lower zone due to prolonged exposure to the sunlight; and snow cover, which buffered the upper zone from extreme temperatures during the winter season.

3.1 Introduction

Alpine vegetation is directly influenced by environmental variables such as temperature, soil moisture, snow cover and solar radiation (Billings & Bliss, 1959; Litaor, *et al*., 2008). The Afro-alpine region has extreme temperature fluctuations which was described by Hedberg (1964, p 9) as "....winter every night, summer every day...." due to its extreme temperature fluctuations. Alpine flora have developed morphological characteristics that enable them to survive under extreme environmental conditions such as below freezing temperatures, high levels of solar radiation, occasional drought, freeze-thaw, extreme winds and high temperatures (Billings & Bliss, 1959; Kudo & Ito, 1992; Körner, 1999; Körner, 2007; Cannone, 2007; Bliss, 2013). Growth forms of alpine species are characteristically dwarf shrubs, graminoids (notably tussock grasses), herbaceous plants with basal rosettes, and mat-forming cushion plants (Körner, 1999; Wahren, 2001; Spehn & Körner, 2005; Becker *et al*., 2012). They are often very small in size and closely attached to the ground — this is a response by the plants to the harsh alpine conditions as their short stature allows them to trap heat (Walsh & Butler, 1994; Körner, 1999; Körner, 2007). Alpine vegetation comprises species that tolerate frost damage, extreme temperatures and often withstand a short growing season due to long-lasting snow cover (Kimball & Salisbury, 1974; Körner, 1999; Wahren, 2001; Keller *et al*., 2005; Olofsson & Shams, 2007; Inouye, 2008). Some alpine species occurring in snow-covered habitats during winter suspend their apical growth when under snow and are therefore not damaged by frost; they are, however, at high risk to frost damage if the snow melts early or there is little snowfall over a winter period (Kimball & Salisbury, 1974; Keller *et al*., 2005; Körner, 2007).

Alpine regions have low species diversity compared to regions at lower altitude, as few species can survive extreme environmental conditions in alpine regions (Moen & Lagerström, 2008). Species diversity is defined as 'richness in species', and is appropriately measured as the number of species in a sample of a standard size' (Whittaker, 1972, p 213). There are three types of diversity, namely: alpha, beta and gamma diversity. Only alpha was measured for this study. Alpha diversity is defined as the number of species within a defined area, while beta diversity can be defined as the extent of species turnover in a community across a gradient (Whittaker, 1972). Gamma

diversity is the overall diversity of different ecosystems in a region, which was not measured here as the study site is within one ecosystem. Indices such as the Shannon-Wiener index of diversity and species evenness may be used to quantify species diversity. Species evenness quantifies how 'equally abundant' are the species in the community. The opposite of evenness is dominance of one or a few species. The scale of the evenness ranges from 0 – 1, representing changes in distribution abundance from uneven to even, where 0 is the most uneven (= dominance) and 1 is the most even (Legendre, 2002). The Shannon-Wiener index is a commonly-used diversity index that accounts for species evenness and relative abundance of the various species present (Legendre, 2002; Mulder & Bazeley; White, 2004).

Species diversity generally decreases with an increase in altitude (Moen & Lagerström, 2008). Although species richness has also been reported to decrease towards the summits in nine mountains in Sweden, 70% of sampled summits in the European Alps in 1992 and 1993 showed an increase in species richness when compared with historic records from the same region (Rahbek, 1995; Pauli, 1996; Grabherr, 2009). Species have been reported to shift to higher altitudes for more favourable conditions; the shift serves as a response to increased temperatures resulting in response to regional climate change (Moen & Lagerström, 2008). Consequently, species' turnover in alpine regions has increased due to species shifting their altitudinal ranges (Thuiller, 2004; Moen & Lagerström, 2008; Grabherr, 2009; Venn *et al*., 2012).

Mountains may serve as refugia during climate change, and for over-harvested or overgrazed species at lower altitudes, and due to their isolation have high numbers of endemics (Schönswetter *et al*., 2005; Holderegger & Thiel-Egenter, 2009; Wesener *et al*., 2011). The DAC is thought to have served as a refugium for Cape elements from a past colder climate (Carbutt & Edwards, 2001) as the climate (low temperatures) associated with high altitude reduces metabolic processes in plants, including nutrient uptake – thereby emulating the nutrient-poor soils characteristic of the Cape Floristic Region (Witkowski & Mitchell, 1987). The DAC has also served as a 'corridor' enabling Cape elements to extend into the mountains of tropical East Africa (Carbutt & Edwards, 2001; Galley *et al*., 2007). The DAC is the fourth richest floristic region in southern Africa comprising ca. 2618 species and has been identified as one of eight biodiversity hotspots

in southern Africa; it is further recognised as a centre for biodiversity and endemism with 334 endemic and 595 near endemic species (Carbutt & Edwards, 2003, 2006; Clark *et al*., 2009).

Alpine species diversity is greatly influenced by topographically induced micro-habitats, with different species adapted to the specific conditions within each micro-habitat. For example, *Ranunculus glacialis*, a perennial herb that occurs in the European Alps and Scandinavia, mainly in snowbed habitats, is highly adapted to alpine environmental conditions as it shows no significant changes in its seed production and growth rate (only leaf width showed significant differences) under prolonged or short periods of snow cover (Totland & Alatalo, 2002). Other species such as the mat-forming shrublet *Helichrysum milfordiae,* growing at high altitude (over 2800 m, pers. obs.) in the Drakensberg, attaches itself to rocks or cliff faces. *Helichrysum milfordiae* leaf rosettes create an environment less exposed to the elements and thick layers of trichomes (indumenta) reduce water loss (Ehleringer, 1976; Gonzáles *et al*., 2008).

Snow distribution is highly uneven in mountain regions due to topographic and micro-climatic controls (Grab *et al*., 2009); it is driven from exposed slopes onto protected slopes where it may last for several weeks to months depending on temperatures and severity of drought, e.g. on the protected pole-ward facing slopes of the Medicine Bow Mountains in the United States of America (USA) (Billings & Bliss, 1959).

Alpine habitat structures are influenced by uneven snow distribution which influences micro-climates and consequently impacts on microhabitats (Billings & Bliss, 1959; Keller *et al*., 2005; Spehn & Körner, 2005; Bliss, 2013). Vegetation micro-zonation is due to the depth and melt-out rate of the snow bank, and habitats with snow cover are more species rich compared to adjacent habitats without snow cover due to protection they receive from snow during winter months (Billings & Bliss, 1959; Ferrari, 1995; Kammer & Mohl, 2002; Spehn & Körner, 2005). In contrast, species occurring in exposed habitats with no snow cover often experience drought in winter as the soil-water is frozen and are subjected to frost damage and very low temperatures (Wahren, 2001; Keller *et al*., 2005; Spehn & Körner, 2005; Jonas *et al*., 2008).

Reduction in the amount and occurrence of snow in alpine regions may lead to local extinctions of species that are unable to migrate to higher elevations or adapt rapidly, (e.g. change their morphological structure to withstand frost or extreme temperatures). Consequently, there is a considerable likely impact associated with projected climate change in alpine regions, and habitats that are currently covered by seasonal snow will be the most affected, as species in these habitats have very low frost tolerance and may become exposed to high levels of solar radiation, combined with extremely high and low temperatures (Kudo & Ito, 1992; Körner, 1999; Spehn & Körner, 2005; Bannister *et al*., 2005; Körner, 2007). Climate change effects are thought to be experienced more in alpine regions than at lower altitudes due to the extreme conditions in these alpine regions; thus alpine environments are the ideal locations for detecting the effects of climate change (Pauli, 1996; Inouye, 2008; Grabherr, 2009; Rangwala & Miller, 2012). There is evidence of species shifting to higher altitudes in alpine areas throughout the world, including Australian and European Alps and north American mountains (Pauli, 1996; Bannister *et al*., 2005; Inouye, 2008; Kala & Ratajc, 2012; Venn, *et al*., 2012). This is the first study to investigate species richness and vegetation cover in a seasonally snow covered area of the DAC, and possibly Africa as a whole. This study will therefore serve as the basis for further studies to monitor the effects of climate change on DAC alpine species surviving under snow for several months of the year.

3.1.1 Aims and objectives

The aim of this study was to investigate plant species composition and diversity beneath winter snow patches at a preselected high altitude site in the Drakensberg Alpine region, viz. on a seasonally snow-covered south facing slope at the base of a rock scarp where snow accumulates and melts differentially down the slope. The following questions are addressed:

c. *What is the plant species composition at this alpine site in the DAC?*
d. *How does the species richness and composition compare across the gradient (i.e. down the slope) below the rock scarp?*
e. *Is there any relationship between species turnover and environmental variables at this site?*

3.1.2 Materials and methods

Percentage vegetation cover (herbs, shrublets, lichens, mosses and grasses), rock and bare ground were measured at the study site using 1 m^2 quadrats along 30 m transects down the south facing slope, starting from the rock scarp. The quadrats were laid on alternating sides for each transect to ensure independent observation. Ten transects were laid out along the scarp, moving in an easterly direction towards the escarpment edge (Figure 3.1).

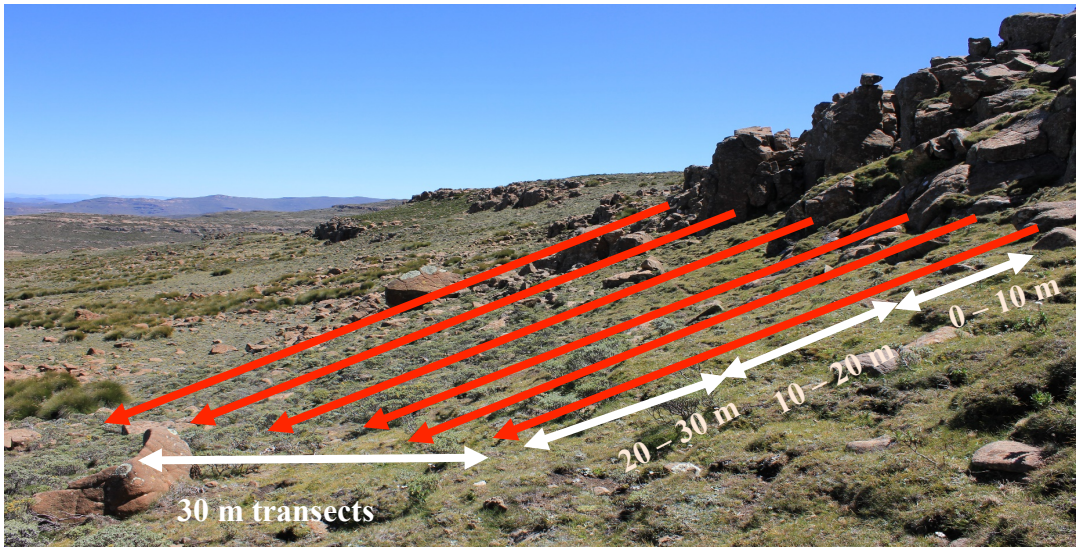

Figure 3.1 Study site, 30 m transects and three zones: upper (0 – 10 m), middle (10 – 20 m) and lower (20 – 30 m) zones.

Percentage aerial/ground cover was recorded for each vascular plant species present, as well as for lichens and mosses (in general) and for rock and bare ground. In addition, the tallest height of the vegetation was measured within every quadrat and the species were classified as grasses, sedges, shrublets or herbs. The vegetation survey was undertaken during the growing season in January and February of 2013 when most plants were in flower, which facilitated identification of the species present. Plants were pre-identified in the field using *Mountain flowers: a field guide to the flora of the Drakensberg and Lesotho* by Pooley (2003), which were then collected and pressed immediately in the field for later confirmation of identification at the C. E. Moss herbarium at the University of the Witwatersrand. A small number of unidentifiable species were taken to the Pretoria National Herbarium (PRE) to be identified with the help of specialists there. Other already identified species were also taken to PRE to confirm their identities using their

more comprehensive specimen collection. Current names (i.e. name changes) were checked for all the plant species using the South African National Biodiversity Institute: Plants of southern Africa online checklist (http://posa.sanbi.org/searchspp.php).

3.1.3. Data analysis

Species richness (the number of species in a defined area), species diversity (Shannon-Wiener diversity index) and species evenness were calculated for (a) each $1m^2$ quadrat from 1 – 30 m along each transect (=1 m^2 scale) and (b) each zone (upper, middle and lower (=10 m^2 scale). These data were then averaged across the ten transects. The Shannon-Weiner index:

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

was calculated where H' is the Shannon index as calculated with natural logarithms, and p_i is the proportion of individuals belonging to the ith species in the dataset (Whittaker, 1972). Species evenness was calculated using

$$E_{var} = 1 - (2 / \pi) \times \arctan(\sum_{s=1}^{S}(\{\ln[x_s] - \sum_{t=1}^{S}\ln[x_t] / S\}^2 / S))$$

where x_s and x_t are the number of individuals s or t, respectively, and S is the number of species (Tuomisto, 2012). E_{var} was selected because it is independent of richness as it is based solely on variance in species' abundances (Tuomisto, 2012). A one-way ANOVA was calculated to measure significant variations in species richness, evenness and diversity across the zones thereafter Tukey-Kramer test, and Fishers LSD from *Graph pad Prism 6* software were also calculated (Süzgeç-Selçuk & Birteksöz, 2011). Species presence (frequency of occurrence) was counted in all quadrats, which totalled 100 per zone. Species percentage cover was also determined from the 100 quadrats per zones.

3.2. Results

3.2.1 Species richness

The study site has relatively low (compared to the lowlands) species richness with a total number of 26 angiosperm species collected along transects across all three zones, a total area of 300 m^2. These comprise 24 dicotyledonous and two monocotyledonous species (Figure 3.2a; Appendix 1 – with all species' authorities included). Five growth-forms were evident amongst the species, viz, evergreen shrublets, forbs (erect herbs), graminoids, geophytes and mat-forming rosette herbs. Twenty four specimens were identified to species level and two are unknown. Asteraceae was the dominant family with 11 species; Crassulaceae was the second largest family with two species. Of the 26 species, 14 were perennial herbs (Figure 3.2b), three species were perennial shrubs, two were graminoids (a perennial grass and a sedge) and another two were annual herbs, while only one species was a perennial geophyte (Figure 3.2b).

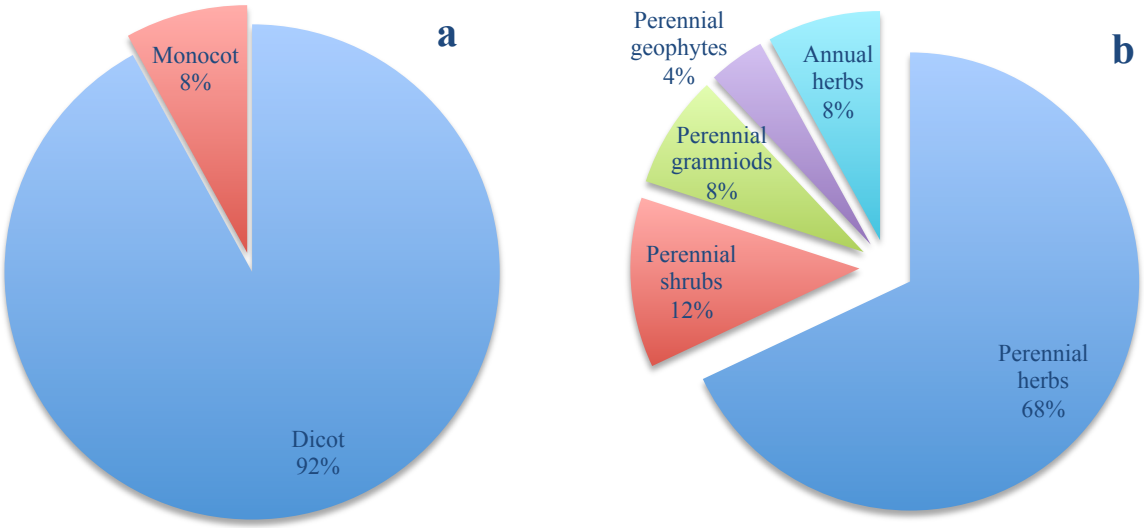

Figure 3.2 (a) Percentage of Monocotyledonous and Dicotyledonous species present at the study site. (b) Percentage of growth forms evident among the angiosperm taxa at the study site. Mosses and lichens are not accounted for in the graphs

Species richness varied somewhat across the three zones (10 m^2 scale): it was highest in the upper zone and decreased along the gradient to the lower zone (Figure 3.3). Species richness was significantly different across the three zones ($F_{2, 27} = 48.51$, $P < 0.001$, The upper zone had a slightly higher number of species (11.11 ± 0.179) compared to the middle (9.65 ± 0.174) and lower (8.77 ± 0.155) zones tested by LSD, where the species numbers ranged between 8 and 10 per m^2. The middle and lower zones had the lowest mean difference (0.88) compared to middle vs. upper zones (1.46) and upper and lower zones (2.34). The higher number of species in the upper zone is possibly due to more favourable environmental conditions such as warmer minimum and average daily temperatures (Figure. 2.7) due to protective snow cover over the winter period and less wind. The insulation from snow and shelter provided by the rock scarp in the upper zone creates a more favourable environment for plant growth and survival compared to the middle and lower zones, which are exposed to more extreme temperatures and drier conditions. Another possibility is that the plant individuals in the upper zone are of a smaller size than in the other zones, which may allow the establishment of more species there.

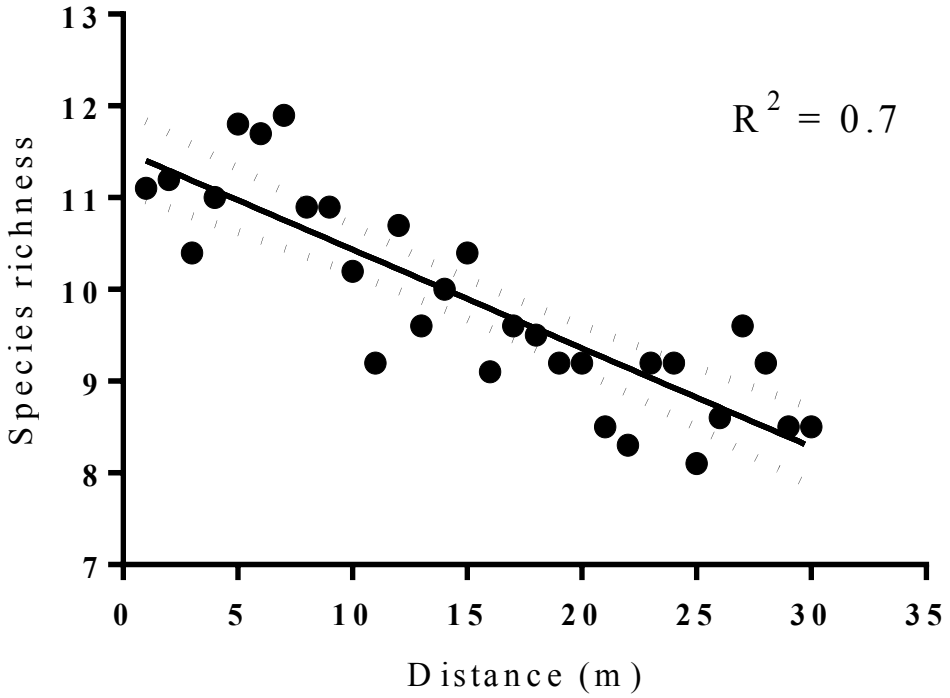

Figure 3.3 Average species richness $1m^2$ (quadrat) scale each distance (0 - 1 m, 1 -2 m…) along ten (30 m) transects from the rock scarp along a 30 m slope across three zones (upper, middle and lower) as recognised by micro-zonation at the study site near Kotisephola Pass (see Figure 3.1).

The study site was dominated by two graminoids (*Dracoscirpoides falsa* and *Merxmuellera drakensbergensis*), three *Helichrysum* species (the mat-forming herb *H. praecurrens,* basal rosette herb *H. albo-brunneum* and shrublet *H. trilineatum*) and *Erica frigida* (Table 3.1). *Dracoscirpoides falsa* was found in all quadrats in the upper and middle zones, and in the lower zone it occurred in 99 of the 100 quadrats (Table 3.1); it was the most widespread species across the study site and had the highest percentage cover across all the quadrats, whether present or absent (Tables, 3.2), as well as the highest percentage cover within only those quadrats that it was present (Table 3.3). *Helichrysum praecurrens* had the second highest percentage cover in all three zones (Tables 3.4 – 3.6). *Helichrysum praecurrens* was one of the dominant species at the study site. This mat-forming herb spread across all three zones and continued to grow further downslope beyond the 30 m transect (i.e. from the rock scarp) amongst the tall tussock

grasses. As previously noted, *Helichrysum* was the most dominant genus in the study site. In addition to *H. praecurrens*, four other perennial herbaceous species of *Helichrysum* were present: the tufted *H. subglomeratum*, and *H. albo-brunneum, H. album* and *H. bellum*, all three with basal leaf rosettes, as well as the spreading shrublets *H. witbergense* and *H. trilineatum*. The mat-forming shrublet *Helichrysum milfordiae* was only found growing on the rocks of the scarp adjacent to the upper zone and so was not included in the species tally down the slope (Table 3.1). *Helichrysum witbergense* only occurred in the upper zone (i.e. it was not found beyond 10 m from the rock scarp) and decreased in abundance with increasing distance from the scarp suggesting intolerance to a snow-free habitat (Table 3.1).

Some species had high frequency (Table 3.1) but low species percentage cover, as summarised in Tables 3.2 and Table 3.3 — including the quadrats which had no percentage cover for each species (Table 3.2), or omitting them and including only quadrats with percentage cover for the selected study species (Table 3.3). Species are presented in order from the most dominant in the upper zone to the least dominant in all three tables. Of the 26 species, 20 occurred across all three zones while three species occurred only in the upper zone, namely, *H. witbergense, H. milfordiae* and *Glumicalyx flanaganii*. In contrast, *Ornithogalum bicornutum* was found in both the upper and the lower zones, but not in the middle zone. Species in the upper zone had a higher percentage cover than the middle and lower zones except for *H. trilineatum* and *H. subglomeratum*, which had their highest percentage cover in the two lower zones (Table 3.1).

Table 3.1 Summary table of species frequency (presence) shown as percentage across the zones.

Species	**Upper zone (%)**	**Middle zone (%)**	**Lower zone (%)**
Helichrysum witbergense Bolus	46	-	-
Ornithogalum bicornutum F.M.Leight.	7	-	2
Helichrysum milfordiae Killick	7	-	-
Glumicalyx flanaganii (Hiern) Hilliard & B.L. Burtt	3	-	-
Unknown Herb	3	1	-
Merxmuellera drakensbergensis	-	3	23
Senecio tugelensis J.M.Wood & M.S.Evans	-	9	-
Crassula papillosa L.Schonland & Baker f.	7	8	4
Helichrysum album Mill. N.E.Br.	12	4	7
Felicia uliginosa Cass. Grau	9	15	5
Erica frigida L. Bolus	13	27	29
Cerastium arabidis E.Mey. ex Fenzl	17	23	15
Unknown Herb	36	34	28
Geranium incanum Burm. f. var. *incanum*	41	35	23
Scabiosa columbaria L.	44	33	14
Helichrysum subglomeratum Mill. Less.	40	73	70
Crassula vaillanti L. (Wild.) Roth	48	32	28
Geum capense L. Thunb.	64	43	39
Psammothropa obtusa Eckl. & Zeyh. Adamson	69	30	33
Gnidia burchellii L. (Meisn.) Gilg	69	54	50
Helichrysum bellum Hilliard	70	59	56
Helichrysum trilineatum DC.	70	87	98
Felicia rosulata Yeo	78	65	59
Helichrysum albo-brunneum S.Moore	80	80	75
Helichrysum praecurrens Hilliard	86	88	71
Dracoscirpoides falsa (CB.Clarke) Muasya	100	100	99

Table 3.2 Summary table of mean percentage cover for all quadrats (including the quadrats where the species was not present).

Species	**Upper zone (%)**	**Middle zone (%)**	**Lower zone (%)**
Helichrysum witbergense	1.1	-	-
Ornithogalum bicornutum	10.3	-	2
Glumicalyx flanaganii	0.03	-	-
Helichrysum milfordiae	0.1	-	-
Unknown Herb	0.02	0.01	-
Senecio tugelensis	-	0.1	-
Merxmuellera drakensbergensis	-	4.7	19.2
Felicia uliginosa	0.02	0.2	0.2
Cerastium arabidis	0.03	0.4	0.2
Crassula papillosa	0.05	0.04	0.01
Crassula vaillanti	0.1	0.1	0.1
Helichrysum album	0.2	0.2	0.2
Scabiosa columbaria	0.2	0.2	0.02
Geranium incanum	0.2	0.3	0.03
Unknown	0.3	0.5	0.1
Helichrysum subglomeratum	0.5	1.3	1.3
Psammothropa obtusa	0.7	0.4	0.2
Helichrysum albo-brunneum	1.1	0.8	0.5
Helichrysum bellum	1.4	1.5	0.7
Erica frigida	1.1	3.9	1.5
Gnidia burchellii	1.6	0.6	0.7
Felicia rosulata	2.1	1.3	1
Geum capense	2.3	0.7	0.6
Helichrysum trilineatum	5.5	8.5	6
Helichrysum praecurrens	8.4	9.4	7.2
Dracoscirpoides falsa	50.2	44.9	47.9

Table 3.3 Summary table of mean percentage cover for the quadrats including only those where the species were present (where a species had 0% cover in a quadrat, these were omitted from the list).

Species	**Upper zone (%)**	**Middle zone (%)**	**Lower zone (%)**
Helichrysum witbergense	2.3	-	-
Ornithogalum bicornutum	2.1	-	1.6
Helichrysum milfordiae	1	-	-
Glumicalyx flanaganii	0.3	-	-
Unknown Herb	0.3	0.08	-
Senecio tugelensis	-	0.8	-
Merxmuellera drakensbergensis	-	34.2	43.4
Felicia uliginosa	0.1	1	1
Cerastium arabidis	0.13	2.2	1.6
Crassula papillosa	0.2	0.3	0.1
Crassula vaillanti	0.3	0.2	0.3
Scabiosa columbaria	0.4	0.7	0.1
Unknown Herb	0.9	2	0.4
Helichrysum subglomeratum	0.9	1.8	1.9
Helichrysum album	1.3	1.7	1
Psammothropa obtusa	1.2	1	0.8
Helichrysum bellum	1.9	2.5	1.4
Geranium incanum	0.4	0.7	0.2
Helichrysum albo-brunneum	1.3	1	0.7
Gnidia burchellii	2.1	1	1.4
Felicia rosulata	2.6	2.1	1.8
Geum capense	3.7	1.6	1.5
Helichrysum trilineatum	6.1	9.8	6.6
Erica frigida	8.8	13	4.9
Helichrysum praecurrens	9.1	9.9	9.9
Dracoscirpoides falsa	50.2	44.9	47.9

Other species such as *H. trilineatum and H. albo-brunneum* occur in all three zones (Table 3.1), although *H. trilineatum* only started appearing towards the lower portion of the upper zone and was most abundant in the middle zone and slightly

decreased in abundance in the lower zone. Similarly *H. albo-brunneum* was most abundant in the upper and middle zones and it decreased in abundance towards the lower zone.

Erica frigida occurred across all three zones but was most dominant in the middle and lower zones it had the lowest percentage cover in the upper zone compared to the middle and lower zones (Table 3.1, 3.2 & 3.3). The tussock-forming perennial 'broom grass', *Merxmuellera drakensbergensis*, which begins to occur ca. 20 m below the scarp, was the second dominant species in the lower zone (Tables 3.1, 3.2 and 3.3). The tussocks reach heights of 91 cm and have a large basal cover; hence the lowest species richness is seen here in the lower zone as these plant species dominate the available space.

Another rank abundance curve was used to assess the relative abundance of the 26 species across the three zones based on species presence within the 300 quadrats in total. *Helichrysum praecurrens* was ranked number first as it had the highest frequency of 8.32% and *H. trilineatum* was ranked second with 6.69% cover, followed *by Erica frigida* at 2.08% and *Felicia rosulata* at 1.2% (Figure 3.7). The curve shows that apart from the 4 most common species, the remaining 22 species each had less than 2% aerial cover (Figure 3.7).

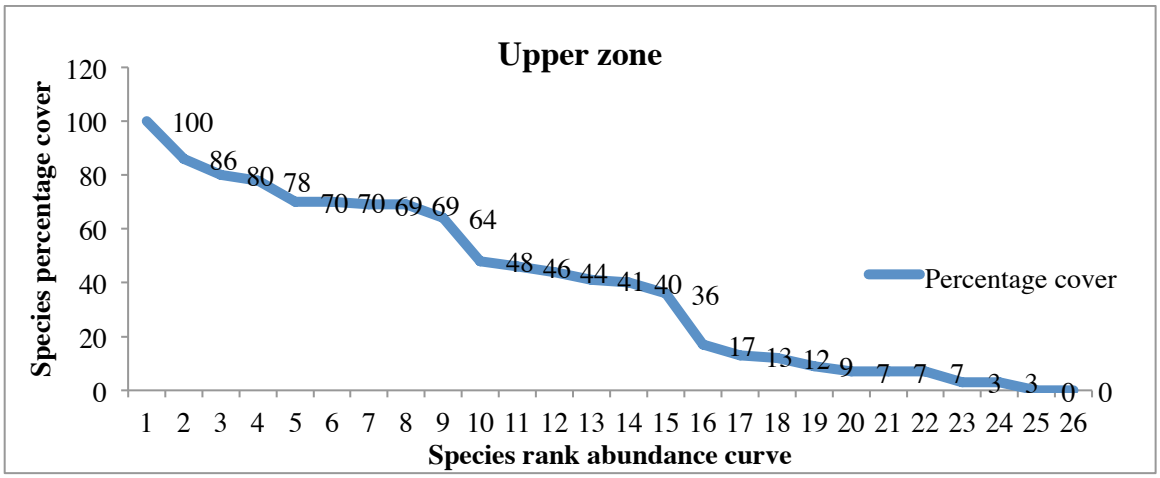

Figure 3.4 Rank-abundance curve for species occurring in the upper zone ranked from 1, the species with the highest frequency to 26, the species with the lowest percentage cover.

Table 3.4 Summary of species rank abundance in the upper zone

Rank abundance	Species	Frequency
1	*Dracoscirpoides falsa* (CB.Clarke) Muasya	100
2	*Helichrysum praecurrens* Hilliard	86
3	*Helichrysum albo-brunneum* S.Moore	80
4	*Felicia rosulata* Yeo	78
5	*Helichrysum trilineatum* DC.	70
6	*Helichrysum bellum* Hilliard	70
7	*Gnidia burchellii* L. (Meisn.) Gilg	69
8	*Psammothropa obtusa* Eckl. & Zeyh. Adamson	69
9	*Geum capense* L. Thunb.	64
10	*Crassula vaillanti* L. (Wild.) Roth	48
11	*Helichrysum witbergense* Mill. Bolus	46
12	*Scabiosa columbaria* L.	44
13	*Geranium incanum* Burm. f. var. incanum	41
14	*Helichrysum subglomeratum* Mill. Less.	40
15	Unknown Herb	36
16	*Cerastium arabidis* E.Mey. ex Fenzl	17
17	*Erica frigida* L. Bolus	13
18	*Helichrysum album* Mill. N.E.Br.	12
19	*Felicia uliginosa* Cass. Grau	9
20	*Ornithogalum bicornutum* L.F.M.Leight.	7
21	*Helichrysum milfordiae* Mill. Killick	7
22	*Crassula papillosa* L.Schonland & Baker f.	7
23	Unknown Herb	3
24	*Glumicalyx flanaganii* (Hiern) Hilliard & B.L. Burtt	3
25	*Senecio tugelensis* J.M.Wood & M.S.Evans	0
26	*Merxmuellera drakensbergensis*	0

Table 3.5 Species rank abundance in the middle zone

Rank abundance	Species	Percentage cover
1	*Dracoscirpoides falsa*	100
2	*Helichrysum praecurrens*	88
3	*Helichrysum trilineatum*	87
4	*Helichrysum albo-brunneum*	80
5	*Helichrysum subglomeratum*	73
6	*Felicia rosulata*	65
7	*Helichrysum trilineatum*	59
8	*Gnidia burchellii*	54
9	*Geum capense*	43
10	*Geranium incanum*	35
11	Unknown Herb	34
12	*Scabiosa columbaria*	33
13	*Crassula vaillanti*	32
14	*Psammothropa obtusa*	30
15	*Erica frigida*	27
16	*Cerastium arabidis*	23
17	*Felicia uliginosa*	15
18	*Senecio tugelensis*	9
19	*Crassula papillosa*	8
20	*Helichrysum album*	4
21	*Merxmuellera drakensbergensis*	3
22	Unknown Herb	1
23	*Glumicalyx flanaganii*	0
24	*Helichrysum milfordiae*	0
25	*Ornithogalum bicornutum*	0
26	*Helichrysum witbergense*	0

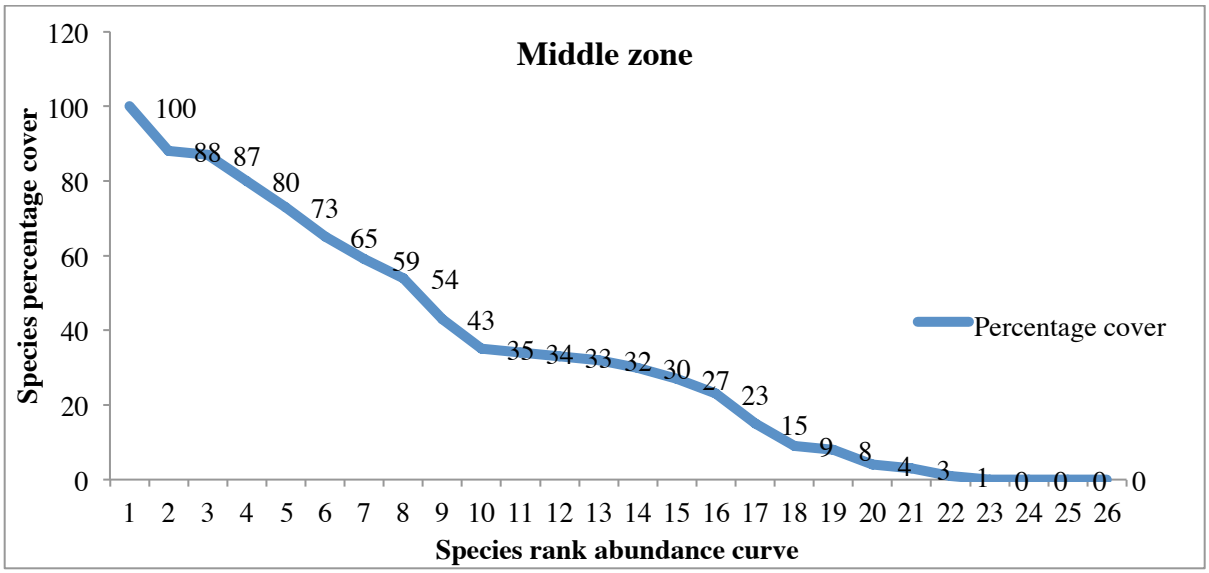

Figure 3.5 Rank-abundance for species occurring in the middle zone ranked from 1, the species with the highest species frequency, to 26, the species with the lowest percentage.

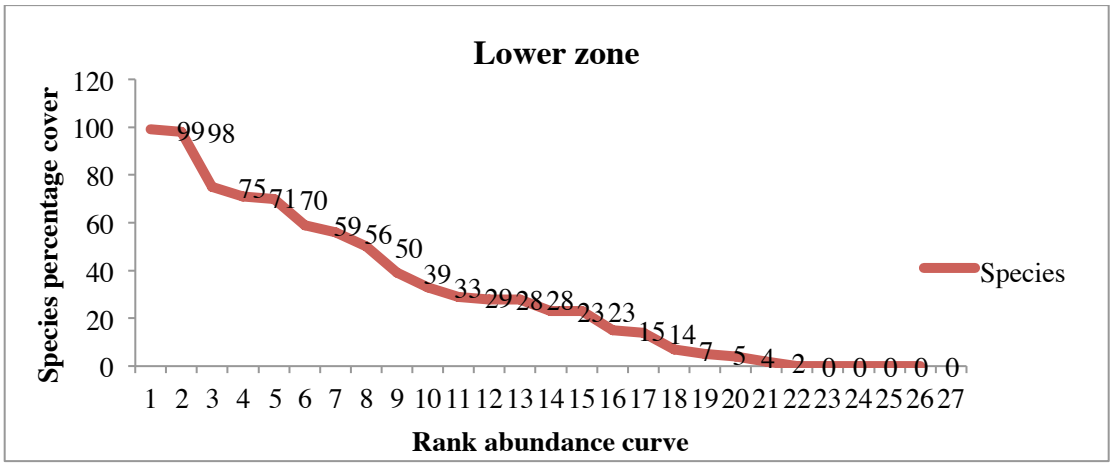

Figure 3.6 Rank-abundance curve for species occurring in the lower zone ranked from 1, the species with the highest percentage cover, to 26, the species with the lowest percentage cover.

Table 3.6 Species rank abundance in the lower zone

Rank abundance	**Species**	Species
1	*Dracoscirpoides falsa*	99
2	*Helichrysum praecurrens*	98
3	*Helichrysum albo-brunneum*	75
4	*Felicia rosulata*	71
5	*Helichrysum trilineatum*	70
6	*Helichrysum subglomeratum*	59
7	*Gnidia burchellii*	56
8	*Psammothropa obtusa*	50
9	*Geum capense*	39
10	*Crassula vaillanti*	33
11	*Helichrysum bellum*	29
12	*Scabiosa columbaria*	28
13	*Merxmuellera drakensbergensis*	28
14	*Geranium incanum*	23
15	Unknown Herb	23
16	*Cerastium arabidis*	15
17	*Erica frigida*	14
18	*Felicia uliginosa*	7
19	*Helichrysum album*	5
20	*Crassula papillosa*	4
21	Unknown Herb	2
22	*Senecio tugelensis*	0
23	*Glumicalyx flanaganii*	0
24	*Helichrysum milfordiae*	0
25	*Ornithogalum bicornutum*	0
26	*Helichrysum witbergense*	0

In all three zones *Dracoscirpoides falsa* was the most dominant species, and *Helichrysum praecurrens* was the second most dominant species (Tables 3.4 – 3.6). The six highest-ranking species are the same across all the zones (Tables 3.4 – 3.6), and species composition did not differ across the zones as 20 species occurred across all the zones and only differed in abundance from zone to zone (Tables 3.4 – 3.6).

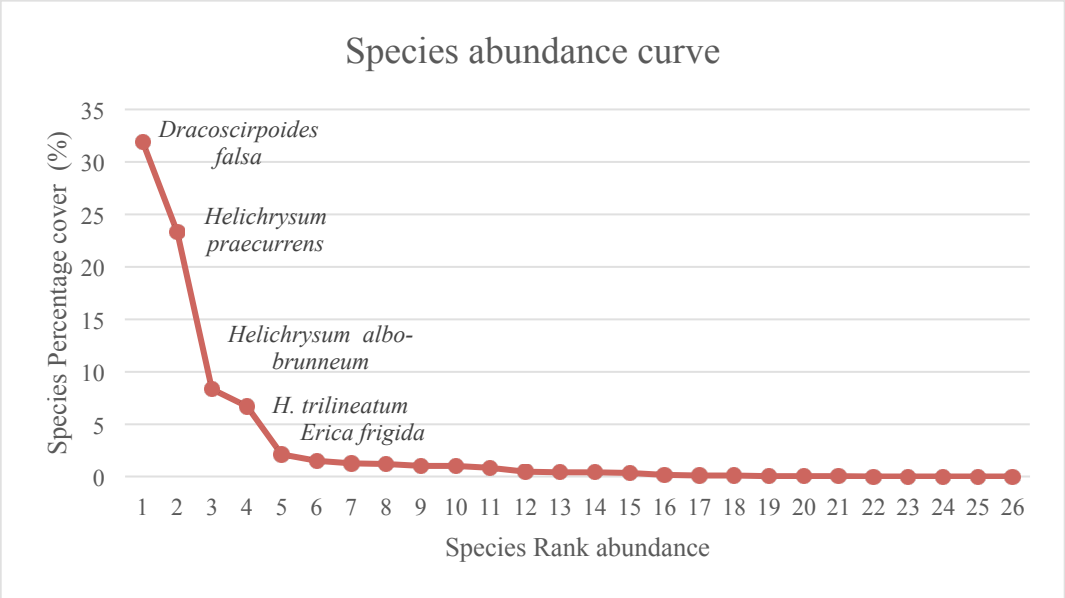

Figure 3.7 Rank-abundance curve for species occurring in the study area, the labelled species have >2% species cover.

3.2.2 Species evenness (E_{var})

There was relatively high species evenness in the vegetation on the south-facing slope below the rock scarp at the study site, ranging from 0.76 to 0.64 (Figure 3.9). This was due to the majority of species being present in small numbers and therefore contributing minimally to percentage cover. The lower zone was significantly different from the middle and upper zone, while there was no significant difference in evenness between the upper and middle zones (P = 0.002; $F_{2, 27}$). The upper zone (0.76 ± 0.032 E_{var}) had the highest evenness, slightly higher than the middle zone (0.74 ± 0.014 E_{var}) while the lower zone (0.64 ± 0.02 E_{var}) had the lowest evenness (Figure 3.8) due to the tussock grasses and *H. trilineatum* species dominating in this zone. Mean species evenness across the three zones combined was 0.71 E_{var}, suggesting relatively high evenness overall (Figure 3.8).

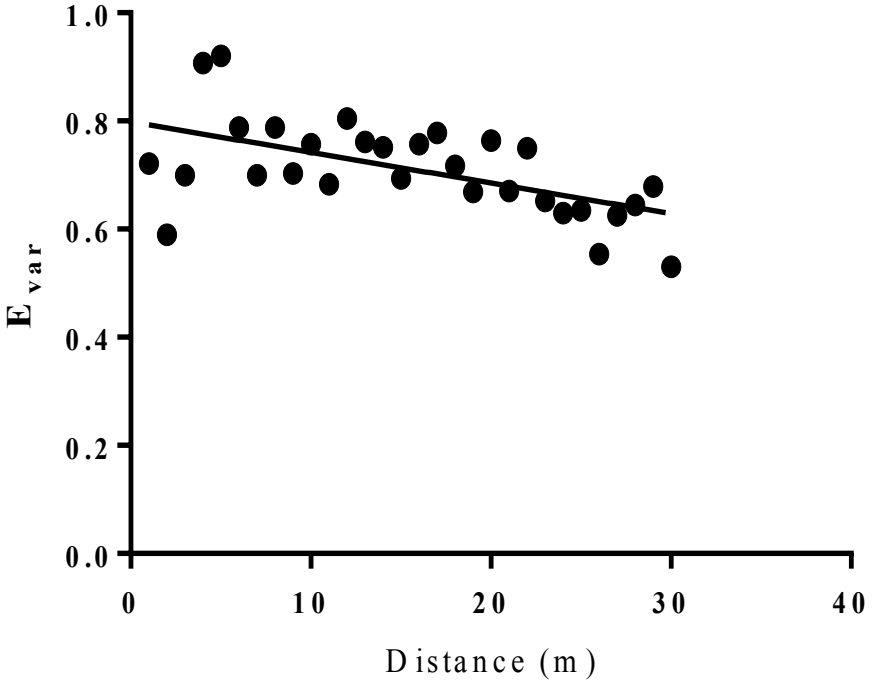

Figure 3.8 Species evenness (E_{var}) along the 30 m gradient across the upper (0 - 10 m), middle (10 - 20 m) and lower (20 - 30 m) zones at the study site near Kotisephola Mountain, Lesotho, $R^2 = 0.319$.

3.2.3 Species diversity as per the Shannon Index (H')

Species diversity in the upper (2.23 ± 0.09 *H*') and middle (2.17 ± 0.04 *H*') zones was not significantly different, however species diversity in the lower zone (1.88 ± 0.06 *H*') was significantly different ($P = 0.002$; $F_{2, 27}$) from both the upper and middle zones (Figure 3.9). The presence of the large clumps of the tussock grass *Merxmuellera drakensbergensis* and the shrublet *Helichrysum trilineatum* are the likely cause of the low species diversity in the lower zone, due to the high abundance (dominance) of these species in this zone.

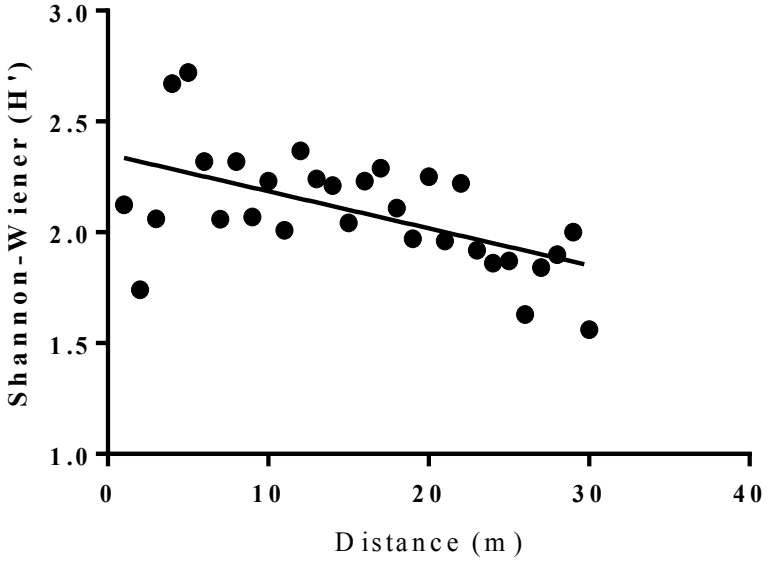

Figure 3.9 Shannon Index (H') of species diversity along 30 m gradient across the upper (0 - 10 m), middle (10 - 20 m) and lower (20 - 30 m) zones at the study site near Kotisephola Mountain, Lesotho, $R^2 = 0.319$.

3.2.4 Species and growth form composition and vegetation cover

The study site is a rocky grassland with very limited bare ground owing to the mat-forming species and graminoids, which cover the ground up to 80% in the various zones (Figures 3.10 & 3.11). They dominated the upper and middle zones providing 32% and 35% cover respectively, while the lower zone was dominated by the large tussock grass *Merxmuellera drakensbergensi*s with a percentage cover of 23 *Merxmuellera drakensbergensis* which occurred from about 20 m from the southeast facing wall of the rock scarp, whereas the small sedge (*Dracoscirpoides falsa*) occurred throughout the site. The total area covered by graminoids ranged from 32 – 37% across all three zones while the lower zone had the highest grass cover followed by the middle zone with 35% (Figure 3.10).

Shrublets were the third most dominant growth form across the upper, middle and lower zones with 5.7%, 6.7% and 5% respectively (Figure 3.10). Herbs had the highest percentage cover of 5.7% in the middle zone, and were lowest in the lower zone at 3.4%. Mosses and lichens had the lowest percentage cover across all three zones, with the percentage cover by mosses ranging from 0.3 – 1.1% (Figure 3.10). Percentage cover of

crustose lichens (occurring only on the rocks) was only 0.2% in the upper zone and 0.1% in both the middle and lower zones.

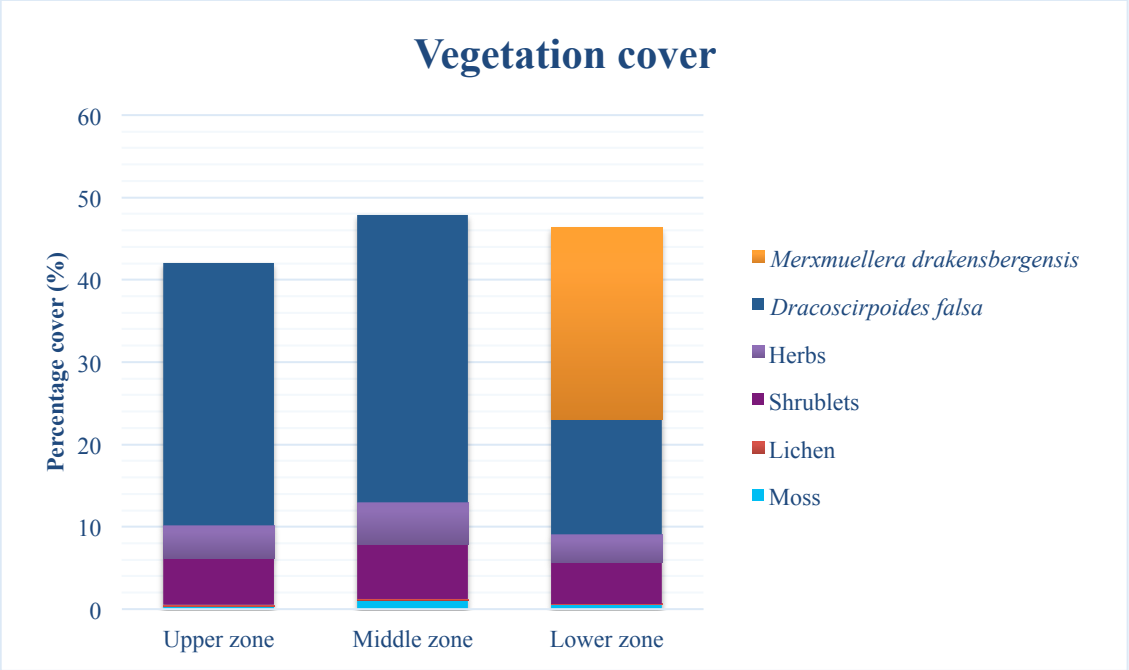

Figure 3.10 Vegetation percentage cover categories (including grasses, sedges, herbs, shrublets, lichens and moss) across the upper, middle and lower zones, of the slope at the study site near Kotisephola Pass at 3325 m.a.s.l.

Shrubs had the highest percentage cover compared to the other three growth forms. Shrubs ($P = 0.02$; $F_{2,27}$) in the middle zone were higher than the upper and middle zone, the middle zone (3.05 ± 0.14) was not significantly different to the upper zone (2.30 ± 0.34), but was significantly different to the lower zone (2.12 ± 0.13). Herbs in the middle zone had a higher percentage cover compared to the upper and lower zones ($P = 0.05$; $F_{2,27}$). The middle zone (1.09 ± 0.06) was not significantly different to the upper zone (1.06 ± 0.08), however it was significantly different to the lower zone (0.86 ± 0.07).

Moss in the upper zone was significantly different from the middle zone ($P = 0.07$; $F_{2,27}$), however the middle and lower zones were not significantly different. Moss had the highest percentage cover in the upper zone (1.19 ± 0.39), compared to the middle (0.34 ± 0.14) and lower zones (0.52 ± 0.20). Lichen was not significantly different across all three zones ($P = 0.5$; $F_{2,27}$). The upper zone had a higher percentage cover (0.67 ± 0.22)

compared to the middle zone (0.48 ± 0.15) and the lower zone had the lowest percentage cover (0.49 ± 0.09).

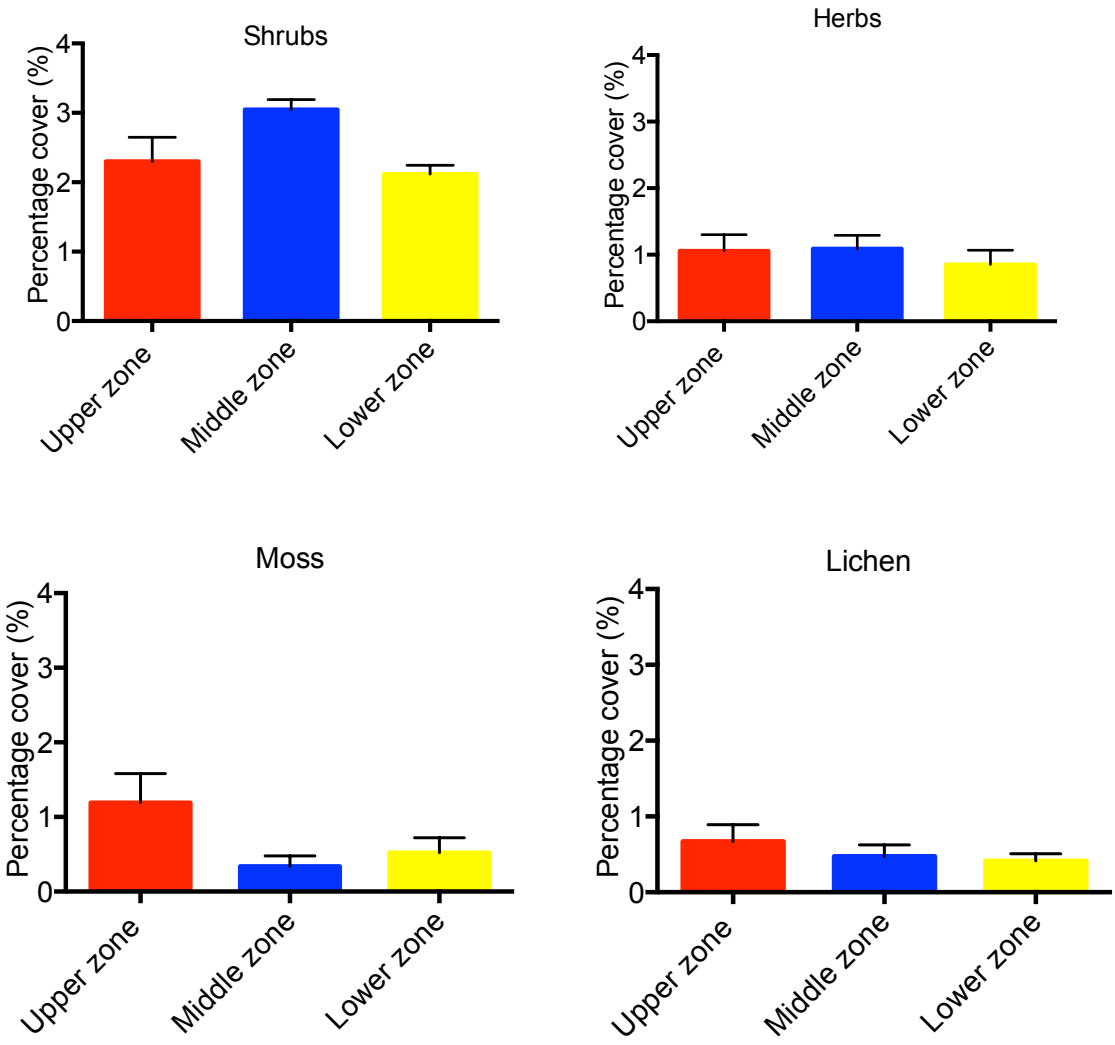

Figure 3.11 Four dominant growth forms including shrubs, herbs, moss and lichen compared across the upper, middle and lower zones.

Rock cover was significantly different between the upper and lower zones, however the middle zone was not significantly different to the neither upper nor lower zone ($P = 0.087$; $F_{2,7}$). The upper zone had the highest percentage rock cover (19.79 ± 2.75), while the middle (15.66 ± 1.63) and the lower zones (13.22 ± 1.91) had lower rock covers. The study area overall was not highly disturbed ($P = 0.90$; $F_{2,27}$), although the lower zone was the most disturbed zone (8.15 ± 0.68). This was probably due to domestic grazing and

pathways created by sheep and shepherds, while the upper (8.55 ± 0.82) and the middle zones (8.58 ± 0.79) were slightly more disturbed (Figure 3.12).

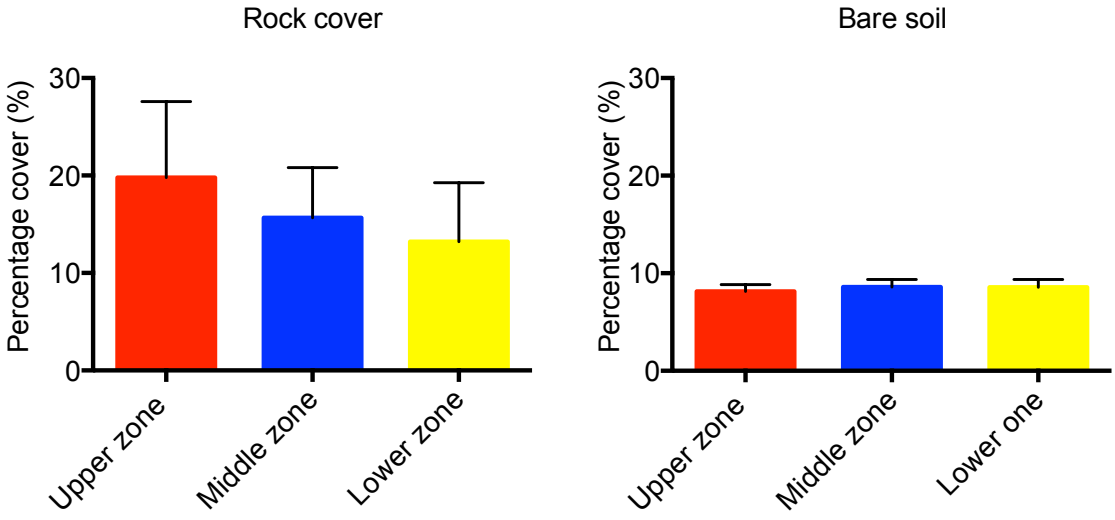

Figure 3.12 Surface percentage cover (bare soil and rock) across the upper, middle and lower zones of the slope at the study site near Kotisephola Pass at 3325 m.a.s.l.

The lower zone had the tallest species in height compared to the middle and the lower zones ($P = 0.0003$; $F_{2, 27}$). The upper zone (18.37 ± 1.2) was significantly different to the middle (26.28 ± 1.2) and the lower zone (28.78 ± 2.3), while the middle and the lower zones were not significantly different (Figure 3.13).

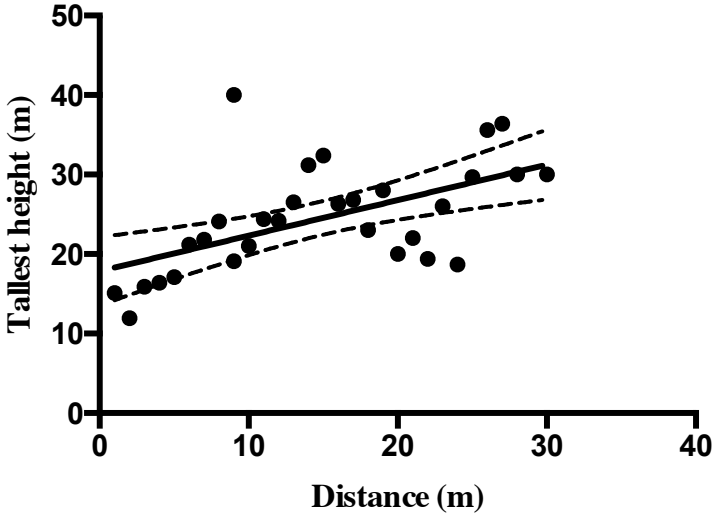

Figure 3.13 Tallest plant height along the 30 m transects across the three zones; upper (0 - 10 m), middle (10 - 20 m); and lower (20 - 30 m), R2 = 0.318.

3.3 Discussion

3.3.1 Species composition and vegetation cover

Species composition and diversity in the alpine regions are typically influenced by cold winters and short growing seasons, except in tropical alpine regions (Kudo & Ito, 1992; Bauer, 2002). Alpine regions have low species richness compared to lowlands (Moen & Lagerström, 2008); this is a result of unfavourable environmental conditions in the mountains, and could explain why only 26 species were collected across the slope from upper to lower zone at the research site for this study in the DAC. Herbaceous plants are the dominant life form in alpine regions as they are one of the plant life forms most suited to alpine climatic conditions (Körner, 1999). Of the 26 species occurring at the study site, 16 species were perennial herbs, including the two grass species. Dwarf shrublets were the second dominant life form in this study, comprising three species; namely, *Helichrysum trilineatum, H. witbergense* and *Erica frigida*. These shrublets are evergreen and cover a relatively large aerial percentage cover. This is because of their stature; shrublets have many small leaves and are highly branched, while herbs have few leaves and basal rosettes and therefore often have less aerial percentage cover. *Helichrysum praecurrens,* a densely tufted, mat-forming herb, was the most dominant

species at the study site. This is to be expected as densely tufted plants (like cushion plants) are very well adapted to this alpine environment. Their compactly rosetted leaves and close attachment to the ground/substrate enable them to trap solar heat and humidity, and restrict air movement (Körner 2003, 2007). These features enhance the plants' ability to withstand the extreme weather conditions, such as the cushion plant *H. milfordiae* which was found attached to the rocks, with a thick woolly indumentum (covering of hairs) on its leaves. The prostrate branches of *H. praecurrens* were closely attached to the ground with narrower smaller leaves compared to *H. milfordiae*.

The upper zone had the highest number of species (11) and, in addition to *Helichrysum witbergense*, was dominated by *H. praecurrens*. *H. witbergense* occurred only in this zone – the leaves of this shrublet are sticky, which indicate some chemical secretion and are also covered in hairs (especially on the ventral surface). The deep channelling of the parallel lateral veins could provide a site for 'sunken stomata', which would reduce transpiration like in *Pinus sylvestris* (Irvine *et al*., 1998).

In contrast, the lower zone had a mean of 8.77/ m^2 species and was dominated by tussock grasses. This zone is exposed to sunlight for several hours of the day, experiences extreme fluctuations of very cold temperatures at night and warm during the day, and high levels of solar radiation. This zone is usually covered by snow only in the first few days after the snowfall. Plants growing in this zone therefore have a very high tolerance to high and low temperatures. Tussock grasses are hardy with an extensive root system and can thrive in dry and poor soil conditions, hence they are a dominant plant life form in the alpine regions, and occur in varying habitats such as wetlands, riverbeds, deserts and tundra (Medek *et al*., 2007; Starr *et al*., 2008).

Alpine vegetation, especially that growing in the snow patches where snow persists into the growing season, is dominated by species that can tolerate short growing seasons; these species include shrublets, cushion plants, graminoids and herbs (Kudo & Ito, 1992; Wahren, 2001). Bannister *et al*. (2005) found that species from snow bank and sheltered habitats have a significantly lower frost tolerance compared to species in windward habitats with no shelter. Plants under snow cover can only start development and flowering after snowmelt, as most plants are dormant when under snow and therefore there is very little plant activity until the snow melts (Richardson & Salisbury, 1977;

Litaor *et al.,* 2008; Jackson *et al.,* 2009; Walker *et al.*, 1995). Species such as *H. witbergense* that only occur in the upper zone which is covered by snow for several months during some years, also start flowering immediately after snowmelt. This is the case for most species in the upper zone, whereas species in the lower zone start flowering earlier due to early snowmelt.

3.3.2. Species richness and turnover relationship with environmental factors

Alpine species richness is very dynamic, it can vary within one community according to varying snow cover and depth (Keller *et al.*, 2005; Venn *et al.*, 2012). At this study site there were c. 11 species per m^2 in the upper zone and 8 species per m^2 in the lower zone (only 10–20 m further down the slope). The higher species richness in the upper zone may be due to the buffer against the elements provided by the snow during winter, and the rock scarp acting as a snow-fence allowing snow banks to build up in front of it and thereby protecting the plants through insulation and providing shade and reducing high solar radiation and increasing soil moisture. The lower zone had the lowest species richness as these species are exposed to hot and cold temperatures and extreme solar radiation. Another possible reason for the low species richness in the lower zone is that the tussock grasses and shrublets are more prevalent in this zone and may be outcompeting the smaller herbaceous plants. Tussock grasses were only found in the lower zone, this could be due to the lower soil moisture temperature in this zone compared to the middle and upper zones, as these grasses are reported to be influenced by this environmental factors (Noble, 1980; Walker *et al.*, 2003). Litter from the tussock grasses and Asteraceae forbs (*Helichrysum trilineatum*) insulates the soil, but the resulting lack of sunlight also prevents new seedlings from growing (Venn *et al.*, 2012).

A study in the Snowy Mountains of the Australian Alps, ranging from 1813 – 2114 m.a.s.l, showed that an average increase of one new species per year occurred between 2004 and 2012 in the alpine zone (Venn *et al.,* 2012). An increase in species richness has also been reported in the European Alps (Moen & Lagerström, 2008; Gottfried *et al.,* 2012; Venn *et al.*, 2012). The increase in species richness in the alpine summits such as European Alps is a result of species shift from lower altitudes (Pauli *et al.,* 1996), however species richness generally deceases with increasing elevation because

of low temperatures resulting to decrease in productivity (Thuiller, 2004; Bertrand *et al*., 2011; Heubes *et al*., 2011; Venn *et al*., 2012). However at this study site, due to the micro-zonation, the opposite was discovered as the tussock grasses and shrublets may have outcompeted species of other, smaller life forms in the lower zone and as a result were the most dominant (Cavieres *et al*., 2005; Sklenar, 2009)

Alpine vegetation responds to one or all of the environmental factors present at the site (Kudo & Ito, 1992; Venn *et al*., 2012). Results from this study concur with these findings as species richness increased with decreased solar radiation and increased soil moisture and minimum temperature. Venn *et al*. (2012) reported that tall herbaceous, shrubby and mat-forming species in the family Asteraceae are predicted to be adaptive with environmental change due to their wide distribution (i.e. range of temperatures, snow cover, solar radiation and soil moisture). Asteraceae is one of the families with species that favors wind dispersal as a result of the morphology of the seeds, groups within Asteracea have been reported to produce diaspores with wing structures, and other diaspores with plumose or comose structures which act as drag enhancing parachutes thereby enhancing wind dispersal (Andersen, 1993). Furthermore, *Helichrysum* has light seeds (ca. 1mm), making them easy to disperse by wind over long distances (Galbany–Casals *et al*., 2009). Asteraceae is the dominant family at this study site with two genera and 11 species. *Helichrysum praecurrens* is the most abundant species covering the largest area of the study site, followed by *H. trilineatum*. The distribution and abundance of four selected *Helichrysum* species will be discussed more fully in Chapter Four.

3.3.3 Habitat structure in relation to slope inclination and rock-scarp

Species' distribution is influenced by snow depth and longevity along a snow gradient, as well as other related environmental factors such as temperature, soil moisture and solar radiation (Billings & Bliss, 1959; Kudo & Ito, 1992; Kudo, 1992; Kudo *et al*., 2010; Bliss, 2013). Plant growth and phenology on a snow bed gradient are dependent on the time of snowmelt (Kudo & Ito, 1992; Kudo, 1992). Three zones were identified as a result of the vegetation differences observed at this study site due to the typically deeper and more persistent snow-cover at the base of the rock providing more favourable conditions in the upper zone. There is a gap in snow cover (several cm in width) which

develops immediately adjacent to the scarp (Figure 2.2) some time after snowfall, possibly due to warmer conditions associated with radiation from the rock and air flow dynamics which differentially ablate and deflate the snow cover adjacent to the rock wall. Consequently, air and ground temperatures in this area remain higher than in the lower zones during winter when there is snow cover. The upper zone was therefore the most species rich zone and species richness decreased down the gradient. Species flowered later in the upper zone compared to the lower zones due to the snow clearing earlier in the lower zones, and possibly also the increased shade from the rock scarp. Plants in the upper zone therefore have a shorter growing period compared to plants in the lower zones due to the timing of snowmelt and daily sunlight. Several studies have found that plant growth and flowering are closely associated with the timing of snowmelt (Kudo & Ito, 1992; Ferrari, 1995; Totland & Alatalo, 2002; Wipf *et al*., 2009). This also helps to explain the phenological differences observed in the upper and lower zones, which will be further dealt with in Chapter Four.

3.4 Conclusion

Notable differences in vegetation were observed across the three zones below the rock scarp due to differences in the snow cover, depth and persistence and several related environmental differences. A vegetation gradient was therefore observed at this site despite the short distance (30 m) that was sampled, owing to the steep environmental gradient at this study site. The study site was a rocky-grassland, mostly covered by short and tussock grasses and scattered rocks. The three zones (upper, middle and lower) that we identified showed significant differences in species richness and evenness. Species composition and diversity also differed across the zones. The upper zone had the highest species richness, very likely because it has the most favourable winter conditions due to the snow that buffers the zone for several months in winter (when it falls in sufficient quantities to persist). Snow, as well as other variables such as temperature, solar radiation and soil moisture have clearly played a significant role in shaping the habitat structure and species diversity at this study site, as some of the plants that occurred in the upper zone were not found in lower zones, and abundance of the various species varied greatly across the zones.

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APPENDIX

List of Species

Species list	**Family**	**Growth form**	**Monocot/ dicot**
Helichrysum witbergense Bolus	Asteraceae	Perennial dwarf shrublet	Dicotyledon
Helichrysum trilineatum DC	Asteraceae	Perennial dwarf shrublet	Dicotyledon
Helichrysum subglomeratum Less	Asteraceae	Perennial herb	Dicotyledon
Helichrysum albo-brunneum S. Moore	Asteraceae	Perennial herb	Dicotyledon
Helichrysum album N. E. Br	Asteraceae	Perennial herb	Dicotyledon
Helichrysum bellum Hilliard	Asteraceae	Perennial herb	Dicotyledon
Helichrysum milfordiae Killick	Asteraceae	Perennial herb	Dicotyledon
Helichrysum praecurrens Hilliard	Asteraceae	Perennial herb	Dicotyledon
Felicia rosulata Yeo	Asteraceae	Perennial herb	Dicotyledon
Felicia uliginosa JM. Wood & MS Evans	Asteraceae	Perennial herb	Dicotyledon
Senecio tugelensis JM Wood & MS Evans	Asteraceae	Perennial herb	Dicotyledon
Crassula vaillanti Schonland & Baker f.	Crassulaceae	Annual herb	Dicotyledon
Crassula papillosa (Wild.) Roth	Crassulaceae	Perennial herb	Dicotyledon
Geranium incanum Burm	Geraniaceae	Perennial herb	Dicotyledon
Glumicalyx flanaganii (Hiern) Hilliard & B.L. Burtt	Scrophulariaceae	Perennial herb	Dicotyledon
Cerastium arabidis E.Mey. ex Fenzl	Caryophyllaceae	Annual	Dicotyledon
Scabiosa columbaria L	Dipsacaceae	Perennial herb	Dicotyledon
Psammothropa obtusa Eckl. & Zeyh. Adamson	Molluginaceae	Perennial herb	Monocotyledon
Dracoscirpoides falsa (C. B. Clarke) Muasya	Cyperaceae	Graminoid	Monocotyledon
Merxmuellera drakensbergensis drakensbergensis (Schweick.) Conert	Poaceae	Graminoid	Dicotyledon
Geum capense L. Thunb.	Rosaceae	Perennial herb	Dicotyledon
Erica frigida L. Bolus	Ericaceae	Perennial shrub	Dicotyledon
Gnidia burchellii L. (Meisn.) Gilg	Thymelaeaceae	Perennial dwarf shrub	Dicotyledon

Ornithogalum bicornutum L.F.M.Leight.	Hyacinthaceae	Perennial geophyte	Dicotyledon
unknown	Unknown	Perennial herb	Dicotyledon
unknown	Unknown	Perennial herb	Dicotyledon

CHAPTER 4 – Morphology, Ecophysiology and Phenology of four alpine *Helichrysum* species

Abstract

Helichrysum is the largest genus (102 species) in the Drakensberg Alpine Centre (DAC), an area renowned for its rich flora and high levels of endemism. Thus, *Helichrysum* was the largest genus at the study site near Kotisephola Mountain in eastern Lesotho in the DAC, with eight species collected and identified between 2012 and 2013. The aim of this study was to compare the morphology, ecophysiology and phenology of the four selected *Helichrysum* species: *H. witbergense, H. trilineatum, H. albo-brunneum* and *H. subglomeratum* between the three zones. Two of the four selected species, *Helichrysum albo-brunneum* and *H. subglomeratum*, are herbaceous plants while *H. trilineatum* and *H. witbergense* are shrublets, and one of each pair is widespread whereas the other is locally endemic or near-endemic. Leaf area and thickness of fresh leaves and leaf dry mass were measured, as well as chlorophyll content in fresh leaves using a SPAD meter. *Helichrysum witbergense* and *H. trilineatum* (the shrublets) had many small leaves, while *H. subglomeratum* and *H. albo-brunneum* (perennial herbs) had fewer leaves with larger leaf areas compared to the shrublets. Furthermore, the leaves of the two herbaceous plants had higher chlorophyll content compared to the shrublets. Leaf surface area of the four *Helichrysum* species was significantly different across the three zones while leaf thickness and dry mass were not significantly different. Specific leaf area (SLA) was also not significantly different across the four species; *Helichrysum witbergense* had the highest SLA while *H. albo-brunneum* had the lowest SLA. Most plants were flowering in January 2013; plants in the lower zones flowered earlier than plants in the upper zone, possibly due to exposure to sunlight for longer hours. *Helichrysum trilineatum* and *H. witbergense* were already flowering in mid-November 2012, while *H. subglomeratum* and *H. albo-brunneum* started flowering in mid-January 2013. The difference in the environmental factors across the three zones did not result in significant differences in the phenology and morphology of the plants, except for the leaf surface area, which varied significantly across the zones.

4.1 Introduction

Helichrysum Mill. (Tribe: Gnaphalieae, Asteraceae) is an important component of the alpine flora in the DAC as it is the largest genus with ca. 102 species that occur from lower altitudes to the alpine zone [Carbutt 2004; SANBI's Integrated Biodiversity Information System (SIBIS): South African Biodiversity Information Facility (SABIF)]. The genus comprises ca. 600 species and is widely distributed, occurring mainly through much of the eastern mountain sector of Africa, South Africa, Madagascar and in parts of Europe, Asia and Australia (Bremer, 1994; Bayer *et al.,* 2007). In Southern Africa, *Helichrysum* has ca. 254 species, 133 in KwaZulu-Natal and 76 species have been recorded in Lesotho (Carbutt & Edwards, 2004; SIBIS: SABIF). *Helichrysum* is predominantly found in mountainous regions such as the Tecer mountain in Turkey, through the north African mountains (e.g. Morocco and Algeria), the East African rift system from southern Cape through to Eritrea (Hedberg, 1964; Meyer & Dilika, 1996; Tepe *et al*., 2005; Galbany-Casals & Romo, 2008; Galbany-Casals *et al*., 2009; Süzgeç-Selçuk & Birteksöz, 2011), and the southern African mountains such as the Drakensberg, Sneeuberg and the Cape Fold Mountains (Hilliard & Burtt 1987; Pooley, 2003; Clarck *et al*., 2009).

The name *Helichrysum* is derived from the Greek words '*helisso*' (turn around) and '*chrysos*' (gold) (Aiyegoro & Okoh, 2010), referring to the fact that papery bracts of their capitula (flower heads) are frequently golden-yellow (but also white, brown or pink). *Helichrysum* has several life forms: herbs and shrublets or subshrubs, and cushion-forming dwarf shrubs. The plants often have greyish-woolly leaves, which are usually alternate, rarely opposite and always entire (Hilliard, 1977; Hilliard, 1983; Hilliard & Burtt, 1987; Pooley, 2003). Their capitula may be solitary or arranged in lax corymbs, homogamous, i.e. with either unisexual or bisexual florets but not both, or heterogamous, often with bisexual outer florets and unisexual inner florets (Hilliard 1981; Galbany-Casals & Romo, 2008).

Helichrysum species often have aromatic leaves and are well known for their medicinal value (Meyer & Dilika, 1996; Afolayan & Meyer, 1997; Aslan *et al*., 2007; Aiyegoro & Okoh, 2010; Albayrak *et al*., 2010). For at least 2000 years various *Helichrysum* species have been known to treat gall bladder disorder, remove kidney

stones, alleviate diabetes symptoms and treat herpes zoster, while others are used to heal bruises (Meyer *et al.,* 1996; Aslan *et al.,* 2007; Tepe *et al.,* 2005; Albayrak *et al*., 2010). *Helichrysum* is also known for its anti-inflammatory, antioxidant and antimicrobial activities, and is used as a herbal tea in some parts of the world (Tepe *et al.,* 2005; Albayrak *et al*., 2010). *Helichrysum aureonitens* (common in the montane to subalpine zones of the DAC) is one of the widely used species by indigenous people of South Africa for treating herpes and as an antibacterial medicine (Meyer *et al.,* 1996; Afolayan & Meyer, 1997). Because *Helichrysum* is one of the dominant genera in the DAC and at the study site, four of its species occurring at the study site were selected for detailed study of their morphology, ecophysiology and phenology.

The selected *Helichrysum* species occur in the alpine areas and survive under extreme weather conditions. Alpine species have morphological features that enable them to survive under harsh environmental conditions such as strong winds, prolonged snow cover, high levels of solar radiation, extreme diurnal temperature ranges and frost damage (Billings & Bliss, 1959; Bliss, 1971; Körner, 2007). These morphological characters include thick indumenta of woolly hairs, rosette leaves attached to the ground, and cushion plants, which tend to trap solar heat enabling them to survive cold temperatures (Körner, 2007). Cushion plants further trap air humidity and restrict air movement creating a humid environment, which allows for a photosynthesizing environment (Körner, 2007). Alpine plants such as cushion plants and shrubs often have deep roots; enabling them to access deep soil moisture during the dry season, particularly in snow beds (Oberbauer & Billings, 1981). Deeply rooted species such as *Polygonum bistortoides* have been reported to have high leaf conductance and survive on lee and windward slopes (Oberbauer & Billings, 1981). Some small herbs with shallow roots have sufficient access to water in the shallow soils as it is adequate for their full development (Oberbauer & Billings, 1981). Alpine plants in snow bed areas have a small stature as a response to cold temperature and therefore often experience little reduction in meristem temperature due to increased resistance to extreme weather conditions (Hedberg, 1964). These morphological features commonly seen in alpine plants, such woolly hairs, thick and viscid (sticky) leaves are found in most *Helichrysum* species. Examples include *H. milfordiae* – a cushion plant with woolly hairs, *H. witbergense* – a

shrublet with sticky leaves, and the herb *H. albo-brunneum* with woolly hairs on its basally rosetted and cauline leaves.

Phenology (flowering period or leaf fall) may be used as a tool to monitor impacts of climate change on plants as it measures the period of the growing season, flowering stage and intervals at which flowering and leaf fall occur; these data can be linked to environmental variables such as temperature, snow cover, solar radiation and soil moisture (Leith, 1974). The phenology of alpine species is highly influenced by the date of snowmelt, as there is minimal growth under snow (Kudo, 1991; Rixen *et al.,* 2001; Inouye, 2008). Phenology is also strongly influenced by micro-climate which is controlled by factors such as slope orientation which affects snow accumulation and longevity (Rixen *et al*., 2001; Dunne *et al.,* 2003; Inouye, 2008; Hülber *et al*., 2010).

Flowering period governs a plants' reproductive success, as it influences their fitness, e.g. by flowering in the right season for mating and pollinators (Dunne *et al*., 2003; Inouye, 2008). Plant phenology can be measured by observing and recording recurring growth stages of yearly cycles of plant development (Leith, 1974). Low air and soil temperatures and late snowmelt delay flowering as the plant's development starts after snowmelt and with temperatures above the freezing point (Kudo, 1991; Rixen *et al.,* 2001: Hülber *et al*., 2010). In snow rich mountain environments, snow is the primary controlling factor of the growing season and phenology; in some cases plants remain dormant under snow cover and start flowering after snow disappearance (Billings & Bliss, 1959; Kudo, 1991; Dunne *et al.,* 2003; Hülber *et al.,* 2010).

Ecophysiological characteristics such as specific leaf area (SLA) usually correlate with environmental conditions as it is an indicator of the plant's stress tolerance, for example plants with low SLA are more stress tolerant (Scheepens *et al.,* 2010). Furthermore, an increase in SLA indicates a decreased leaf thickness and density as SLA decreases with increasing altitude, relative growth rate, and leaf longevity (Scheepens *et al.,* 2010). The increase of SLA with decreasing altitude is the response triggered largely by increasing temperatures and a change in water availability; SLA is reportedly higher in areas with late snowmelt due to faster decomposition (Baptist *et al.,* 2009; Scheepens *et al.,* 2010).

4.1.1 The study species

Asteraceae dominated the study site (see chapter 3) with 11 species and 10 of them were *Helichrysum species*. Consequently, four *Helichrysum* species of varying life forms that occur at the study site were selected for this aspect of the research: *H. albo-brunneum, H. subglomeratum, H. witbergense* and *H. trilineatum*. Of these four species, two are shrublets — *H. witbergense* and *H. trilineatum,* whilst the other two (*H. subglomeratum* and *H. albo-brunneum*) are herbaceous plants (Figure 4.1).

Helichrysum albo-brunneum is herbaceous with basal leaf rosettes, grey-woolly leaves, a solitary flowering stem, and its height ranges from 15 – 30 cm (Hilliard 1977, Hilliard & Burtt 1987; Pooley 2003). It occurs in damp rocky grassland on summit plateaus between 1670 – 3355 m.a.s.l., mainly in Lesotho and adjoining high mountain areas of KwaZulu-Natal, the Eastern Cape and Free State (Figure 4.2; Hilliard & Burtt 1987; Pooley, 2003). The second herbaceous species, *Helichrysum subglomeratum,* occurs in stony grasslands, and ranges from 10 – 60 cm in height. It is the most widespread of the four selected species and is widely distributed across South Africa, Lesotho and highlands of Zimbabwe (Figure 4.2) at altitudes between 5 and 3475 m.a.s.l. *Helichrysum subglomeratum* has several basal leaf rosettes with a grey-woolly, silky, felted indumentum on its linear-lanceolate leaves and several flowering stems bearing compact clusters of capitula with yellow bright involucral bracts (Hilliard, 1977; Hilliard & Burtt 1987; Pooley, 2003).

Helichrysum witbergense is a dwarf shrublet confined to shady, moist habitats and grows up to 90 cm high (Pooley, 2003). The leaves of *H. witbergense* are very sticky with conspicuous parallel veins, and the capitula have bright yellow involucral bracts (Hilliard, 1977; Pooley, 2003).

Figure 4.3 Selected study species: (A1 & A1) *Helichrysum witbergense*, (B & B1) *H. trilineatum*, (C) *H. subglomeratum* and (D) *H. albo-brunneum*. All photographs were taken at the study site.

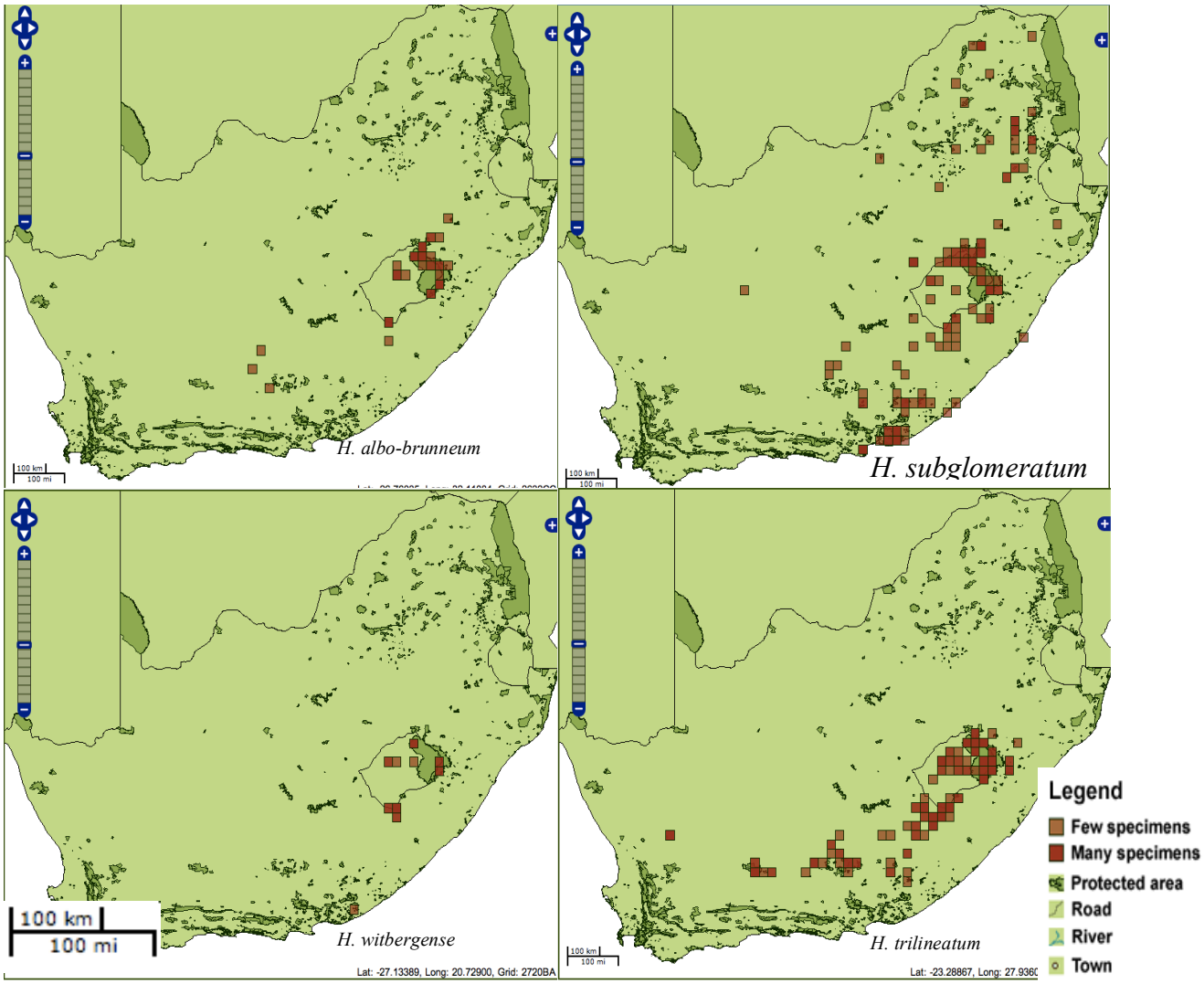

Figure 4.4 Distribution maps for the four *Helichrysum* study species (A) *Helichrysum albo-brunneum* (B) *Helichrysum subglomeratum* (C) *Helichrysum witbergense* and (D) *Helichrysum trilineatum* across South Africa and Lesotho. Source: http://sibis.sanbi.org/

Helichrysum witbergense occurs at very high altitudes ranging from 2600 – 3475 m.a.s.l., mainly in Lesotho, but with some extension into the KwaZulu-Natal Drakensberg, and is often found growing on dry rocky grassland slopes (Pooley, 2003). *Helichrysum witbergense* is very similar morphologically to *H. trilineatum* which is also a perennial dwarf shrub; this species grows up to 1.2 m in height (Hilliard, 1977; Pooley, 2003). The leaves of *H. trilineatum* have three distinct veins above and below the leaf and are grey-woolly on both sides. The leaf indumentum of this species is very variable, and as a result this species is often confused with three other *Helichrysum* species

namely: *H. tenuifolium, H. splendidum* and *H. montanum* (Hilliard, 1977). *Helichrysum trilineatum* has a relatively wide distribution ranging in altitude from 1250 to 3355 m.a.s.l.; it occurs in three South African provinces: the Eastern Cape, Free State and KwaZulu-Natal, and also in Lesotho (Figure 4.1).

The aim of this study was to investigate and compare the morphology, ecophysiology and phenology of four selected alpine plant species that persist within winter snow patches in the cline adjacent to the rock scarp at the Black Mountain Pass study site, in and between the three zones, by addressing the following questions:

f. What are the leaf morphological features that characterise the four selected *Helichrysum* species, which survive under snow patches in the alpine region of the DAC?
g. How do selected ecophysiological features of the selected species vary across the zones of the study site?
h. What are the flowering patterns of the selected *Helichrysum* species across the zones at the study site?

4.1.2 Materials and methods

4.1.2.1 Leaf morphology and ecophysiology

Three sets of leaves from five plants of each species were collected in sealed plastic bags to retain moisture for measuring surface area, thickness and dry mass. Leaf thickness was measured when the leaves were still fresh using a digital Vernier calliper, and trace-graph paper was used to measure leaf surface area also from a fresh leaf. Leaves were then pressed in a small plant press and placed in a drying oven for 24 hours at the C.E. Moss herbarium, after which dry mass was measured using a Sartorius (2200, 00g) scale. Lastly, Leaf Specific Mass (LSM) was calculated by dividing leaf surface area by dry mass and Specific Leaf Area (SLA) was calculated by dividing dry mass by leaf surface area. Leaf area, thickness, dry mass, SLA and LSM were compared between the four *Helichrysum* species within and between the zones by one-way ANOVA and

Fisher's LSD, using GraphPad Prism 6, a statistical scientific software by GraphPad Software Inc.

Chlorophyll content measurements were taken in the field using a portable Minolta SPAD-502 DL Plus meter. Five readings from each plant were taken on mature fresh leaves (still attached to the plant); this was repeated on five plants of each of the study species across the three zones. However, readings for *Helichrysum witbergense* were restricted to the upper zone as the species only grows in this zone. All readings were taken in the morning between 10 and 11 am. To test for significant differences on SPAD meter readings across the species, one-way ANOVA and Fishers LSD from Graph Pad Prism 6 was used.

4.1.2.2 Phenology

A phenology survey of the four selected study plants (*Helichrysum subglomeratum, H. albo-brunneum, H. witbergense* and *H. trilineatum*) was conducted along fourteen line transects (each 30 m long) in October 2012, and again in January 2013 along two line transects. Quadrats of 1 m^2 were laid out on alternating sides along the transect line to ensure independent observation. To categorise the flowering stages of the plants, five flowering stages were established: no buds, bud emergence, bud burst, flower emergence, and full bloom. Each of the four species was then scored according to the presence or absence of each flowering stage within each quadrat. The average per species was obtained from the 1 m^2 quadrats at equivalent distances along the 30 metre transect over 14 transects in November 2012 and two transects in January 2013.

4.2 Results

4.2.1 Leaf morphological features

The four *Helichrysum* study species differed considerably in terms of leaf area, weight, thickness, and leaf specific mass (Figures 4.3 – 4.6). The largest leaf surface areas were found in the perennial herbs *H. albo-brunneum and H. subglomeratum,* while the evergreen shrublets (*H. witbergense* and *H. trilineatum*) had the smaller leaf surface areas (Figure 4.2).

The three species of *Helichrysum* that occurred in all three microzones at the study site (viz. *H. trilineatum, H. albo-brunneum and H. subglomeratum*) showed no significant differences in leaf thickness and dry mass across the zones (Table 4.1). However, significant differences were observed in leaf area: both *H. albo-brunneum* and *H. trilineatum* had their highest leaf area in the upper zone compared to the middle and lower zones, whereas *H. subglomeratum* exhibited its lowest leaf surface area in the upper zone (Table 4.1). There were no significant differences in leaf thickness in any the species across the zones; the dry mass for *H. albo-brunneum* and *H. subglomeratum* was significantly different across the zones while *H. trilineatum* was not significantly different across the zones (Table 4.1).

Leaf surface area was significantly different across all four species ($F_{3, 56} = 63.44$; $P < 0.0001$). The two herbaceous species, *H. albo-brunneum* (3.57 ± 0.30 cm^2), and *H. subglomeratum* (2.30 ± 0.17 cm^2) had larger leaf surface areas, while *H. witbergense* (0.97 ± 0.59 cm^2) and *H. trilineatum* (0.42 ± 0.002 cm^2) had smaller leaf areas (Figure 4.2). Leaf thickness of *H. albo-brunneum* (0.04 ± 0.001 mm) was significantly different ($F_{2, 56} = 78.83$; $P < 0.0001$) from the other three species: *H. subglomeratum* (0.02 ± 0.002 mm), *H. witbergense* (0.019± 0.002 mm) and *H. trilineatum* (0.02 ± 0.001 mm). Leaf dry mass was also significantly different across the four *Helichrysum* species ($F_{2,56} = 36.56$; $P < 0.0001$), with *H. albo-brunneum* (0.03 ± 0.002 g) and *H. subglomeratum* (0.02 ± 0.002 g) having the highest dry mass. *Helichrysum witbergense*'s dry mass was slightly higher than that of *H. trilineatum* but they were not significantly different (Figure 4.5; 0.007 ± 0.001 g).

Leaf specific mass varied significantly across the four *Helichrysum* study species ($F_{3, 60} = 3.95$, $P = 0.012$). *Helichrysum trilineatum* had the highest leaf specific mass (0.025 ± 0.001 g/cm^2) and was significantly different from *H. albo-brunneum* (0.008 ± 0.0006 g/cm^2) and *H. subglomeratum* (0.015 ± 0.005 g/cm^2), while *H. witbergense* (0.02 ± 0.004 g/cm^2) had the second highest leaf specific mass, but was not significantly differently from the other three species (Figure 4.6). Specific leaf area (SLA) was not significantly different ($F_{3, 92} = 0.35$, $P = 0.786$) across the four species (Figure 4.7). *Helichrysum witbergense* (156 ± 63.46 cm^2/g) had the highest SLA followed by *H.*

subglomeratum (151 ± 51.72 cm^2/g), while *H. albo-brunneum* (98.09 ± 4.6 cm^2/g) had the lowest SLA following *H. trilineatum* (99.81 ± 46.64 cm^2/g).

Table 4. 1 Summary of the leaf size and texture variables across the three zones (mean ± standard error). Comparisons by one-way ANOVA, D.F. = 2, 45. Values with the same superscript letters within rows are not significantly different between the treatments across the zones (Fishers LSD, $p<0.05$). Note that *H. witbergense* was not included in the table, as it does not occur in the middle and lower zones.

Leaf sizes	***Species***	**Upper zone**	**Middle zone**	**Lower zone**	**F**	**P**
Leaf area (cm^2)	*H. albo-brunneum*	4.95 ± 0.42^{a}	2.96 ± 0.13^{b}	2.80 ± 0.24^{b}	16.83	**0.0003**
	H. subglomeratum	1.71 ± 0.04^{b}	2.29 ± 0.35^{a}	2.90 ± 0.03^{a}	8.42	**0.0052**
	H. trilineatum	0.52 ± 0.02^{a}	0.42 ± 0.01^{b}	0.33 ± 0.02^{c}	28.77	**<0.0001**
Leaf thickness (mm)	*H. albo-brunneum*	0.04 ± 0.001^{a}	0.34 ± 0.001^{a}	0.04 ± 0.002^{a}	2.57	0.1176
	H. Subglomeratum	0.02 ± 0.03^{a}	0.01 ± 0.001^{b}	0.02 ± 0.002^{ab}	3.52	0.0628
	H. trilineatum	0.02 ± 0.001^{a}	0.02 ± 0.001^{a}	0.02 ± 0.001^{a}	2.32	0.141
Leaf dry mass (g)	*H. albo-brunneum*	0.04 ± 0.003^{a}	0.03 ± 0.002^{ab}	0.02 ± 0.004^{b}	6.40	**0.0128**
	H. subglomeratum	0.02 ± 0.0^{b}	0.02 ± 0.002^{b}	0.03 ± 0.002^{a}	6.50	**0.0122**
	H. trilineatum	0.004 ± 0.002^{a}	0.01 ± 0.0^{b}	0.008 ± 0.002^{ab}	2.80	0.1005
Specific Leaf Mass (g/cm^2)	*H. albo-brunneum*	0.01 ± 0.0002^{a}	0.01 ± 0.0006^{a}	0.01 ± 0.001^{a}	2.078	0.17
	H. subglomeratum	0.19 ± 0.18^{a}	0.01 ± 0.001^{a}	0.01 ± 001^{a}	1.004	0.37
	H. trilineatum	0.02 ± 0.001^{b}	0.03 ± 0.002^{a}	0.03 ± 0.0^{a}	13.52	**0.0008**
Specific Leaf Area (cm^2/g)	*H. albo-brunneum*	85.5 ± 2.0^{a}	102.5 ± 7.7^{a}	106.3 ± 9.7^{a}	2.31	0.14
	H. subglomeratum	123.6 ± 3.7^{a}	93.3 ± 5.2^{a}	140.1 ± 40.2^{a}	0.39	0.18
	H. trilineatum	52.2 ± 2.01^{a}	41.6 ± 1.4^{b}	32.8 ± 1.9^{c}	28.77	**0.0001**

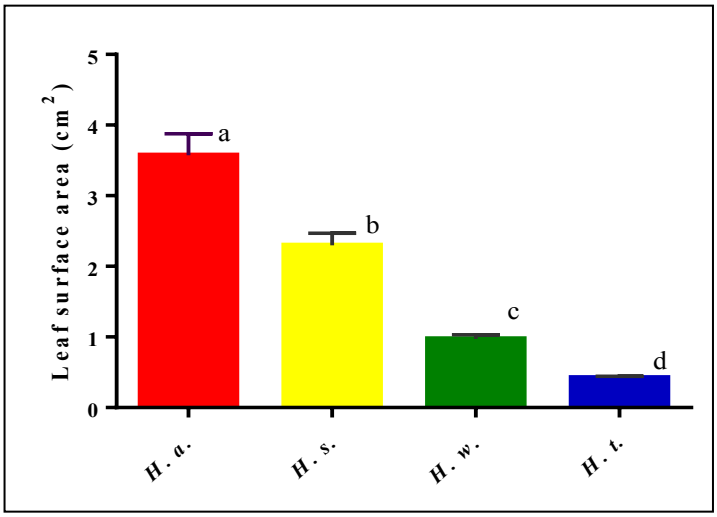

Figure 4.3 Average leaf surface area of the study plants: *Helichrysum albo-brunneum* (*H. a.*), *H. subglomeratum* (*H. s.*), *H. witbergense* (*H. w.*) and *H. trilineatum* (*H. t.*). Measurements were taken from five plants per species (three leaves per plant). The letters on the bars represent Fischer's Least Significant Difference (LSD), same letters mean no significant difference and different letters mean the opposite.

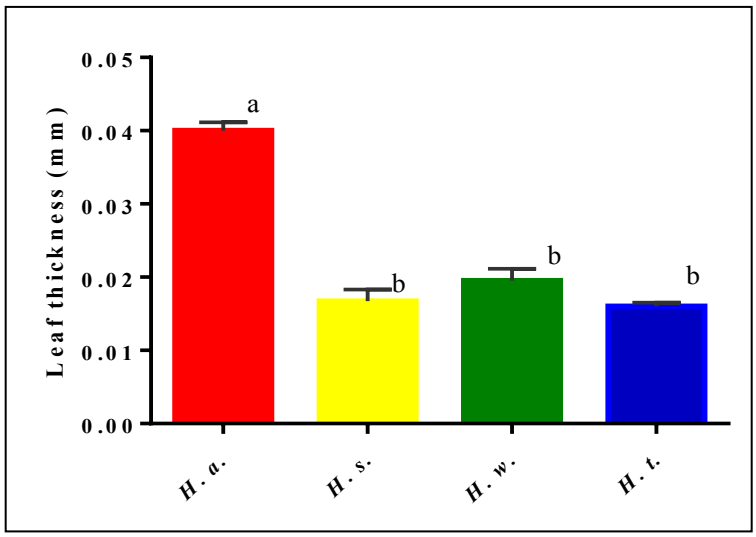

Figure 4.4 Mean leaf thickness of the study plants: *Helichrysum albo-brunneum* (*H. a.*), *H. subglomeratum* (*H. s.*), *H. witbergense* (*H. w.*) and *H. trilineatum* (*H. t.*). Measurements were taken from five plants per species (three leaves per plant). The letters on the bars represent Fischer's Least Significant Difference (LSD).

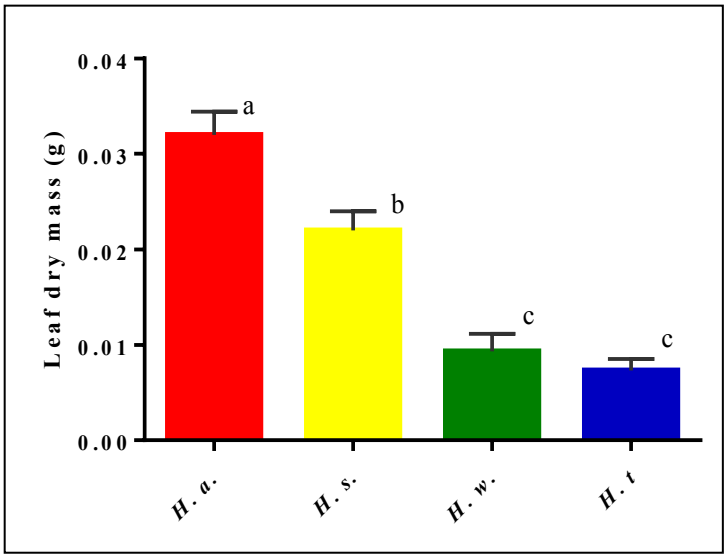

Figure 4.5 Mean leaf dry mass of the study plants: *Helichrysum albo-brunneum* (*H. a.*), *H. subglomeratum* (*H. s.*), *H. witbergense* (*H. w.*) and *H. trilineatum* (*H. t.*). Measurements were taken from five plants per species (three leaves per plant). The letters on the bars represent Fischer's Least Significant Difference (LSD).

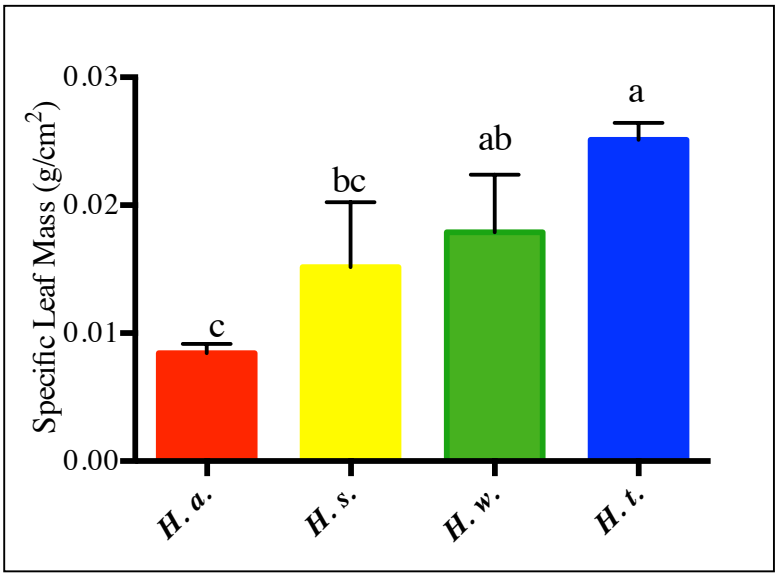

Figure 4.6 Mean leaf specific mass of the study plants: *Helichrysum albo-brunneum* (*H. a.*), *H. subglomeratum* (*H. s.*), *H. witbergense* (*H. w.*) and *H. trilineatum* (*H. t.*). The letters on the bars represent Fischer's Least Significant Difference (LSD).

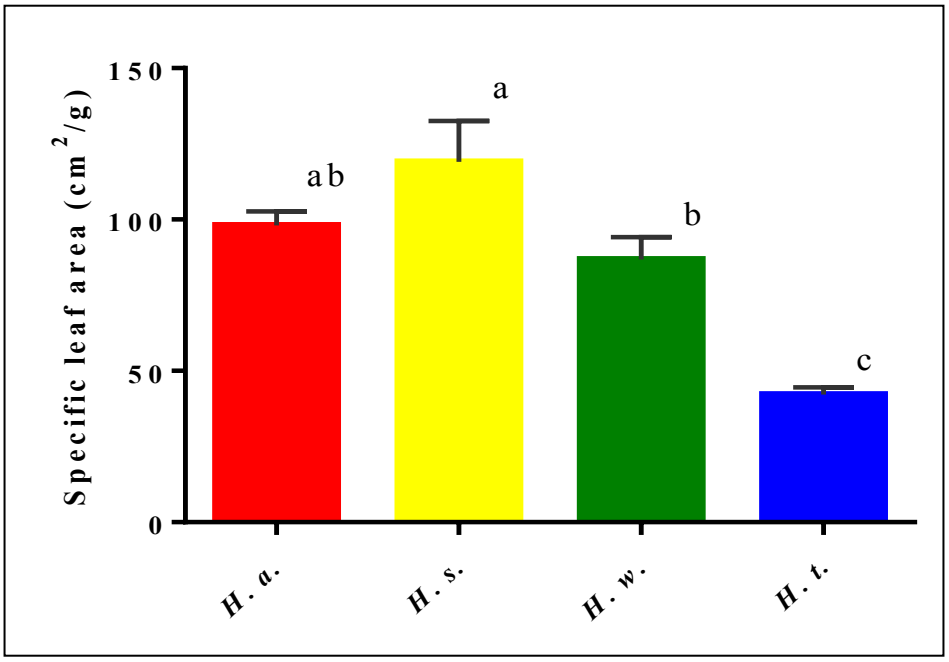

Figure 4.7 Mean Specific Leaf Area of the study plants: *Helichrysum albo-brunneum* (*H. a.*), *H. subglomeratum* (*H. s.*), *H. witbergense* (*H. w.*) and *H. trilineatum* (*H. t.*). The letters on the bars represent Fischer's Least Significant Difference (LSD).

4.2.2 Chlorophyll content

Chlorophyll content of the leaves differed significantly across all the species ($F_{3, 96}$ = 123.7, P < 0.0001), and ranged from 21 – 57 SPAD units across the four species (Figure 4.8). Species with larger leaf areas had higher chlorophyll content, viz. *Helichrysum albo-brunneum* (57.7 ± 1.0 SPAD) and *H. subglomeratum* (56.74 ± 1.13 SPAD) (Figure 4.7). *Helichrysum trilineatum* (21.6 ± 1.8 SPAD) had the lowest chlorophyll content among the four species; possibly due to its small leaf area (Figure 4.2) slightly lower than *H. witbergense* (36.5 ± 1.9 SPAD).

4.2.3 Phenology

Flowering season at the study site was noted from November 2012 – March 2013. The first phenology observations were conducted in late November 2012 along 14 transects. However, only *Helichrysum trilineatum* and *H. witbergense* were flowering at this stage, and most plants were in the early flowering stages. *H. trilineatum* was flowering in the lower zone while *H. witbergense* was in the upper zone as it only occurs there (Figure 4.8)

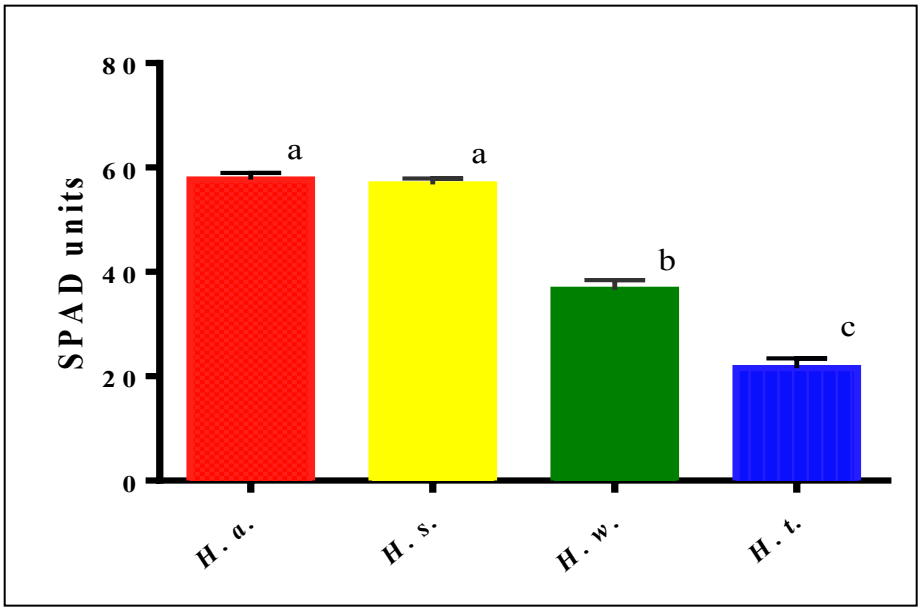

Figure 4. 8Means and standard deviation of leaf chlorophyll content of the four study species: *Helichrysum subglomeratum* (*H. s.*), *H. albo-brunneum* (*H. a.*), *H. trilineatum* (*H. t.*) and *H. witbergense* (*H. w.*) measured with a SPAD-502 Measurements taken from five plants per species (five leaves per plant). The letters on the bars represent Fischer's Least Significant Difference (LSD).

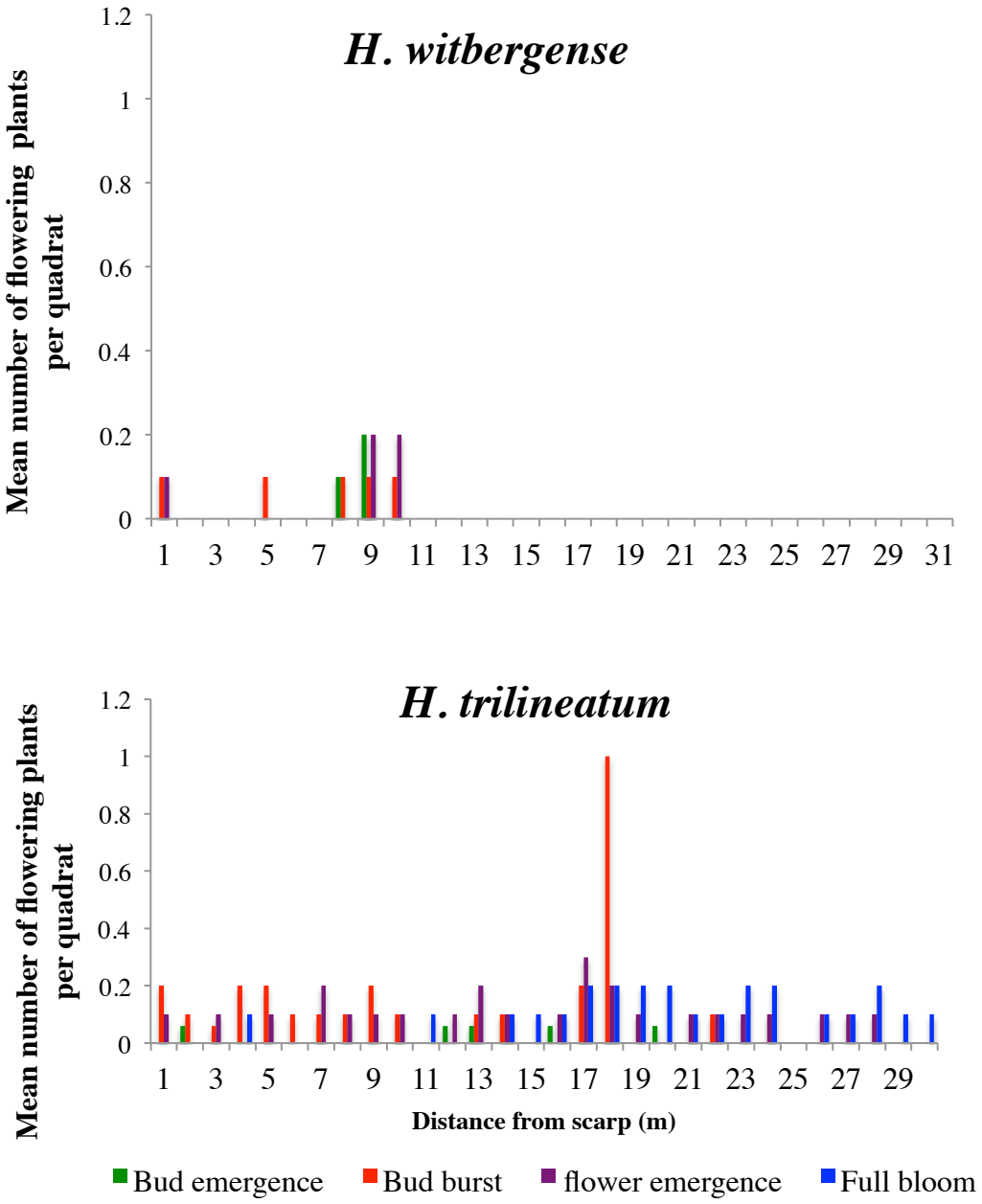

Figure 4.9 Flowering stages of *Helichrysum trilineatum* and *H. witbergense* in November 2012 at distances from the rock scarp down the slope to the tussock grasses (across the three zones) at the study site near Kotisephola Mountain

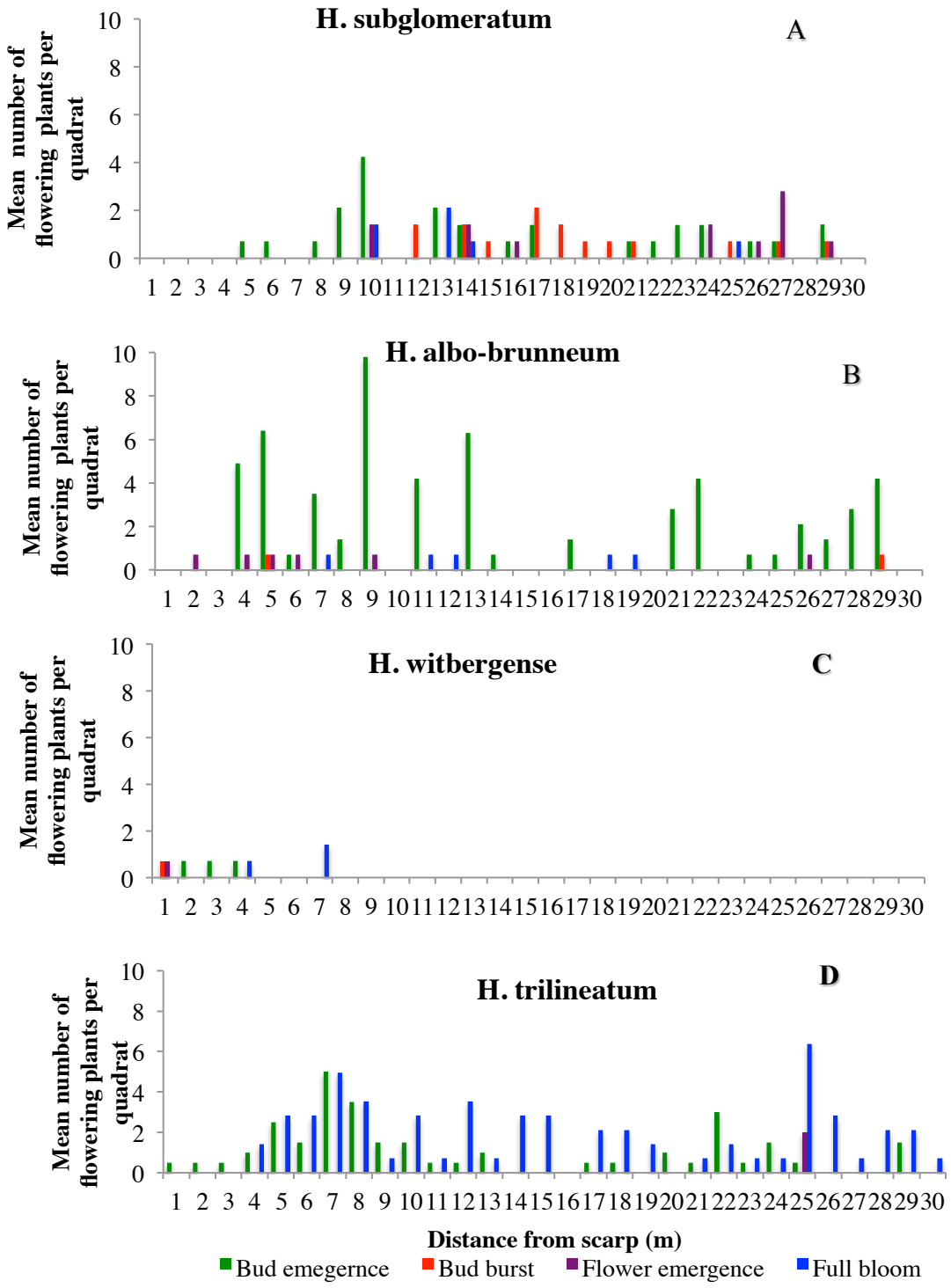

Figure 4.10 Flowering stages of (A) *Helichrysum subglomeratum*, (B) *H. albo-brunneum*, (C) *H. witbergense &* (D) *H. trilineatum* in January 2013 at distances from the rock scarp down the slope to the tussock grasses (across the three zones) at the study site near Kotisephola Mountain.

Helichrysum albo-brunneum and *H. subglomeratum* were recorded flowering in January 2013, when the second phenology survey was conducted. *Helichrysum trilineatum* and *H. witbergense* were both in full bloom in January, the former across all three zones and the latter in the upper zone, where it occurs (Figure 4.9). *Helichrysum subglomeratum* was spread across all the zones and was in full bloom in the lower zone, whereas in the upper zone buds were still emerging, and its flowering stages matured progressively towards the lower zone (Figure 4.9). Most *H. albo-brunneum* species were at the first flowering stage across all three zones, however, four plants in full bloom were observed in the upper and middle zones (Figure 4.9).

4.3 Discussion

4.3.1 Morphological features that characterise the selected Helichrysum species that survive under the snow patches

The alpine ecosystem is dominated by cushion, mat-forming, deep rooted, dwarf rosette plants and perennial herbs with basal rosettes (Billings & Bliss, 1959; Bliss, 1971; Oberbauer & Billings, 1981; Wahren, 2001; Körner, 2007; Baptist *et al.,* 2009). As noted in the previous chapter, this study site was dominated by a mat-forming herb, *Helichrysum praecurrens*, and the second most dominant species was the shrublet, *H. trilineatum*. The four selected *Helichrysum* study species have two different growth forms: dwarf shrublets and perennial herbs. *Helichrysum witbergense* and *H. trilineatum*, the two dwarf shrublets, have numerous evergreen leaves, whilst the perennial herbs have fewer leaves, some of which do not persist over the winter. *H. subglomeratum* has numerous vertically erect, tufted leaf rosettes and *H. albo-brunneum* has basal leaf rosettes, with both species also having cauline leaves on a flowering stem that dies off over winter. These morphological features enable these plants to survive under snow for several months and also enable them to survive harsh alpine environmental conditions (Körner, 2007).

Alpine species often have trichomes, which reduce water loss from the plants, decrease radiation absorbance, and some possess chemicals that act as a deterrent to some herbivores (Press, 1999). They further trap sunlight and heat over the leaf surface, and at night the trichomes maintain leaf temperatures above the ambient air temperature (Levin,

1973; Press, 1999; Gonzáles *et al*., 2008). Trichomes are described as "traits related to water control and resistance against herbivory in several plant species" (Gonzáles *et al*., 2008, p. 129). *Helichrysum albo-brunneum* and *H. subglomeratum* both have dense layers of trichomes in the form of long woolly hairs on both leaf surfaces, which may account for their high chlorophyll content as the trichomes prevent the sunlight from penetrating through the leaf surface (Körner, 1999, 2007). Herbivory?

Evergreen plants have a longer leaf life span due to their slow photosynthetic ability and their ability to store carbohydrates, and as a result evergreen species dominate in the alpine regions and leaf life span is further correlated with growing conditions of the plant (Chabot & Hicks, 1982; Kudo, 1991). *Helichrysum trilineatum,* an evergreen species, was indeed one of the most dominant species in this study site; evergreen species tend to have leaves that persist for years before they are shed due to their slow leaf turnover and the ability to maintain the physiological capacity in changing environmental conditions (Chabot & Hicks, 1982).

4.3.2 Ecophysiology of the study plants in relation to snowmelt and shading

Helichrysum subglomeratum and *H. albo-brunneum* had higher chlorophyll content as indicated by the SPAD units due to their higher specific leaf area (SLA) and thicker leaves compared to the other two species. These results concur with results reported by others on the effects of leaf thickness, succulence, specific leaf area, specific leaf mass and leaf water content on chlorophyll meter readings, i.e., that SPAD meter readings increase with fresh leaf thickness (Marenco *et al*., 2009). *Helichrysum albo-brunneum* and *H. subglomeratum* were therefore observed to have the higher chlorophyll content because of their thicker leaves and higher SLA. However, a study conducted by Wang *et al*., (2005) in Florida on estimating plant quality using SPAD-502 found no correlation between leaf thickness and SPAD values. *Helichrysum witbergense* was only exposed to the sun up to five hours a day, and had higher chlorophyll content compared to *H. trilineatum*. This does not concur with the experiments conducted by Sarijeva *et al*. (2006) who reported species (*Ginkgo biloba L.* and *Fagus sylvatica L.*) had higher chlorophyll when exposed to the sunlight for longer periods compared to when under the shade for prolonged periods. *Helichrysum witbergense* and *H. trilineatum,* have higher

SLA compared to *H. subglomeratum* and *H. albo-brunneum*, which does not concur with the findings from a study in the European Alps in which transplantation to different altitudes and local measurement of SLA reported that an increase in SLA indicated a decrease in leaf thickness, however, the opposite is true for LSM, where the decrease in LSM indicates increase in leaf thickness (Scheepens *et al.,* 2010).

4.3.3. Effects of snow cover on phenology

Phenology is associated with plant growth and plays a crucial role in the functioning of alpine plant ecosystems (Inouye, 2008). Timing of snowmelt controls flowering phenology in alpine regions as most plants remain dormant under snow and only start growing and flowering after the snow has cleared (Walker *et al*., 1995; Nautiyal *et al*., 2001; Rixen & Stoeckli, 2001; Inouye, 2008). Plants under snow-bed areas start their flowering later than plants on windward slopes which often start their flowering in early spring (Walker *et al.,* 1995; Nautiyal *et al.,* 2001; Inouye, 2008). During this study, the upper zone had long lasting snow for more than four months (in 2012), and as a result, plants in this zone started their flowering later than plants in the lower zones, which had been exposed to sunlight for longer periods.

Plants experiencing below freezing air and soil temperatures delay their flowering until the snow has cleared as an adaptation strategy (Walker *et al*., 1995; Nautiyal *et al*., 2001; Cleland *et al*., 2007; Inouye, 2008; Hülber *et al*., 2010; Wilsey *et al*., 2011). There were differences in terms of the amount of snow cover and depth between the two years (2012 & 2013) of data collection for this study, as 2012 had higher snowfall quantity and the snow lasted for four months longer than in 2013. Flowering after the heavy snowfall in the winter of 2012 started in January 2013 for *H. subglomeratum* and *H. albo-brunneum,* as the snow only cleared in October 2012 from the upper zone, but *H. trilineatum* and *H. witbergense* were already flowering in November 2012. This could be a feature related to the growth form of the shrublets as they flower earlier than the herbaceous plant species due to their higher tolerance of extreme weather conditions; the shrubs also have more leaves than herbs and therefore do not have to produce more leaves and an erect stem before flowering (Körner, 2007). This concurs with the study conducted by Dunne *et al* (2003), where phenological responses to climate change were

studied using snow manipulation and natural snow melt, and it was found that graminoids and shrublets flower earlier and for longer periods than herbs.

In contrast, after the light winter snowfall of 2013, plants might have flowered earlier, however we do not have phenological data for that spring/summer. A more detailed phenological survey of plants at this study site is still required for a comprehensive understanding of responses to snow patterns. Increase in temperatures and early snowmelt resulting from global climate change is a potential threat to these plants, especially *H. witbergense,* as it is mostly restricted to high altitudes, and is frequently (but not always) under snow for several months of the year. It might therefore be negatively affected by higher temperatures, less snow accumulation and early snow melt. The species may need to adapt morphologically and physiologically to withstand drought and frost damage or it may be at risk of extinction in those alpine areas previously covered by snow for much of the winter. *Helichrysum* species in the upper zones were least exposed to high solar radiation and high soil moisture while the opposite is true for species in the lower zones, which could also be a reason for early flowering of species in the lower zones as they were exposed to the sun for longer hours.

4.4 Conclusion

Helichrysum is the dominant genus at the study site owing to its diverse morphological features, which enable the plants to survive in the alpine regions under extreme weather conditions. The herbaceous species, *H. albo-brunneum* and *H. subglomeratum,* had larger and thicker leaves compared to the shrublets *H. witbergense* and *H. trilineatum*; as a result there were notable differences between these species' leaf morphology and ecophysiology. The herbaceous plants had higher chlorophyll content compared to the shrublets *H. witbergense* and *H. trilineatum*. Environmental factors such as snow depth and snow cover duration at this study site played a significant role in the microzonation and response of selected species phenologically and morphologically. Plants in the lower zones started flowering much earlier than plants in the upper zone where snow lasted for longer periods and there was more shading by the rock scarp. In addition, the shrublets *H. trilineatum* and *H. witbergense* flowered for longer periods than

the herbaceous plants. SLA was highest in *H. witbergense* due to the prolonged snow cover and deep shade in the upper zone compared to other species in the lower zone, while SLM was lowest in *H. witbergense* and *H. trilineatum* (overall). SLA was significantly higher in the upper zone compared to the middle and lower zones in the three species that occurred in all three zones. This study therefore contributes to our understanding of the significance of snow cover duration and depth in the alpine ecosystem of the Drakensberg Alpine Centre of southern Africa. Further, more detailed studies of the ecophysiology, phenology and morphology of these alpine plants are needed to develop our knowledge and understanding of the role that snow and topographic shading play in this region.

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CHAPTER 5 – Discussion & Conclusion

Climate change is predicted to increase temperatures to a level among the highest in the earth's history (Halloy & Mark, 2003; Cannone *et al*., 2007). It is predicted that temperatures will rise 0.6 – 4.0 °C by 2100 (IPCC, 2007). Mountain regions are one of the most vulnerable environments to climate change, especially mountain areas which are covered by snow for several months in the year (Keller *et al*., 2005). Climate change in the alpine regions has implications for snow depth and longevity (Inouye, 2008). Decrease in snow cover will expose species that are currently buffered by snow during winter against extreme temperatures and may result in increased risk of frost damage and desiccation (Bannister *et al*., 2005). Future projections for the alpine regions suggest that snowfall days and continuous snow cover may decline in the future as a result of increase in temperatures (Ziervogel, 2004; Baptist *et al*., 2009; Rammig *et al*., 2010). Increase in average temperatures has been recorded in the alpine regions over the past decades (Sjursen *et al*., 2005; Sicart *et al*., 2008) and temperatures in the Arctic regions are predicted to increase to a mean temperature of ca. 40 °C in the next 40 years (Sjursen *et al*., 2005).

This study in the alpine region of the Drakensberg Alpine Centre (DAC) provides a first, albeit very localized, account of environmental conditions and species diversity at a site adjacent to a south facing rock scarp, where snow commonly collects and persists for several months in winter. Snow clears gradually further away from the rock scarp, resulting in differences in environmental conditions such as temperature, soil moisture, solar radiation and snow cover along the slope. This results in changes in vegetation down the slope both in species composition and richness. Snow is an important factor in differentiating plant communities in alpine areas, as areas not commonly covered by snow will not have similar plant species as those areas frequently covered by persistent snow (Tablot *et al*., 1992). The north facing slopes in the alpine region of the DAC seldom have snow persisting for very short periods and consequently are very different from the south-facing slopes represented by this study. They are hotter and drier, the vegetation appears more uniform than on the south-facing slopes, and the tussock grasses extend higher up the slopes. The species on the north facing slopes are less likely to be affected by climate change, as they do not experience long periods of winter snow cover,

however they are exposed to high levels of solar radiation and evaporation (Billings & Bliss 1959).

This study therefore focused on a seasonally snow-covered, south-facing slope at the base of a rock scarp on a high altitude ridge in the DAC. The aim was to investigate plant species composition and diversity on this slope and to compare the habitats, morphology and ecophysiology of selected alpine plant species in the cline created by snow accumulation adjacent to the rock scarp. The study site was divided into three zones, as a result of differences in environmental variables, particularly the depth and persistence of snow, and the vegetation present at these zones. Three zones were identified namely: upper, middle and lower zones.

The first objective of the study was to determine the composition and diversity of plant species present and percentage surface covering at this site, as measured and compared across the three zones. Species richness generally on the mountain summits is relatively low compared to species richness at lower altitudes (Moen & Lagerström, 2008), this may be due to the extreme weather and harsh environmental conditions in the alpine regions (Körner, 1999). The upper zone had higher species richness compared to the middle and lower zones due to the cushion provided by snow against the extreme temperature conditions (Wahren, 2001). The lower zone had the lowest species richness, which might be due to the more extreme variation in daily temperatures, lower soil moisture, and increased solar radiation. Plants in the lower and middle zones are commonly not cushioned from extreme winds and are exposed to frost damage when the snow has melted (Kudo, 1991).

Species in alpine habitats in different regions of the world adapt differently to climate change compared to species in the lower altitudes; in the European Alps, shrublet range expanded in response to permafrost degradation and increased precipitation (Cannone *et al*., 2007). The middle and lower zones had more shrublets while the upper zone had more herbaceous plants. The shrublets have higher species percentage cover compared to herbaceous plants at the study site across the three zones. Plants respond to climate change in several ways, namely; migration to more suitable temperatures, persistence in the changed climate and extinction (Theurillat & Guisan, 2001). Species in the upper zone are frequently under snow for several months during the winter snow

season; these plants are thus protected from extreme weather conditions, especially in winter (Kudo, 1991). However these species would be exposed to extreme weather conditions and be at risk of local extinction with the rise in temperature due to global climate change, as they will be exposed to the harsh environment the species in the lower zones experience should less snow fall or melt more rapidly (Bannister *et al*., 2005).

Species have been reported to migrate to higher altitudes due to increased temperatures; such shifting of species is due to seed dispersal via vectors, such as herbivores and wind. Seeds could also be dispersed downhill with water from melting ice and gravity. Shepherds herding sheep and goats commute past the study site; this could be playing a significant role in dispersing seeds from lower altitudes to upper altitudes and also from upper to lower altitudes. Fire also plays a significant role in seed dispersal and seed germination (Pfab & Witkowski, 1999), however the upper zone is less exposed to fires compared to the lower zones, due to the shelter from the rocks, and the continuous snow cover during winter season, as well as the low fuel load due to the absence of tussock grasses. Skinks and lizards were observed occasionally on the rocks at the study site; these might play a role in seed dispersal both up and down the slope, this was noted by Godinez-Alvarez (2004), on a review of studies published in the past 15 years on seed dispersal and pollination by lizards. Wind plays a significant role in seed dispersal in the alpine regions particularly in the Asteraceae (Galbany-Casals *et al*., 2009); long distance wind seed dispersal has been reported for *Helichrysum,* where seeds have reached the Macaronesian islands from African mainland through wind dispersal. *Helichrysum* seeds are suited for wind dispersal as they are ca. 1 mm light with a fluffy pappus comprised by fine bristles (Galbany-Casals *et al*., 2009; Galbany-Casals *et al*., 2014).

No herbivores were observed grazing at the study site, as it is generally colder than surrounding areas and with no tall grasses for grazing. Most of the grazing was done on the north facing slopes because they are warmer and grasses are more abundant further down the south facing slopes. Only when the shepherds approached to observe us did the livestock occasionally graze at or near the actual study site.

There are often positive interactions among plants in the alpine regions as plants in these regions are exposed to harsh environments, and they therefore co-depend on other species for survival (Bruno, *et al*., 2003; Cavieres *et al*., 2005). Ecological facilitation was prominent at this study site; it was evident between the mat forming species and the erect herbs and shrublets. Mat-forming species such as *Dracoscirpoides falsa* and *Helichrysum praecurrens*, covering 31% and 23 % of the study site respectively, may have had a positive impact on other species as their mat-like contact with the ground reduces soil erosion and retains soil moisture. This in turn benefits species growing adjacent to them. However, there may also be negative interactions resulting from competition for space and nutrients between the mat forming species and other plants.

The upper zone was found to have the highest temperatures in winter during heavy snow periods, as it was buffered by snow for over four months (in the winter of 2012), while the middle and lower zones were on more exposed slopes and as a result were exposed to more extreme temperatures, both cold and warm. The snow has thus played a major role in shaping the habitat structure at the study site and influenced the diversity and composition of the vegetation down the slope due to the differences in environmental conditions (Kudo, 1991; Keller *et al*., 2005). These zones showed significant differences in several environmental characteristics, i.e. the upper zone was exposed to the sunlight for a maximum of five hours, whereas the lower and middle zones were exposed to the sunlight for more than ten hours a day. Solar radiation across the three zones was significantly different due to the shade from the rock scarp and snow cover that lasted for several months; the upper zone had the lowest solar radiation compared to the middle and lower zones. The high solar radiation played a role in snow melt in the middle and lower zones, as high solar radiation means exposure to sunlight, which will in turn increase the melt of snow (Wahren, 2001; Bannister *et al*., 2005; Huss *et al*., 2009). Increase in temperatures due to climate change may lead to increased solar radiation, which will result in a higher rate of snow melt in areas usually covered by snow. Soil moisture is strongly affected by rapid snow melt, as it depends on precipitation such as rainfall and snow (Wipf *et al*., 2009; Wipf & Rixen, 2010). Increase in temperatures due to climate change will cause the snow to melt faster and cause water surface run off, with the result that the soil will not retain enough moisture for drought

periods, whereas where there are long periods of snow cover and slow snowmelt, the soil retains the moisture for several months reducing potential of drought (Jonas *et al*., 2008).

Another objective of this study was to characterise the morphology and phenology (flowering period) of four selected plant species that persist within the winter snow patches. Phenology was observed across the three zones on the four *Helichrysum* species. The first phenological observations were conducted in November 2012; during this period only *H. witbergense* and *H. trilineatum* were flowering. The second observation was conducted in January when most species were then flowering. The shrublets' (*H. witbergense* and *H. trilineatum*) flowering period lasted longer than the herbaceous plants, as these plants were already flowering in the November whereas the herbaceous plants were observed flowering only in January. Phenology was affected by the environmental variables across the zones, i.e. plants started flowering earlier in the lower zones as they are exposed to sunlight for longer. Some plants remain dormant under snow for several months and only start flowering after the snow has cleared (Kudo, 1991); hence plants in the upper zone flowered later than plants in the lower zones.

Leaf surface area of all the selected *Helichrysum* study species was significantly different across the zones, and the leaves of *H. albo-brunneum* and *H. trilineatum* in the upper zone had larger surface areas. However, this was not the case with leaf thickness and leaf dry mass, as they were not significantly different across the zones; this could be due to the short distance that was measured (0 – 30 m) at the site. The environmental variables therefore had no significant impact on the leaf thickness and dry mass across the zones. The two shrublets (*H. witbergense* and *H. trilineatum*) had higher Specific Leaf Area (SLA) compared to *H. albo-brunneum* and *H. subglomeratum*, which might be due to the leaf thickness and leaf size of these species. These findings do not concur with results from other studies where an increase in leaf thickness indicated a decrease in SLA (Scheepens *et al*., 2010).

This study was limited to a single site in the alpine region of the DAC, however it represents many other similar south-facing slopes adjacent to rock scarps where snow accumulates and persists for part or all of the winter months. There was high species diversity below the rock scarp as a result of the persistent winter snow cover; due to the

shade created by the rock scarp. The plants on the south-facing slope were also cushioned from harsh weather conditions hence the higher species diversity compared to species habitats that were not adjacent to the rock scarp. There is one species that can be argued to be a specialist; *Helichrysum witbergense*. This species only occurred in the upper zone, which is under shade for several hours of the day and covered by snow for much longer periods that the lower zones. This species was not observed in the lower zones of this site, however it was spotted along ridges (at lower altitudes) with similar environmental conditions such as persistent winter snow and continuous shade during the day.

Increase in temperatures due to climate change would likely have a negative impact on species occurring mainly in the upper zone. These species are often buffered by snow, however in the case of less frequent or persistent snow, they would be exposed to the alpine harsh weather conditions. The ridge creates favorable conditions for species occurring there; the species have higher soil moisture throughout the year compared to species in lower zones, and are further protected from strong winds and therefore the moisture is retained for longer periods. During winter, minimum temperatures in the upper zone are higher than temperatures in the lower zone; this is as a result of the prolonged snow, which buffers against cold temperature. As a result of these favorable conditions, the upper zone had higher species richness and diversity compared to the lower zones. Studying these species in the alpine regions will give us understanding of how they are likely to respond to climate change, as currently more is known about the climate change than its effects on organisms (Urban *et al*., 2011).

Even though the snow patch that was sampled was relatively small, it provides us with some insight into the changes in both environmental factors and species diversity that occur over a relatively small distance down a slope at high altitude and provides important results that may form a basis for further studies in the DAC. Studies covering several ridges comparing the north-facing slopes (where snow does not accumulate) with south-facing slopes at the same altitude and at lower altitudes could be done to extend our knowledge of the alpine environment in the DAC. A more detailed morphological study of the alpine plants is also desirable as this study focused mainly on the leaf morphology. This study was tailored to meet the requirements of a Masters project. However, the

south-facing patch that was surveyed is very likely representative of other south facing slopes adjacent to rock scarps on the summit plateau, where snow accumulates and persists for some time over the winter period. As previously mentioned in the earlier chapters, this study is the first of its kind in the DAC, and the results and methods used in this research provide a baseline for future research in the DAC. Monitoring the environmental variables and species composition at this site in the future could reveal the effects of climate change on the plants at the summit of the alpine region in the DAC and deepen our understanding of what future climate may hold.

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