Regional temperature and precipitation trends in the Drakensberg alpine and montane zones: implications for endemic plant species

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Declaration

I, Patricia Marsh, declare that this research report, apart from the contributions mentioned in the acknowledgments, is my own, unaided work. It is submitted for the Degree of Master of Science by coursework and research report to the University of the Witwatersrand. It has not been presented before for any degree or examination to any other University.

(Signature of candidate)

1st day of November 2017

Abstract

Mountains are complex environments owing to their varying topography and geographic range, and as a result are havens for a variety of eco-systems and biodiversity. Mountain systems around the globe are potentially transforming due to increasing pressure from human-driven climate change. The possible effects of these pressures and overall consequences of the changes are difficult to predict due to the complexity of mountain habitats. Previous studies have recorded increasing temperatures in mountain systems as one of the consequences of climatic change. As a consequence of this warming trend, plant species that typically grow in lower altitudes may migrate to higher altitudes as those habitats become suitable. There are many different effects this may have on the local eco-system, such as the possibility of the migrating species outcompeting the local species or even hybridization occurring, resulting in a new species. Regardless, the movement of species from low to high elevations will have a direct effect on plant community dynamics in the area. South Africa is experiencing warming temperatures and has experienced a reported increase in mean annual temperature by 0.96 ºC over the last five decades.

This research aims to understand the implications of inter-annual temperature and precipitation trends in the alpine, upper and lower montane thermal zones in the Drakensberg on two endemic plant genera, *Rhodohypoxis* (Hypoxidaceae) and *Glumicalyx* (Scrophulariaceae). A thermal zone refers to a temperature gradient at a specific altitude in a mountain system. Temperature and precipitation data from 1994 to 2014 were collected from four weather stations: Sani Pass (2874 m), Shaleburn (1614 m) and Giants Castle (1759 m) in South Africa, and Mokhotlong (2209 m) in Lesotho. These sites represent three thermal zones; Sani Pass is in the alpine zone, Mokhotlong is in the upper montane zone, and Shaleburn and Giants Castle are in the lower montane zone. The objectives of this research are to analyse and compare the temperature and precipitation trends, inter-annual variability, and annual number of frost days at each data collection site from 1994 to 2014, as well as infer the potential impact these changes may have on the local endemic plant genera. Results show a more pronounced increase in temperature in the lower thermal zones and a larger decrease in precipitation in higher thermal zones. The lower montane zone experienced the highest increase in temperature of up to 0.6 ºC over two decades. The alpine zone showed the largest decrease in precipitation of on average 27.5 mm of rainfall

per annum over 20 years, while the lower montane zone displayed the largest inter-annual variability in both temperature and precipitation variables. The upper montane zone had a larger decrease in frost days over the 20 year period relative to the lower montane zone. Interestingly this work showed an increased warming pattern in the lower thermal zones relative to upper zones, which contrasts with work in other mountain ecosystems. This warming may create larger intermediate regions which could encourage the movement of endemic flora into neighbouring thermal zones. Movement between thermal zones may increase hybridization within plant genera which could change the structure of the plant communities and possibly result in altered floral populations.

Keywords: Climatic change, Drakensberg, endemic flora, thermal zones, temperature and precipitation trends, inter-annual variability

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Glossary of terms and list of abbreviations

CFR – Cape Floristic Region

CoV – Coefficient of Variance

DAC – Drakensberg Alpine Centre

GC – Giants Castle

MANOVA – Multivariate Analysis of Variance

MK – Mokhotlong

PCA – Principle Component Analysis

SD – Standard Deviation

SH – Shaleburn

SP – Sani Pass

Afroalpine – the highest delineation in African mountains that includes a specialised group of plants that differ from the vegetation of lower altitudes. This group of plants survive from 3500 m above sea level and above.

Afromontane - delineation based on shared plant species' distribution and high elevation areas with great floral endemism.

Allopatric – (of plants or animals, regarding related species or populations) occurring in isolated or non-overlapping geographical locations.

Alpine – delineation in high mountains regarding climatic and biogeographic factors.

Altitude – a point related to sea level or ground level, or height of an object.

Altitudinal zones – delineation of high mountains with regards to height about sea level as these delineations will have different vegetative and climatic conditions.

Angiosperms – large group of plants that have flowers and fruit, as well as an enclosed seed.

Anthropogenic – originating from or in human activity.

Aspect – (relative to physical geology) is the compass direction that a slope faces.

Austroalpine – the highest delineation of temperate African mountains according to the specific floral species and climatic conditions.

Autecology – the study of an individual organism or species and its interactions with the biotic and abiotic factors of its environment.

Biodiversity – the variability of living organisms (flora and fauna) in the world or in a specific habitat.

Biome – a naturally occurring community of plants and animals occurring across a large area in a particular region.

Drakensberg – an Afrikaans name given to the eastern part of the great escarpment in southern Africa.

Eco-system – a community of living organisms interacting amongst themselves and the non-living elements in a particular area.

Elevation – the height above a given level, specifically sea level.

Endemic/endemism – native to an area or confined to a certain place/region.

Escarpment – a steep slope or long cliff at the edge of a plateau or separating two areas of land with different heights.

Extinct – a species or group of organisms having no existing/living members.

Fauna – the animal life of a particular region or place.

Flora – the plant life of a particular region or place.

Fynbos – a small belt on the southern tip of Africa of distinctive hardleaf shrubland or heathland vegetation.

Genre – singlular: genus. A taxonomic category ranking that is below family and above species.

Geomorphic – natural structures on the surface of the earth with regard to the form of the landscape.

Geophyte – a perennial plant with a concealed underground storage organ such as a rhizome or bulb.

Germinate – to start to develop or grow after a period of dormancy.

Habitat – the natural or preferred environment of an organism or population.

Hemicryptophyte – a perennial plant that carries its buds at the soil surface.

Hemisphere – half of the earth, usually divided into northern and southern halves or eastern and western halves.

Heterogeneous – diverse in content or character

Homogeneous – alike or similar in content or character

Hybridization – the process of a plant or animal reproducing with an individual of another species or genetic variety.

Insolation – the solar radiation that reaches the earth's surface.

Interannual variability – the change in climatic conditions between years or from one year to the next.

Intercellular – occurring or located between cells.

Interspecific – occurring or existing between different species.

Intracellular – occurring or located within a cell or cells.

Intraspecific – occurring or existing within a species.

Introgression – the exchange of genetic material from one species to another by the process of hybridization between the species, and repeated backcrossing.

Lower Alpine – one of the seven life zones in mountains defined by climate, the climatic characteristics of this zone are a mean growing season temperature below 6.4 ºC and a growing season of less than 94 days.

Lower Montane – one of the seven life zones in mountains defined by climate, the climatic characteristics of this zone are a mean growing season temperature between 10 and 15 ºC and a growing season of less than 94 days.

Metabolic threshold temperature – minimum temperature at which an organism or plant is able to function and metabolise successfully.

Metabolism – chemical processes in living organisms in order to maintain life.

Microbe – is a microorganism, predominantly a bacterium causing fermentation.

Microclimate – the climate of a small or restricted area, usually differing from the surrounding climate.

Morphological – relating to the form of living things and relationships between their structures.

Nival – a region characteristic of continuous snow.

Phenological – study of cyclic and seasonal phenomena, in relation to climate and living organisms.

Physiological – regarding the way a living organism or their body parts function.

Phytogeographical – branch of botany relating to the geographical distribution of plants.

Prezygotic – relating to before fertilization.

Radiation – the emission of energy as electromagnetic waves or rays.

Snowline – a particular altitude above which snow remains on the ground year round.

Snowmelt – water that results from the melting of fallen snow.

Speciation – a course of evolution regarding the formation of new and distinct species.

Sub-sahelian – the area below the Sahel, the semi-arid region on the southern end of the Sahara desert that stretches across six countries from Senegal to Chad.

Symbiotic (relationship) – unique interactions between species that can be benefical or harmful, they are essential to the survival of many organisms and eco-systems.

Topography – the arrangement or distribution of physical features (both natural and artificial) in an area.

Upper Montane - one of the seven life zones in mountains defined by climate, the climatic characteristics of this zone are a mean growing season temperature between 6.4 and 10 ºC and a growing season of less than 94 days.

Vapour – a substance suspended or difused in the air, usually liquid.

Vicariance – the geographical separation of a population, usually by a physical barrier.

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Chapter 1

General Introduction and Literature Review

Literature Review

Mountains are some of the most delicate and complex environments on Earth, as they comprise a wide spectrum of diverse topography and environmental conditions that provide opportunities for the diversification of life (Spehn *et al.*, 2010). They are a haven for biodiversity, endangered species, and ecosystems (Beniston, 2003). Mountains influence regional climates in the surrounding areas and are sources of water, minerals, agriculture, areas of recreation, among other environmental services. Mountain systems around the globe, from the Himalayas to the Andes, are experiencing some form of environmental deterioration due to increasing human populations and the associated increase in pressure on natural resources and ecosystem services (Beniston, 2003). Climatic change is an effect natural environments are experiencing due to human influences; these changes are now reaching beyond the boundaries of natural variability (Karl & Trenberth, 2003). The effect climatic change may have on mountain systems is still unclear due to the complexity of mountain environments and the diversity of specialized fauna and flora that inhabit them (Theurillat and Guisan, 2001).

Previous research has shown that an increase in temperature at high altitudes results in the creation of suitable habitat for several lower altitude plant species, thus enabling these lower altitude plants to migrate to higher altitudes (Beniston, 2003; Gehrig-Fasel, 2007; Gomez *et al.*, 2015). Many examples of the movement of plant species due to climate change have been documented. The three following examples illustrate the effects of climate change on mountain environments from different parts of the world. First, in the Swiss Alps the growth of trees has occurred at higher elevations and there has been a significant increase in tree cover in areas between 1650 m and 2450 m above sea level (a.s.l.) within the sub-alpine and alpine altitudinal zones (Gehrig-Fasel, 2007). The expansion of tree species into the alpine zone could be due to the increase of temperature in the area (Gehrig-Fasel, 2007). The movement of plant species suggests that the zone is expanding upslope and sub-alpine species are moving into alpine areas. In general the alpine vegetation zone is climatically determined, and the shift of tree species further up the mountain is a strong indication of changing temperature (Gehrig-Fasel, 2007).

In a second example, the snow line in the Andes mountain range in Venezuela has moved 600 m upslope over the last 118 years. In 1885, the snow line was recorded at 4100 m a.s.l.,

whereas in 2003 the snow line was reported at 4700 m a.s.l. (Beniston and Fox, 2003). The third example is in the Australian Alps, where warming temperatures have been recorded over the last forty years in all three altitudinal zones, with the largest increase in the alpine zone. Altitudinal zones describe the environmental conditions or ecosystems that occur at different altitudinal gradients in mountainous areas (Körner *et al.,* 2011). The snowline, currently documented at 1460 m a.s.l., is predicted to rise in elevation to between 1490 m and 1625 m in the year 2020 (Hennessy *et al.,* 2008). The movement of the snowline upwards suggests warming temperatures, which may lead to a shift of vegetation into higher altitudes as the climate and soil become suitable for plant growth. These examples illustrate how warming temperatures are directly related to the movement of plant species into higher altitudes and have important parallels to the mountain regions of southern Africa. These examples suggest that if temperatures and precipitation trends change in southern African mountains, there may be an upward shift of species within the altitudinal zones.

Climatic Change in South Africa

Climatic trends in southern Africa have changed over the last few decades, particularly with regard to temperature and precipitation. Studies of temperature patterns from 1851 revealed a long-term warming trend over the entire southern hemisphere (Jones *et al.,* 1986). The monthly mean surface air temperature in the southern hemisphere was recorded from the year 1851 to 1984 and a warming trend of 0.5 ºC over that period was observed. A similar trend is seen across the African continent. Historical and instrumental temperature data from the late 19th to early 21st centuries showed slowly increasing temperatures (Nicholson *et al.,* 2013), but the rate of temperature increase accelerated from the end of the 20th century to the early 21st century. These mean annual temperatures were 1–2 ºC higher in the last few decades than in previous years. South Africa has reported an increase in mean annual temperatures of 1.5 times the global average of 0.65 ºC over the last five decades from 1960 to 2010, putting South Africa's increase at 0.96 ºC for that period (DEA, 2013). The frequency of extreme low temperatures annually has decreased over the same period of time, but with a significant increase in the frequency of high temperature extremes, thus depicting an increasing temperature over time (DEA, 2013). The south-western Cape of South Africa, for example, has recorded temperature increases of +0.45 ºC per decade in the early spring months of the year (August/September) from 1973 to 2009

(Grab and Craparo, 2011). These records confirm that temperatures in South Africa are rising and that the rate of increase has accelerated in recent years.

Rainfall patterns in South Africa have also changed over the last few decades. Precipitation trends in South Africa over the last 200 years have shown a decrease over time (Neukom *et al.*, 2014). An example of this decreased precipitation trend can be seen in Grootfontein in the eastern Karoo. Monthly rainfall analysed from 123 years of data showed higher rainfall in the late 1800's than in the 20th century, with predicted decreases continuing over the next 20 years (Du Toit and O'Connor, 2014). The Department of Environmental Affairs (DEA) reported that there was a decrease in rainfall in the autumn months (late February to April) across the country from 1960–2010, however there was no significant annual rainfall trend over that time. The DEA also reported a significant decrease in the number of rain days over the same period (DEA, 2013); this implies an increased intensity of rainfall events with increased dry spell duration.

Rainfall in mountain systems, such as the Drakensberg, can be more variable than in low altitude areas due to topographical and altitudinal influences (Körner and Ohsawa, 2005). This variability may cause difficulty when analysing precipitation trends in mountain systems. In previous studies, precipitation has been noted to vary greatly from year to year (Killick, 1978). For example, the mean annual rainfall at Sani Pass, in the Drakensberg, was recorded at 1441.6 mm for the rainfall period 1938/39, in comparison to 439.3 mm for 1944/45. Another site in the Maluti mountains on the Lesotho side of the Drakensberg recorded 1663 mm for the rainfall period 1956/57 and 701 mm for 1965/66 (Killick, 1978). These records show a substantial variation of ±1000 mm of rainfall between years, which makes it difficult to identify an increasing or decreasing trend. More recent data from Sani Pass and Sentinel Peak (in the southern and northern Drakensberg respectively) recorded the mean annual rainfall from 2001 to 2005 to be 767.8 mm and 753.2 mm respectively (Nel and Sumner, 2008). Even though these estimates are lower than in previous years, additional long-term data are needed for the decrease in rainfall to be considered a trend, as this may be due to a temporary dry spell (Nel and Sumner, 2008). Consequently, the differences in the mean annual precipitation at various sites in the Drakensberg make it difficult to identify rainfall trends. However, the differences do provide evidence for possible change in rainfall over the years as estimates from the late 1970's for the Drakensberg were between 1000–2000 mm of rainfall per annum, which is higher than current

records (Nel and Sumner, 2005). Data from previous studies therefore aid in the understanding and interpretation of current climate data and trends, as climatic changes have important consequences for the vegetation and biodiversity of mountain systems (Messerli and Winiger, 1992).

Factors that influence plant growth in mountain environments

High-altitude mountains with extreme temperatures and variable microclimates can be a harsh environment to survive in, yet mountain flora have adapted to these conditions with a variety of specialized traits to tolerate the harsh environment (Körner, 2003; Larcher, 2010). Several factors, both natural and anthropogenic, create these harsh conditions that affect plant growth in mountain environments. Natural factors include high altitudes, low soil depth, variable precipitation and low temperatures. Some examples of anthropogenic factors are pollution, land-use, increasing populations, as well as increasing atmospheric CO_2 (Thuiller, 2007). Given that this research focuses on temperature and precipitation changes within the Drakensberg and the implications on plant species, it is important to understand how specific natural factors affect plant growth (i.e., altitude, temperature, water availability and precipitation, and aspect).

Altitude

Altitude often influences other environmental factors. Körner (2007) described two categories of environmental change that occur at different altitudes: 1) physical changes with altitude and, 2) changes that are not altitude specific. Physical changes include temperature (see below), cloud cover and atmospheric pressure. Cloud cover may affect how much sunlight or short wave radiation plants are exposed to (Gale, 2004). Shortwave radiation increases with altitude; as a result there is more radiation available for leaves to absorb in plants that grow at higher altitudes, leading to increased photosynthetic rates (Gale 2004). An increase in photosynthesis can lead to an increase in the growth rate of the plant. However, these consequences should be considered in conjunction with other factors such as moisture and temperature. Atmospheric pressure affects the cells and organelles in the leaves of a plant, and therefore may affect the rates of photosynthesis and respiration in a plant, thus affecting the growth rate (Takeishi *et al.*, 2013). In addition, these reactions should be considered in conjunction with other factors such as temperature, CO_2 and O_2 levels.

A second category of changes that are not altitude specific include moisture, hours of sunshine, season length, wind, and geology (Körner, 2007). Moisture refers to precipitation and water available to plants and will be discussed below. Hours of sunshine and season length will affect the period of time in which plants have to grow, and will influence the germination (the sprouting of a seedling from a seed) capacity of plants (Vera, 1997). Therefore, reproductive efficiency of plants at high altitudes will be affected. Plants occurring at higher altitudes germinate at faster rates than those at lower altitudes, due to the plant adapting to short growing seasons (Vera, 1997). Altitude affects many different facets of plant growth and survival; these facets should be taken into account when studying plant dynamics and communities.

Temperature

Temperature influences which plant species survive in mountain systems as each species has a minimum temperature at which it is able to function and metabolise (e.g., metabolic threshold temperature). When frost occurs and the temperature falls to below the metabolic threshold temperature, there is an increased probability of intracellular ice formation, causing mortality due to the rupturing of cell membranes of the plant (Woodward and Williams, 1987). Frost occurs when the temperature falls below the freezing temperature of water, which is usually 0 °C (Inouye, 2000). When temperatures decrease, frost is formed from water vapour, it usually coats the plants and ground with a layer of crystals, also known as 'hoarfrost'. The size of the frost crystals is dependent on other climatic factors such as temperature and moisture in the air. Under certain conditions, a more damaging form of frost can occur without visible signs of the formation of crystals. This can cause intracellular ice formation and the mortality of the plant, a condition known as 'black frost' (Inouye, 2000).

As altitude increases, the temperature decreases and thus low temperatures have a direct influence on the growth processes of a plant (Körner and Larcher, 1988). Therefore, plants growing at high altitudes with cooler temperatures will be smaller in size than plants at lower altitudes with warmer temperatures. Low temperatures also affect plant survival by way of the length of the growing season, as this has ideal temperatures for plant growth. Plants need to make the most of a growing season and minimise damage in the non-growing season. Mountains in temperate areas, like South Africa, have a seasonal climate with a clear growing season and non-growing season duration (Pauli, 2003). To adapt to the non-growing season conditions

plants may enter a dormant state or adopt morphological, physiological or phenological qualities that aid in their protection (Körner and Larcher, 1988; Inouye, 2000).

Increased temperature may also have an effect on the local flora as these changes affect the soil in which the plants survive. Changes in soil temperature alter the composition of the microbial communities in the soil (Zogg *et al.,* 1995). Soil microorganisms are important for plant survival as they play a role in the nutrient cycling and fertility of the soil. Microbes also regulate plant productivity as well as plant community dynamics and diversity, as some plants depend on the symbiotic relationship with microbes to survive (Van Der Heijden *et al.,* 2007). This suggests that if a change in temperature alters the microbial structure of the soil it may result in a change of the plant community dynamics, as microbes may determine plant abundance (Van Der Heijden *et al.,* 2007). Plants that are adapted to the warmer temperatures will therefore have a higher chance of survival in the areas with warming soils. Therefore, temperature is a limiting factor for plant growth in mountain habitats and the knowledge of temperature trends in various altitudinal zones are vital to understand mountain flora and their temperature thresholds (Larcher, 2010).

Water

Another variable that influences plant survival is water; specifically the amount of water available dictates which plant species survive. With South Africa being an arid country, most plants will suffer water deficits rather than surpluses, it can be assumed that water is a large driver of plant survival and diversity. Water availability may have an effect on the functioning of an ecosystem with regard to nutrient cycling and population dynamics (Schwinning *et al.,* 2004). If water is not available this will affect growth of the plant and in severe cases cause mortality of the plant. The presence of water in the soil and water availability are two different factors, as soil may have water present but that water may be unavailable to the plants due to low temperatures, causing it to be present only in the form of ice and snow. Consequently, plants may suffer from water stress (Körner, 2003). Snow has both positive and negative effects on mountain plants. A positive effect is that a layer of snow may insulate the soil and prevent freezing when ambient air temperatures are below 0 ºC; an obvious negative effect is the shortening of the growing season (Körner, 2003). Snowmelt also has both positive and negative effects as it may stimulate the growth of plants in a dormant phase, or it may cause water-logging of soils. Therefore, the

presence of snow in mountain environments could also be a limiting factor on plant growth and distribution.

Another important effect precipitation may have is the ability to break the dormancy of a plant (Opler *et al.*, 1976; Walck *et al.*, 2011). The increase in soil moisture with precipitation or snowmelt may trigger plant growth or flowering (Opler *et al.*, 1976; Stinson, 2005). This is true of *Rhodohypoxis* Nel., which grows soon after the first rains (Nordal, 1998), developing from an underground corm-like tuber. Precipitation may also have an effect on the ecosystem processes such as the cycling and storage of carbon (Harper *et al.*, 2005). The carbon dioxide (CO_2) in the soil is an important part of an eco-system and is greatly influenced by climate. In a study done in the tall grass prairies of Kansas USA over four years (1998-2001), the soil showed a decrease in CO_2 when the growing season rainfall decreased and the frequency of extreme rainfall events increased. The frequency of extreme rainfall events may increase if the number of rain days decrease. The decrease of CO_2 in the soil resulted in a decrease in plant productivity, which was also affected by the decrease in the amount of rainfall and the alteration of rainfall timing (Harper *et al.*, 2005).

Another factor that influences water availability is soil depth as it is associated with water retention capacity and precipitation (Khan *et al.*, 2012). If soil depth is not sufficient there will be less retention of water and a greater runoff, thus less water available to the plant. An equally important factor is the soil type as this will influence soil permeability. Given the importance of water to plant growth in mountain systems, an understanding of how different precipitation and water availability trends affects plant growth is important for gauging how mountain ecosystems will respond to changing climate patterns.

Aspect

Aspect refers to the orientation of the slope. This affects how much sunlight is available to the plant (Khan *et al.*, 2012). Sunlight is essential for most plants' survival as it enables them to photosynthesize (Mishra, 2004). The sunlight received on a slope has an influence on temperature and water movements in the area. A slope with a higher insolation (the solar energy that reaches the earth's surface) will be warmer and have a higher evaporation rate than a slope with lower insolation (Holland and Steyn, 1975). For that reason, a slope with higher insolation (i.e., north facing slope in the southern hemisphere) may have a higher plant growth rate as

compared to a slope with a lower sunlight income (i.e., south facing slope in the southern hemisphere; Hasler, 1982). Temperature, as well as water movement and availability, influence the growth, composition and structure of vegetation, and should be taken into account when studying plant communities in high mountains.

The Drakensberg Alpine Centre (DAC)

The Drakensberg Alpine Centre (DAC) is a mountain region previously recognised as being above 1800 m a.s.l. (Carbutt and Edwards , 2004), but has more recently been defined as to be above 2800 m a.s.l., (Carbutt and Edwards, 2015). The DAC expands over a large area of the eastern interior of southern Africa (Carbutt and Edwards, 2004). The Drakensberg is part of the Great Escarpment, which occurs along the eastern margin of the southern African plateau (Carbutt and Edwards, 2004). The Great Escarpment extends for almost 5000 km with many geomorphic variations due to the geology and climate of the area (Bussmann, 2006; Grab, 2010). The DAC (as previously circumscribed) comprises a high altitude range of hills, escarpments and plateaus covering approximately 40,000 km² and including the highest part of the Great Escarpment. The DAC is home to 2 520 native angiosperm species, 595 of which are near-endemic and 334 are endemic, and it is recognised as a world heritage site for both its biological and cultural qualities (Carbutt and Edwards, 2006; Nel, 2007). Many of the endemic angiosperms are rare and have very specific habitats, which likely played an important role in plant speciation and biodiversity of the area (Carbutt and Edwards, 2006).

The DAC forms part of the 'Afromontane archipelago' as recognised by White (1978, 1981), that comprises a number of mountains scattered across the African continent with similar floristic attributes and high levels of endemism (Grimshaw, 2001). The Afromontane archipelago includes seven mountain systems stretching across the continent from Sierra Leone in West Africa through Sudan in North Africa, Tanzania in East Africa and ending in South Africa. The Drakensberg is the southernmost mountain system in the archipelago, as the archipelago includes the DAC and the Cape forests in the Cape Floristic Region (CFR; Carbutt and Edwards, 2015). The comparison between a network of mountains and an 'archipelago', or group of islands surrounded by sea, is one that describes how mountains have similar characteristics and are separated by vast expanses. The vast expanses are not comprised of water but rather geographical terrain including different vegetation biomes, such as savanna and grassland, which

are barriers for the movement of high mountain plant species (Carbutt and Edwards, 2015). The term ‘archipelago’ describes how the mountainous areas are separated by other vegetation, but share similar floral species.

The recognition of the ‘Afromontane’ floristic region in African mountains put forth by White (1978) has been challenged by Carbutt and Edwards (2015). The delineation was based on shared plant species’ distribution and areas with great floral endemism at high elevations. However, this delineation was problematic as it included two different spatial scales, namely, phytogeographical and ecological scales. A ‘phytogeographical’ scale describes centres of plant endemism and diversity while an ‘ecological’ scales describes the vegetation structure and landscape, thus the phytogeographical scale is on a relatively smaller scale than the ecological. These two different scales make it difficult to accurately describe a variety of landscapes (Carbutt and Edwards, 2015). Carbutt and Edwards (2015) suggest that only the montane zones should be recognised in the Afromontane region, excluding the higher and lower zones, as the alpine plant species differ from the montane species. The authors redefine the ‘Afromontane’ region in southern Africa as an area that occurs between ±1300 m and ±2800 m a.s.l. Additionally, Carbutt and Edwards (2015) argue for clarification on the term ’Drakensberg Alpine Centre’ as it does not solely include the alpine zone, but starts from a seemingly random elevation of ±1800 m a.s.l. first coined by Killick (1963, 1978). Carbutt and Edwards (2015) proposed that the DAC should exclude the upper and lower montane zones and only include the lower alpine zone from ±2800 m to 3482 m a.s.l. Their redefined DAC still supports a large number of endemic species, however this is currently being reassessed considering the exclusion of the montane belts.

Different altitudinal zones in high-altitude mountains are characterised by specialised habitats, due to the extreme environmental and climatic conditions. The delineation of altitudinal zones has changed over the years. Previously, White (1978) described the highest altitudinal zone as ‘Afroalpine’; this delineation included a specialised group of plants, different from the vegetation of lower altitudes. This group of plants (surviving from 3500 m a.s.l. and above) are well adapted to temperate climate and are characterised by a high degree of endemism due to their unique habitat (Hedberg, 1970; White, 1978). The use of the term ‘Afroalpine’ in the context of South African mountains has since been considered incorrect, as ‘Afroalpine’

encompasses both tropical and temperate mountain systems (Carbutt and Edwards, 2015). The alpine areas of South African mountains are more accurately described as the 'Austroalpine region' as they have different daily and seasonal temperature than tropical mountains (Carbutt and Edwards, 2015). In the Drakensberg, Killick (1963) defined the centre of floristic endemism from 1800 m a.s.l. to the Drakensberg's highest point (3482 m a.s.l.; Carbutt and Edwards, 2015), and then delimited the alpine belt in the Drakensberg as occurring above about 2800 m a.s.l. The vegetation from 1800 m to 2800 m was defined by Killick (1978) as 'sub-alpine' and that below 1800 m as 'montane', and was characterised by their particular climax plant communities, i.e. the final stage of plant succession (the sequential change in the dominant plant species in an area over time; Huston and Smith, 1987). In the DAC, the sub-alpine altitudinal zone is characterised by the presence of *Passerina-Philippa-Widdringtonia* shrubs and the alpine altitudinal zone by the presence of *Erica-Helichrysum* heath (Killick, 1963, 1978; Carbutt and Edwards, 2004).

New delineations of the altitudinal zones and floristic regions have been determined, challenging the previous classifications. Körner *et al.* (2011) proposed a new model of seven life zones in mountains, the zones are defined by climate, excluding elevation. The most defined biome boundary in mountains is the high elevation climatic treeline or 'thermal treeline', which separates the alpine areas with no trees from the montane belts. This thermal treeline is the main reference for the seven thermal belts of life (nival, upper alpine, lower alpine, upper montane, lower montane, remaining area with frost and remaining area without frost; Körner *et al.*, 2011). The transition between the life zones is co-defined by mean temperature and duration of the growing season. The new model of thermal belts changes the previously accepted alpine altitudinal zone in the Drakensberg to lower alpine (<6.4 ºC mean growing season temperature, growing season < 94 days), which will be here referred to as 'alpine' as there is no upper alpine zone in the Drakensberg. The sub-alpine zone is now referred to as the 'upper montane' zone (>6.4 ≤10 ºC mean growing season temp., growing season (GS) > 94 days), and montane as the 'lower montane' zone (>10 ≤15 ºC mean growing season temp., GS > 94 days). The new thermal belts of life are a simple, temperature defined zonation of mountains which enable comparison of mountain life on a global scale (Körner *et al.*, 2011; Figure.1).

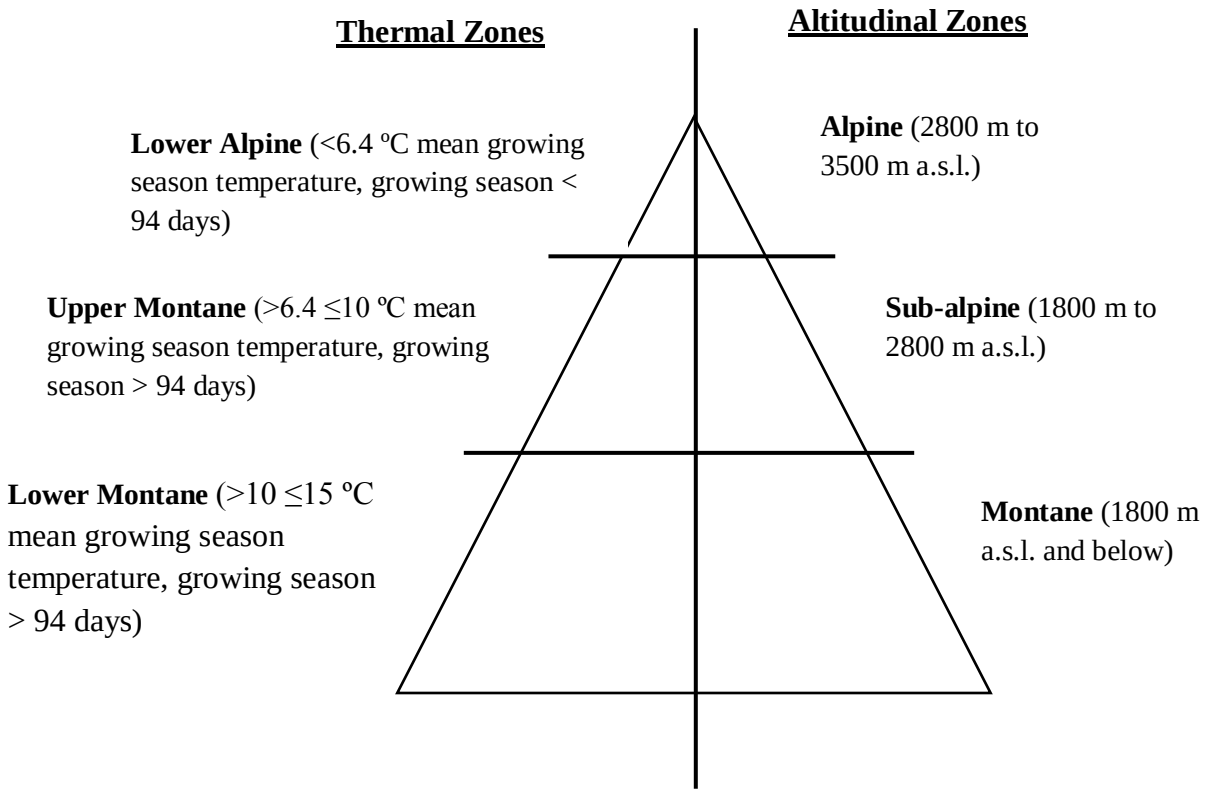

Figure 1. Diagram comparing thermal zones and altitudinal zones.

The Drakensberg region, along with the CFR, is part of a corridor of mountain habitats that is central to the speciation (the formation of new species) of lower montane flora within sub-Sahelian Africa (Carbutt and Edwards, 2015). The CFR is in the south-west of southern Africa (Snijman *et al.,* 2013), the vegetation in this winter rainfall area is commonly known as 'fynbos' (sclerophyllous vegetation). These species are referred to as the 'Cape element' as they are concentrated in the south-western tip of South Africa (Carbutt and Edwards, 2001; Snijman *et al.*, 2013). There is evidence of Cape species in the DAC, these elements in the DAC migrated from the south of Africa (Carbutt and Edwards, 2001) by long distance dispersal (White, 1981). There are three hypotheses how Cape species may have moved through Africa: 1) the species originated in tropical areas and migrated southward towards the Cape, 2) the species have a Cape origin and have migrated northward, or lastly 3) vicariance, the geographical separation of a species usually by a physical barrier such as a river or mountain (Galley *et al.*, 2007). Galley *et*

al. (2007) found there were 18 migrations of Cape species from the Cape into the Drakensberg and 12 migrations of Cape species from the Drakensberg northward beyond the Limpopo. Strong evidence for both ancient and current connections between the Drakensberg and the CFR was revealed in a study done on the interconnectivity of the Drakensberg and the CFR, focusing on three possible pathways (north-west, Matjiesfontein, and south-east). The south eastern pathway (Which involves the Zuurberg, Groot Wintershoekberge, Grootrivierberge, Baviaanskloofberge, and the Tsitsikammaberge) appears to be the most likely route, as compared to a north-western route or one via Matjiesfontein (Clark *et al.,* 2011). Clark *et al.,* 2011 suggest that the climate may be more of an influence on florist connectivity than the continuity of physical features. These findings show movement of plant species between mountainous areas and suggest that a change or disruption in the climate and biodiversity in the Drakensberg may have an effect on the future biodiversity in the Cape and/or in mountain regions to the north of it.

Hybridisation as a result of climate change

As warming temperatures lead to an upward migration of plant species, lower altitude species may come into contact with related species that occur in higher altitude zones. This could create competition for resources as high mountain plant species are restricted to a particular altitudinal zone and are spatially and climatically limited (Gomez *et al.,* 2015). Species movement may also disrupt prezygotic reproductive isolation mechanisms as allopatric species that have never been in contact may come into closer proximity and potentially result in the hybridisation and introgression of species (Rhymer and Simberloff, 1996; Honnay *et al.,* 2005). Reproductive isolation is when a species is unable to breed successfully with a related species due to a variety of geographical, physiological, genetic and/or behavioural barriers (Boughman, 2001). A hybrid is an organism resulting from the inter-breeding or cross-fertilization between two genetically different species or varieties (Rhymer and Simberloff, 1996; Rieseberg, 1997). Introgression is the movement of genetic material from one species to another by the breeding of an interspecific hybrid (a hybrid between different species in the same genus) with one of its parent species. (Rhymer and Simberloff, 1996).

Previous studies (e.g., Hughes, 2000; Walther *et al,* 2005; Gomez *et al.,* 2015) have observed trends that the migration to higher elevations and new contact of species may result in three possible outcomes. First, both higher and lower altitude plants cohabit and survive at higher

altitudes with the limited resources (Walther *et al*, 2005). Second, the contact between closely related endemic mountain species and lower altitude species may lead to interspecific hybridisation (Gomez *et al.*, 2015). Lastly, lower altitudinal plants could migrate to higher altitudes and outcompete the endemic species in that area (Hughes, 2000).

Hybridisation is often associated with extinction of species and loss of genetic diversity, however, there can be both positive and negative consequences of hybridisation with regard to biodiversity (Rieseberg, 1997). Some of the positive outcomes include the formation of new species, the formation and transfer of genetic adaptation, an increase in intraspecific (between individuals of a single species) genetic diversity, an increase in interspecific diversity (between individuals of different species) and the strengthening of reproductive barriers (Rieseberg, 1997; Whitham *et al.*, 1999; Chunco, 2014). One such example of an increase in interspecific diversity is that of the genus *Eucalyptus* in Australia. The *Eucalyptus* hybrid supports a larger diversity of fungal and insect species, thus enhancing biodiversity (Whitham *et al.*, 1999). Whitham *et al.* (1999) mentions that the *Eucalyptus* hybrid attracts an equal or greater abundance of symbiotic biodiversity than the parent species.

Negative consequences of hybridisation include the extinction of parent species, introgression and the loss of intraspecific genetic diversity, weakening of reproductive barriers, the loss of genetic adaptation, and lowering of genetic fitness. An example of introgression and loss of intraspecific genetic diversity is that of the mallard duck (*Anas platyrhynchos*) in Australia and New Zealand. Mallard ducks were introduced into natural areas which resulted in their interbreeding and ensuing introgression with the endemic duck species with smaller distribution ranges. This has resulted in the decline of the endemic species' populations such as the New Zealand grey duck (*A. superciliosa* subspecies *superciliosa*), as well as a physical change as the local ducks look more mallard-like in appearance. Such genetic disturbances can also occur in plant species, an example is that of the many endangered sunflower species of the genus *Helianthus*. In California, USA, many endangered *Helianthus* species (such as *H. petiolaris*) hybridise with the widely distributed weed *H. annuus.* The wide distribution of these weeds has been mainly due to human activities and the resulting hybridisation and introgression has led to a decrease in the endangered species populations (Rhymer and Simberloff, 1996; Poverene *et al.*, 2009; Chunco, 2014). These examples outline hypotheses to predict outcomes

for the endemic plant genera in the Drakensberg range in a changing climate. However, hybridisation is a case-specific process that needs to be studied in detail to understand the ecological implications.

Plants have developed many ways in which to survive harsh and changing conditions. For instance, migration is one method and another is the plant life form itself. Plant life forms can play an important role in their ability to adapt to changing climatic conditions. Two life forms that through which plants have adapted to harsh conditions are hemicryptophytes and geophytes. Hemicryptophytes are herbaceous perennials with dormant buds at or near the soil line (Raunkiær, 1907; Smith, 2013). The aboveground herbaceous part of the plant dies back during unfavourable weather conditions or during the cold season. Many hemicryptophytes are well equipped to survive harsh conditions such as arid deserts as well as high mountain habitats (Gutterman, 2002). Geophytes are herbaceous plants that survive part of their annual life cycle as dormant bulbs or corms well below (relative to other surface dwelling flora) ground (Raunkiær, 1907). The life cycle of a geophyte includes periods of dormancy ranging from weeks to months, as this plant is adapted to a seasonal climate with a distinct growing and non-growing season (Dafni *et al.*, 1981). The bulb or corm, which allows the plant to lie dormant in unfavourable conditions, is a storage organ that contains food and nutrient reserves that enables rapid growth when the growing season begins (Dafni *et al* 1981).

This research explored the pressures that a changing climate could have on high altitude plant species' distributions. As such, my study focused on two Drakensberg near endemic and endemic plant genera, *Rhodohypoxis* and 2) *Glumicalyx* Hiern (Hilliard & Burtt 1987; Hilliard & Burtt 1977) in the families Hypoxidaceae and Scrophulariaceae, respectively. *Rhodohypoxis* species are geophytes while *Glumicalyx* species are hemicrytophytes. These genera were chosen because of documented cases of hybridization within each genus at the species and/or varietal level. This is an important factor as species within each genus have the potential to hybridize which may affect the biodiversity of the area. Additionally, the species in each genus (and varieties of *Rhodohypoxis*) occur in the three thermal zones in the Drakensberg (Hilliard & Burtt, 1987). The study focused on the KwaZulu-Natal portion of the Drakensberg region and the potential implications climatic changes have on two endemic plant genera. Consequently, the aim was to assess recent climatic trends between the alpine, upper and lower montane thermal zones in the Drakensberg from 1994 to 2014 and predict the potential effects on hybridization

possibly occurring between the plant species due to shifting or merging of thermal zones in the region.

This aim was achieved by analysing temperature and precipitation data over a 20 year period (1994–2014) from four weather stations in the Drakensberg range that encompass each thermal zone. The analyses included temperature and precipitation trend lines, inter-annual variations, as well as the number of frost days within the thermal zones. Results from these analyses provided information as to whether the thermal zones have changed over the 20 year period and to what extent. The resulting trends in temperature and precipitation in the region have implications for the survival of plant species as well as the structure of the plant communities in these areas. To address this issue this study focused on how the temperature and precipitation changes may potentially affect two endemic plant genera in the Drakensberg that have records of hybridization between co-occurring species and/or varieties, namely *Rhodohypoxis* and *Glumicalyx*.

References list

Beniston, M. & Fox, D.G., 2003. Impacts of climate change on mountain regions: a review of possible impacts. *Climate Change.* 59 (1-2): 5–31.

Boughman, J.W., 2001. Divergent sexual selection enhances reproductive isolation in sicklebacks. *Nature.* 411: 944–948.

Bussmann, R.W., 2006. Vegetation zonation and nomenclature of African mountains – an overview. *Iyonia-Journal of Ecology and Application.* 11 (1): 41–66.

Carbutt, C. & Edwards, T.J., 2001. Cape elements on high-altitude corridors and edaphic islands: historical aspects and preliminary phytogeography. *Systematics and Geography of Plants.* 71 (2): 1033–1061.

Carbutt, C. & Edwards, T.J., 2004.The flora of the Drakensberg Alpine Centre. *Edinburgh Journal of Botany.* 60 (3): 581–607.

Carbutt, C. & Edwards, T.J., 2006. The endemic and near-endemic angiosperms of the Drakensberg Alpine Centre. *South African Journal of Botany.* (72): 105–132.

Carbutt, C. & Edwards, T.J., 2015. Reconciling ecological and phytogeographical spatial boundaries to clarify the limits of the montane and alpine regions of sub-Sahelian Africa. *South African Journal of Botany.* (98): 64–75.

Chunco, A.J., 2014. Hybridization in a warmer world. *Ecology and Evolution.* 4 (10): 2019–2031.

Clark, V.R., Barker, N., and Mucina, L., 2011. Taking the scenic route – the southern Great Escarpment (South Africa) as part of the Cape to Cairo floristic highway. *Plant Ecology and Diversity.* 4 (4): 313-328.

DEA (Department of Environmental Affairs), 2013. Long-Term Adaptation Scenarios Flagship Research Programme (LTAS) for South Africa. *Climate Trends and Scenarios for South Africa*. Pretoria, South Africa.

Du Toit, J.C.O., and O'Connor, T.G., 2014. Changes in rainfall pattern in the eastern karoo, South Africa, over the past 123 years. *Water SA.* 40 (3): 452–460.

Dafni, A., Cohen, D. & Noy-Meir, I., 1981. Life-cycle variation in geophytes. *Annals of the Missouri Botanical Garden.* 68 (4): 652–660.

Gale, J., 2004. Plants and altitude – revisited. *Annuals of Botany.* 94 (2): 199.

Galley, C., Bytebier, B., Bellstedt, D.U., & Linder, H.P., 2007. The Cape element in the afrotemperate flora: from Cape to Cairo? *Proceedings of Royal Society B: Biological Sciences.* 274 (1609): 535–543.

Gehrig-Fasel, J., Guisan, A., and Zimmerman, N.E., 2007.Tree line shifts in the Swiss Alps: climate change or land abandonment*? Journal of Vegetation Science.* (18): 571–582.

Gomez, J.M., Gonzalez-Megias, A., Lorite, J., Abdelaziz, M., and Perfectti, F., 2015. The silent extinction: climate change and the potential hybridization-mediated extinction of endemic high mountain plants. *Biodiversity Conservation.* (24): 1843–1857.

Grab, S.W., and Craparo, A., 2011. Advance of apple and pear tree full bloom dates in response to climate change in the southwestern Cape, South Africa: 1973-2009. *Agricultural and Forest Meteorology.* 151: 406–413.

Grab, S., 2010. Geomorphic landscapes: Drakensberg escarpment. Springer International Publishing, Switzerland.

Grimshaw, J.M., 2001. What do we really know about afromontane archipelago? *Systematics and Geography of Plants.* 71 (3): 949–957.

Gutterman, Y., 2002. Adaptations of desert organisms: survival strategies of annual desert plants. Springer-Verlag Berlin, Heidelberg.

Harper, C.W., Blair, J.M., Fay, P.A., Knapp, A.K., and Carlisle, J.D., 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in grassland eco-system. *Global Change Biology.* 11 (2): 322–334.

Hasler, R., 1982. Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. *Oecologia.* (54): 14–22.

Hedberg, O., 1970. Evolution of Afroalpine flora. *Biotropica.* 2 (1): 16–23.

Hennessy, K., Whetton, P., Walsh, K., Smith, I.N., Bathols, J.M. Hutchinson, M.and Sharples, J., 2008. Climate change effects on snow conditions in main-land Australia and adaptations at ski resorts through snowmaking. *Climate Research.* (35): 255–270.

Hilliard, O.M. & Burtt, B.L., 1973. Notes on some plants of southern Africa chiefly from Natal III. Rhodohypoxis. *Notes from the Royal Botanic Garden Edinburgh.* 32: 305–314.

Hilliard, O.M. & Burtt, B.L., 1977. Notes on some plants of southern Africa chiefly from Natal: VII. *Notes from the Royal Botanic Gardens Edinburgh.* 43: 201–206.

Hilliard, O.M. & Burtt, B.L., 1977. Notes on some plants of southern Africa chiefly from Natal: VI: 221–227. Glumicalyx. *Notes from the Royal Botanic Gardens Edinburgh.* 35: 155–172.

Hilliard, O.M. & Burtt, B.L., 1978. Notes on some plants of southern Africa chiefly from Natal: VII: 233–244. Rhodohypoxis. *Notes from the Royal Botanic Garden Edinburgh.* 36: 43–76.

Hilliard, O.M. & Burtt., B.L., 1987. Notes on some plants from southern Africa chiefly from Natal. *Notes from the Royal Botanical Gardens Edinburgh.* 1: 233–244.

Holland, P.G. & Steyn, D.G., 1975. Vegetational responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography.* 2: 179–183.

Honnay, O., Jacquemyn, H., Bossuyt, B., and Hermy, M., 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist.* 166 (3): 723–736.

Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution.* 15 (2): 56–61.

Inouye, D.W., 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters.* 3 (5): 457–463.

Jones, P.D., Raper, S.C.B, and Wigley, T.M.L., 1986. Southern hemisphere surface air temperature variations: 1851-1984. *American Meteorological Society.* 25: 1213–1230.

Karl, T.R., and Trenberth, K.E., 2003. Modern global climate change. *Science.* 5651 (302): 17190–1723.

Khan, S.M., Page, S., Ahmad, H., Shaheen, H., and Harper, D., 2012. Vegetation dynamics in the western Himalayas, diversity indices and climate change. *Science, Technology and Development.* 31 (3): 232–243.

Killick, D.J.B., 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. *Memoirs of the Botanical. Survey of South Africa.* 34: 178.

Killick, D.J.B., 1978. Notes on the vegetation of the Sani Pass area of the southern Drakensberg. *Bothalia.* 12: 537–542.

Killick, D.J.B., 1978. Further data on the climate of the alpine vegetation belt of eastern Lesotho. *Bothalia.* 12 (3): 567–572.

Körner, C., & Larcher, W., 1988. Plant life in cold climates. *Symposia of the Society for Experimental Biology*. (42): 25–57.

Körner, C., 2003. Alpine plant life: functional plant ecology of high mountain ecosystems. Springer-Verlag Publishers. Berlin, Germany.

Körner, C., & Ohsawa, M., 2005. Ecosystems and human well-being: current state and trends, mountain systems. *Millennium Ecosystem Report.* 24: 681–716.

Körner, C., 2007. The use of 'altitude' in ecological research. *Trends Ecol. Evol*. 22: 569–574.

Körner, C., Paulsen, J., and Spehn, E.M., 2011. A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany.* 121 (2): 73–78.

Larcher, W., Kainmuller, C., & Wagner, J., 2010. Survival types of high mountain plants under extreme temperatures. *Flora – Morphology, Distribution, Functional Ecology of Plants.* 205 (1): 3–18.

Messerli, B., and Winiger, M., 1992. Climate, environmental change, and resources, of the African mountains from the Mediterranean to the equator. *Mountain Research and Development.* 12 (4): 315–336.

Mishra, S.R., 2004. Photosynthesis in plants. Discovery Publishing House.

Nel, W., 2007. On the climate of the Drakensberg: rainfall and surface temperature attributes and associated geomorphic effects. *Department of Geography, Geoinformatics and Meteorology, University of Pretoria.*

Nel, W., and Sumner, P.D., 2005. First rainfall data from the KZN escarpment edge (2002 and 2003). *Water SA.* 31 (3): 399–402.

Neukom, R., Nash, D.J., Endfield, G.H., Grab, S.W., Grove, C.A., Kelso, C., Vogel, C.H. and Zinke, J., 2014. Multi-proxy summer and winter precipitation reconstruction for southern Africa over the last 200 years. *Climate dynamics.* 42: 2713–2726.

Nicholsom, S.E., Nash, D.J., Chase, B.M., Grab, S.W., Shanahan, T.M., Verschuren, D., Asrat, A., Lezine, A. and Umer, M., 2013. Temperature variability over Africa during the last 2000 years. *The Holocene.* 23 (8): 1085–1094.

Opler, P.A., Frankie, G.W. and Baker H.G., 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography.* (3): 231–236.

Pauli, H., Gottfried, M., and Grabherr, G., 2003. Effects of climate change on the alpine and nival vegetation of the Alps. *Journal of Mountain Ecology.* 7: 9–12.

Poverene, M., Cantamutto, M. and Seiler, G.J., 2009. Ecological characterization of wild *Helianthus annuus* and *Helianthus petiolaris* germplasm in Argentina. *Plant Genetic Resources.* 7(1): 42–49.

Raunkiær, C., 1907. Planterigets livsformer og deres betydning for geografien. *Gyldendalske Boghandel - Nordisk Forlag, København and Kristiania. Pp*: 104–132.

Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics.* 27: 83–109.

Rieseberg, L.H., and Carney, S.E., 1998. Plant hybridization. *New Phytologist.* 140: 599–624.

Rieseberg, L.H., 1997. Hybrid origins of plant species. *Annual Review of Ecology and Systematics.* 28: 359–389.

Schwinning, S., Sala, O.E., Loik, M.E., and Ehleringer, J.R., 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid eco-systems. *Oecologia.* (141): 191–193.

Smith, W.G., 2013. Raunkiaer's "Life Forms" and statistical methods. Retrieved from http://www.britishecologicalsociety.org/100papers/100_Ecological_Papers/100_Influential_Papers_026.pdf.

Snijman, D.A., 2013. Plants of the greater Cape floristic region, 2: the extra Cape flora. *Strelitzia,* SANBI, Pretoria.

Spehn, E.M., Rudmann-Maurer, K., Körner, C., Maselli, D., 2010. Mountain biodiversity and global change. GMBA-Diversitas, Basel.

Stinson, K.A., 2005. Effects of snowmelt timing and neighbour density on the altitudinal distribution of *Potentilla diversifolia* in Western Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research.* 37 (3): 379–386.

Takeishi, H., Hayashi, J., Okazawa, A., Harada, K., Hirata, K., Kobayashi, A., and Akamatsu, F., 2013. Effects of elevated pressure on rate of photosynthesis during plant growth. *Journal of Biotechnology.* 168 (2): 135–141.

Theurillat, J.P. & Guisan, A., 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic change.* 50 (1-2): 77–109.

Thuiller, W., 2007. Biodiversity: Climate change and the ecologists. *Nature.* 448: 550–552

Van Der Heijden, M.G.A., Bardgett, R.D., and Van Straalen, N.M., 2007. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial eco-systems. *Ecology Letters.* 11 (3): 296–310.

Vera, M.L., 1997. Effects of altitude and seed size on germination and seedling survival of heathland plants in north Spain. *Plant Ecology.* 133: 101–106.

Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K., and Poschold, P., 2011. Climate change and plant regeneration from seed. *Global Change Biology.* 17 (6): 2144–2162.

Walther, G., Bieβner, S., & Burga, C.A., 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science.* 16: 541–548.

White. F., 1978. Biography and ecology of southern Africa: the afromontane region. *Monographiae Biologicae.* (31): 463–513.

White, F., 1981. The history of the afromontane archipelago and the scientific need for its conservation. *African Journal of Ecology.* (19): 33–54.

Whitham, T.G., Martinsen, G.D., Floate, K.D., Dungey, H.S., Potts, B.M. and Keim, P., 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. *Ecology.* 80 (2): 416–428.

Woodward, F.I. & Williams, B.G., 1987. Climate and plant distribution at global and local scales. *Vegetation.* (69): 189–197.

Zogg, G.P., Zak, D.R., Ringelberg, D.B., White, D.C., MacDonald, N.W., and Pregitzer, K.S., 1995. Compositional and functional shifts in microbial communities due to soil warming. *Soil Science Society of America Journal.* 61 (2): 475–481.

Chapter 2

Research and Analysis

Introduction

Mountain environments are a haven for biodiversity, endangered species and ecosystems (Beniston, 2003). Climatic change is one of the effects that natural environments experience due to human influences (Beniston, 2003; Karl & Trenberth, 2003). Previous research has shown that an increase in temperature at high altitudes results in the formation of suitable habitats for several lower altitude plant species, thus enabling these lower altitude plants to migrate to higher altitudes (Beniston, 2003; Gehrig-Fasel, 2007; Gomez *et al.,* 2015). Such migration of mountain plant species has been documented in the Swiss Alps, the Andes mountain range in Venezuela, the Australian Alps and the Asian Himilayas (Xu *et al.,* 2009). These documented cases illustrate how warming temperatures are directly related to the movement of plant species into higher altitudes, and are important parallels to the mountain regions of southern Africa. This suggests that if temperatures and precipitation trends change in southern African mountains, there may be an upward shift of species within the altitudinal zones.

South Africa has several mountainous areas, one of which is the Drakensberg range. Within this mountain range is the Drakensberg Alpine Centre (DAC). The DAC is a mountain region previously recognised to be above 1800 m a.s.l. (Carbutt and Edwards, 2004), but has more recently been restricted to above 2800 m a.s.l., (Carbutt and Edwards, 2015). The DAC comprises a high altitude range of hills, escarpments and plateaus covering approximately 40,000 km², including the highest part of the Great Escarpment, is home to 2 520 native angiosperm species, 595 of which are near-endemic and 334 are endemic and is recognised as a world heritage site (Carbutt and Edwards, 2006; Nel, 2007). Many of these endemic angiosperms are rare and have very specific habitats which play an important role in plant speciation and biodiversity of the area (Carbutt and Edwards, 2006). Killick (1963) defined the centre of floristic endemism in the DAC from 1800 m a.s.l. to the Drakensberg's highest point, 3482 m a.s.l. (Carbutt and Edwards, 2014), and then delimited the alpine belt in the Drakensberg as occurring above about 2800 m a.s.l. The vegetation from 1800 m to 2800 m was defined as 'sub-alpine' and vegetation below 1800 m as 'montane' (Killick, 1978). Vegetation was characterised

by climax plant communities, i.e. the final stage of plant succession (the sequential change in the dominant plant species in an area over time; Huston and Smith, 1987).

In more recent years the delineation of the altitudinal zones and the classification of the floristic regions have been challenged. Körner *et al.* (2011) employed a new model of seven thermal life zones in mountains; the zones are defined by climate, excluding elevation (although climate and elevation are tightly correlated). This model changed the previously known montane altitudinal zone to the lower montane thermal zone (>10 ≤15ºC mean growing season temperature, growing season (GS) > 94 days), the sub-alpine altitudinal zone to the upper montane thermal zone (>6.4 ≤10ºC mean growing season temp., GS > 94 days). The alpine altitudinal zone changed to the lower alpine thermal zone (< 6.4ºC mean growing season temperature, growing season < 94 days). The new thermal life zones are simple and defined by climate rather than elevation, this enables comparison of mountain life on a global scale (Körner *et al.*, 2011).

The DAC forms part of the formally known 'Afromontane archipelago' (White, 1978, 1981), that comprises a number of mountains scattered across the African continent with similar floristic attributes and high levels of endemism (Grimshaw, 2001). The recognition of the 'Afromontane' floristic region in African mountains has been challenged as its delineation was based on shared plant species distribution and areas with great floral endemism at high elevations (Carbutt and Edwards, 2015). Species distributions and floral endemism function on two different scales and make it difficult to accurately describe such a variety of landscapes (Carbutt and Edwards, 2015). Carbutt and Edwards (2015) suggest the 'Afromontane' region in southern Africa between ±1300 m and ±2800 m a.s.l. Carbutt and Edwards (2015) also proposed that the DAC should exclude the upper and lower montane zones and only include the lower alpine zone from ±2800 m to 3482 m a.s.l. The alpine areas of South Africa are more accurately defined as 'Austroalpine' as the term 'afroalpine' encompasses both tropical and temperate mountain systems (Carbutt and Edwards, 2015).

The mountainous regions in South Africa experience various temperature and precipitation regimes, which have an effect on which plant species are able to survive in those regions. The growing (wet) season in the summer rainfall areas of the southern Africa begins

around October and ceases around March (Shongwe *et al.,* 2009). The length of the growing season may decrease with altitude and thus the non-growing season length may increase. For this research, the growing season was defined as six months of the year from October to March, and non-growing season from April to September, to enable a comparison between the alpine, lower and upper montane thermal zones. The number of frost days in the year (January to December) was measured as frost does occur in the Drakensberg and may have a detrimental effect on plant survival (Woodward and Williams, 1987; Boelhouwers, 1991; Hanvey & Marker, 1992).

Over the last few decades, climatic trends in South Africa have shown an overall increase in temperature and decrease in precipitation with such changes accelerating in recent years (Grab & Craparo, 2011; DEA, 2013; Nicholson *et al.,* 2013; Neukom *et al.,* 2014). Changing climatic conditions in South African mountain environments are likely to affect the distribution of plant species in the thermal zones. The effect this will have on the Drakensberg ecosystems is unclear due to the complexity of these systems (among other reasons; Theurillat and Guisan, 2001; Pauchard *et al.,* 2009). Previously recorded climatic changes in mountain systems have shown a variety of results with both positive and negative consequences for biodiversity. The adaptive ability of endemic plant species is key to their long-term survival in a changing climate, as species with low responsive rates to environmental conditions may be particularly vulnerable to changing climatic conditions (Totlan & Alatalo, 2002). Plants may adapt to changing climatic conditions through hybridization and this is true for some Drakensberg species such as *Jamesbrittenia breviflora* and *J. pristisepala* which frequently hybridize where they co-occur (Verboom *et al.,* 2016). Hybridization may have a positive or negative effect on the floral species composition of the area and therefore may affect the biodiversity (Hilliard & Burtt 1977, 1987; Johnson & Hobbhahn, 2010).

This study focuses on two plant genera *Rhodohypoxis* Nel. and *Glumicalyx* Hiern as they occur in the three thermal zones and have been known to hybridise between species and/or varieties. *Rhodohypoxis* (Hypoxidaceae) occurs in the Drakensberg of South Africa and the Lesotho Plateau (Hilliard and Burtt, 1987). This genus consists of herbaceous perennial geophytes with red, pink, or white flowers. It is a small genus of six recognised species, viz. *Rhodohypoxis baurii* (Baker) Nel, *R. milloides* (Baker) Hilliard & B.L.Burtt, *R. thodiana* (Nel) Hilliard & B.L.Burtt, *R. incompta* Hilliard & B.L.Burtt, *R. rubella* (Baker) Nel and *R. deflexa*

Hilliard & B.L.Burtt. *Rhodohypoxis baurii* is the most widespread and comprises three varieties. Two of the species occur in the lower montane and upper montane zones: *Rhodohypoxis milloides* and two varieties of *R. baurii,* viz. *Rhodohypoxis baurii* (Baker) Nel var. *platypetala* (Baker) Nel and *R. baurii* (Baker) Nel var. *baurii.* The other four species (*Rhodohypoxis incompta, R. rubella, R. thodiana* and *R. deflexa*) as well as *R. baurii* var. *confecta* Hilliard & B.L.Burtt occur in the alpine zone. It has been suggested that each of these species and varieties has adapted to a specialised microhabitat (Hilliard and Burtt, 1987). *Rhodohypoxis milloides* grows on hill sides in spring flushes or near moving water, however cannot handle continuous flooding. *Rhodohypoxis baurii* var. *baurii* is found predominantly on moist, shaded cliff faces; *R. baurii* var. *platypetala* is often found in dry areas with shallow stony soils, while *R. baurii* var. *confecta* grows on damp grass slopes or on the summit plateau in short damp turf (Hilliard and Burtt, 1978). *Rhodohypoxis incompta* thrives on the outskirts of grass or sedge tussocks on the boarder of the rock sheets or silt patches. *Rhodohypoxis thodiana* has been observed in turf on gentle slopes near wet areas, and *R. rubella* grows in shallow seasonal pools in fine sandy or damp silt soils. *Rhodohypoxis deflexa* is found growing in marshy damp areas usually besides moving streams (Hilliard and Burtt, 1978). The second case study genus, *Glumicalyx* (Scrophulariaceae) has six species that occur in the DAC and Afromontane areas of the Drakensberg, three predominantly in the alpine zone and three in the upper montane zone (Hilliard and Burt, 1977; Carbutt and Edwards, 2004). *Glumicalyx* species are characterised by a broad terminal inflorescence of trumpet-shaped flowers. The flowers have different colour variations including red, orange and yellow (Carbutt and Edwards, 2004). Two species, *Glumicalyx gloseloides* (Diels) Hilliard & B.L.Burtt (1900 – 2600 m), *G. montanus* Hiern (2042 – 3050 m), occur predominately in the upper montane zone, although the latter has been recorded in the alpine zone. *Glumicalyx gloseloides* is found growing among the boulders of mountain streams as well as other open gravel areas, and *G. montanus* grows in rocky areas on thinly grassed slopes (Hilliard and Burtt, 1987). Three species, *Glumicalyx nutans* (Rolfe) Hilliard & B.L.Burtt (2440 – 3220 m), *G. flanaganii* (Hiern) Hilliard & B.L.Burtt (2440 – 3215 m), and *G. lesuticus* Hilliard & B.L.Burtt (2590 – 3110 m; Pooley, 2003) occur predominately in the alpine zone, with slight overlap into the higher upper montane altitudes. *Glumicalyx nutans* prefers to grow in short turf, in bare gravel, around rock sheets or in silt patches (Hillard and Burtt, 1977). *Glumicalyx flanaganii* grows in damp rocky areas, often in the gullies of streams or along the

foot of a cliffs, *G. lesuticus* however is found in gravel patches in grassland or thinly grassed slopes. The sixth species, *Glumicalyx apiculatus* (E.Mey.) Hilliard & B.L.Burtt is found between 2133 m and 3350 m, i.e., in the upper montane and alpine zones, and grows in silt or bare gravel patches or in patches of turf around rock sheets. Little is known about the biology of this species and it is either under-collected or the rarest in the genus (Hilliard and Burtt, 1977; 1987).

Hybridization among plant species in the Drakensberg has been suggested as an adaptation to changing climatic conditions (Hilliard & Burtt 1977, 1987; Johnson & Hobbhahn, 2010). There is a record of hybridization between *Glumicalyx nutans* and *G. goseloides* at ca. 2200 m a.s.l. within the upper montane thermal zone in the northern Drakensberg near the Sentinel where they co-occur (Hilliard & Burtt 1977). However, there have not been as many documented cases of hybridization in *Glumicalyx* as in *Rhodohypoxis*, with one documented hybrid between *Glumicalyx* species and six recorded hybrids between *Rhodohypoxis* species or varieties. As few hybrids of *Glumicalyx* species have been recorded, if the species started to hybridize more frequently than previously recorded, this could be used as an indicator of change. *Rhodohypoxis* species have been observed to hybridise within their thermal zones, but not between the thermal zones (Hilliard & Burtt 1978; E. Uys, *pers. comm*.). The hybrid offspring often occur in intermediate habitats, but do not merge with the two parent populations (E. Uys, *pers. comm.)*. However, if the thermal zones were to become less distinct in terms of climatic variables, or if the alpine zone becomes more inhabitable for upper montane species, it is not known whether alpine and upper montane species would hybridise. The presence of hybrids in both genera suggests that if the alpine and upper montane zones merge as a result of future regional temperature trends, the continued existence of the *Rhodohypoxis* and *Glumicalyx* species could be jeopardised if they are not reproductively isolated. These two genera are therefore potential indicators of change in floral diversity and plant community dynamics in the Drakensberg.

Aims and Objectives

This study aims to compare inter-annual (within the last 20 years, 1994-2014) temperature and precipitation trends between alpine, upper and lower montane thermal zones in the southern Drakensberg to better predict future implications for endemic plant genera with regard to climate change.

The aim was met by the following objectives:

- To compare annual temperature trends over 20 years in the alpine, upper and lower montane thermal zones in the Drakensberg and compare temperature-related variables that are important for plant existence (e.g., average monthly temperatures, growing season temperatures).
- To compare the inter-annual variability of temperatures over 20 years in the alpine, upper and lower montane thermal zones in the Drakensberg.
- To compare annual precipitation trends over 20 years in the alpine, upper and lower montane thermal zones in the Drakensberg and compare precipitation-related variables that are important for plant existence (e.g. annual rainfall, growing season rainfall, date of first rainfall).
- To compare the inter-annual variability of precipitation over 20 years in the alpine, upper and lower montane thermal zones in the Drakensberg.
- To compare the annual number of frost days over 20 years in the alpine, upper and lower montane thermal zones in the Drakensberg.
- To identify potential implications of the migration and survival of endemic plant species in the alpine, upper and lower montane thermal zones using *Rhodohypoxis* and *Glumicalyx* as case studies

Methods

Study Area and Data Sources

The focus of this study is the central to southern Drakensberg in South Africa and Lesotho, between latitudes 28º30´S – 31º20´S and longitudes 27º00´E – 29º40´E. Weather data were collected from four weather stations in this region (Figure 2 and 3): Shaleburn and Giants Castle in South Africa, and Sani Pass and Mokhotlong in Lesotho. Shaleburn (1614 m) and Giants Castle (1759 m) are within the lower montane thermal zone, while Mokhotlong (2209 m) is in the upper montane thermal zone, and Sani Pass (2874 m), in the eastern most area of Lesotho, falls within the alpine thermal zone.

The weather records collected consisted of precipitation and temperature data over a 20 year period from 1994 to 2014. This 20 year period was the only length of time for which all four sites had complete data, although some sites had data for longer than the 20 years. The Shaleburn site had temperature data available from 1981 to 2014, and precipitation data from 1993 to 2014. The Giants Castle site had temperature data from 1994 to 2014 and precipitation data from 1993 to 2014. The Mokhotlong site had recorded temperature data from 1959 to 2014 and precipitation data from 1984 to 1993. The Sani Pass temperature data was recorded from 1992 to 2014, however the data were incomplete in 15 of the years over this period , and the precipitation data were recorded from 1994–2014.

The temperature and precipitation data for Shaleburn and Giants Castle data were retrieved from the South African Weather Services from daily automated measurements and are captured using data loggers. The Mokhotlong temperature and precipitation data were retrieved from the Lesotho Meteorological Services, also from automated measurements and are captured using data loggers. The Sani Pass temperature data were collected through two different methods: one by hand, recording the temperature each day, and the second method recorded temperature via automated capture. The hand recorded temperature data from this site is from the Lesotho Meteorological Services (LMS), and the automated data is from a weather station set up by Prof. Stefan Grab (School of Geography, Archaeology & Environmental Studies, University of the Witwatersrand, Johannesburg). The available data spanned 20 years (1994–2014). Both the LMS data and data from Prof. Grab of the temperature data sets received were consolidated into one dataset. If there were overlapping years (where both sources had a temperature for the same year) an average of the two temperatures was calculated and used in the consolidated data set for the Sani Pass data. The LMS temperature data (for the Sani Pass site) spanned the years 1992–2014 with 15 years of data that were incomplete, and the automated data spanned the years 2010–2014, with four years of data that were incomplete. There was no particular pattern identified among the gaps in the data. There were only four years (1995, 1998, 2001 [manual recordings], 2013 [automated recordings]) with complete data (a minimum and maximum temperature reading for each month of the year). Thus these datasets were not sufficient for the temperature analysis because there were many incomplete years. The precipitation data from the Mokhotlong site was also not sufficient as there were many incomplete years and could not be used in the analyses, however the temperature data were comprehensive over 19 of the 20 years and were

included in this study. All data were checked for errors by identifying outliers and missing data. Outliers were identitified by gauging minimum and maximum values and checking whether suspected outliers fell within the expected range. Missing data were identified by performing counts on each data set, confirming there was a value for each year. It is understood that there were no instrument changes over the period of time studied, however the Sani Pass data set was collected by hand and could contain human error.

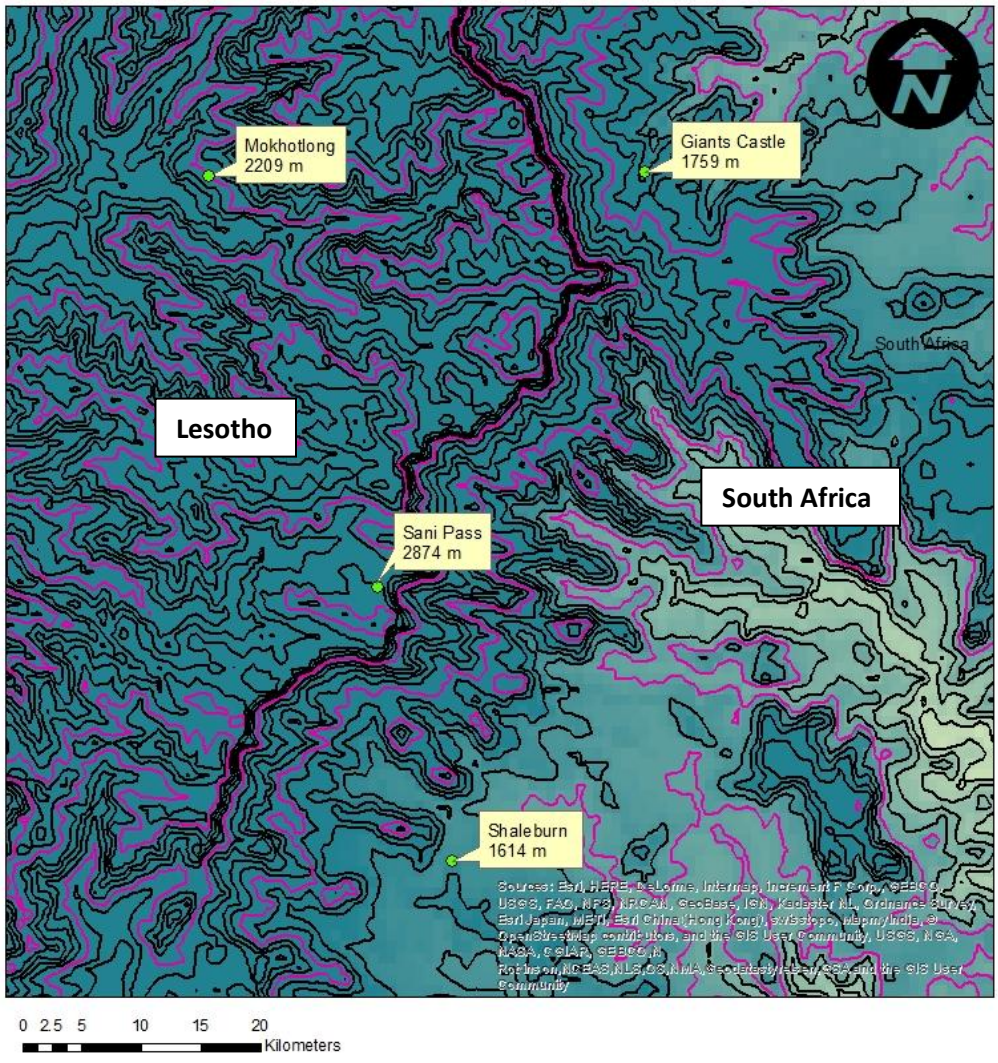

Figure 2. Map showing location of Mokhotlong, Giants Castle, Sani Pass and Shaleburn weather stations showing elevation every 100 m, the pink line represents a 500 m interval.

Figure 3. A large scale regional map of South Africa showing the research area (represented by black box).

Precipitation and Temperature Variables

The precipitation variables chosen for this study included annual rainfall, growing season rainfall, non-growing season rainfall, and number of rain days per annum. Annual rainfall provides information on how much precipitation the plants are surviving on in each thermal zone over a 12 month period from January to December. Growing and non-growing season provide information on how much rain is falling in the wet and dry seasons respectively and therefore how much rain is needed for the plants to survive these seasons. The number of rain days in a year provide information on the frequency of rainfall events, and paired with annual rainfall provide information on intensity of rainfall events. The precipitation variables were calculated as follows. The annual rainfall equals the sum of rainfall on each day of all 12 months, the same method was used for the growing season (October to March) and non-growing season (April to September). All variables were calculated over a 20 year period (1994–2014) for three sites: Sani

Pass (alpine), Shaleburn (lower montane), and Giants Castle (lower montane). Mokhotlong had complete data from 1984 to 1992, but not further, and therefore was excluded for lack of data in the correct time frame.

The temperature variables chosen for this research were mean annual, minimum annual and maximum annual temperatures; mean growing season, minimum growing season, and maximum growing season temperatures; and mean non-growing season, minimum non-growing season and maximum non-growing season temperatures. The mean, minimum and maximum annual temperatures provide information on the average temperatures as well as the hottest and coldest temperatures in which the plants survive across a 12 month period from January to December in each thermal zone. The mean, minimum and maximum growing season temperatures highlight average temperature and the hottest and coldest temperatures in which the plants would survive and grow. The mean, minimum and maximum temperatures give an indication of the range of temperatures for plant growth in each thermal zone. The mean, minimum and maximum non-growing season temperatures provide information on the average temperature and extreme hot and cold temperatures in which the plants survive in the non-growing season (autumn-winter). This gives an indication of the dry season conditions which the plants survive. The precipitation and temperature variables and the graphs associated with those variables are listed in the table below. Mean annual temperature was calculated as an average of the temperatures (both maximum and minimum over 12 months). The annual minimum and maximum temperatures were calculated in the same way using the average temperatures from January to December. Minimum temperature is defined as the lowest temperature of the day (24 hours), the maximum is therefore the highest temperature of the day.

The same process was applied for the growing season variables, however the averages were calculated over a six month period from October to March. The same process was again used for the non-growing variables and the averages were calculated over a 6 month period from April to September. The annual variables were calculated for each year spanning 20 years at three sites: Mokhotlong (upper montane), Shaleburn (lower montane), and Giants Castle (lower montane), Sani Pass being excluded for lack of complete data. Inter-annual variability was estimated using Levene's test, standard deviation, and coefficient of variance. Each test had a different objective, Levene's test was used to determine if one data set had more variability than

the other, standard deviation would determine the variability in the temperature data sets, and coefficient of variance would determine the variability in the precipitation data sets over the period of 20 years.

Data Analyses

Trend Analyses:

In order to identify temperature and precipitation clustering in the lower alpine, upper and lower montane zones, linear regression analyses, multivariate analysis of variance, and principal component analyses were conducted. Linear regressions modelled the relationship between the temperature/precipitation variables and time revealing the trend of the data over the 20 year period. Using the mean values calculated from the temperature and precipitation variables above, regressions were used to determine increasing or decreasing trends within the three thermal zones (lower alpine, upper montane and lower montane) over time. The rates of change in the zones were compared using regression slopes, the slope showed how much change had taken place over the 20 years. This enabled the rate of increase or decrease of each variable to be identified over time in each zone.

Principal component analyses (PCA) were conducted using STATISTICA (StatSoft, Inc., 2013) to highlight the components which account for the most variance in multiple data sets over time. The goal was to see which varibles accounted for the most variance within the three sites. The PCA also showed whether the alpine, upper and lower montane shared multiple variables between the weather data collection sites (Sani Pass, Mokhotlong, Shaleburn and Giants Castle). The temperature PCA included data from three sites (Mokhotlong, Shaleburn and Giants Castle) with nine variables (mean annual, minimum annual and maximum annual temperatures; mean growing season, minimum growing season, and maximum growing season temperatures; and mean non-growing season, minimum non-growing season and maximum non-growing season temperatures), and the precipitation PCA was produced using data from three sites (Sani Pass, Shaleburn and Giants Castle) with four variables (annual rainfall, growing season rainfall, non-growing season rainfall, and number of rain days per annum).

Multivariate analysis of variance (MANOVA) were conducted using STATISTICA to test if there were significant differences between the means of the alpine, upper and lower montane temperature and precipitation variables. The MANOVA showed which means amongst the variables had a higher variation over the time period. A Bonferroni correction was used as a post hoc test to reduce the chances of a false positive result that may occur when multiple pair wise tests are performed. The Bonferroni Correction required an adjusted alpha level; the alpha level was divided by the number of comparisons being made, in this case there were three sites and therefore three comparisons ($P = 0.05/3$).

The precipitation data were found to violate the assumption of homogeneity of variances for the one-way MANOVA and the linear regression. Previous studies have shown that linear regressions and MANOVA's are robust with respect to the violation of the homogeneity of variance if sample sizes are equal (Box, 1953; Rutherford, 2001), and my sample sizes across stations for precipitation are equal (i.e. there are four variables with 21 samples of rainfall in each).

Inter-annual Variability Analysis

The second aim of the study was to understand the inter-annual variability of temperature and precipitation ranges at different altitudes. To do so, a Levene's test and comparisons of the coefficient of variation and standard deviations for the precipitation data and temperature data were conducted. The Levene's test was used to test if the different samples have equal variances (or homogeneity of variance), which is indicative of whether one data set has more variability than another over a 20 year time period. To understand how much the temperature variables for Mokhotlong, Shaleburn and Giants Castle sites deviated from the mean, a standard deviation (SD) was calculated for each variable.

In addition, a coefficient of variation (CoV) was then calculated to understand the variability of the precipitation variables for Sani Pass, Shaleburn and Giants Castle sites. The coefficient of variation was calculated by dividing the standard deviation by the mean of each precipitation variable. This number was then multiplied by 100, which resulted in the coefficient of variation expressed as a percentage. This was done for each site (Sani Pass, Shaleburn, and Giants Castle) for all precipitation variables. The temperature and precipitation variables were tested to find out whetherthe higher thermal zones (upper montane and alpine) have a higher

variation from the mean, as previous studies (Beniston, 2003; Gehrig-Fasel, 2007; Gomez *et al.*, 2015) have found more variable climate and temperature and precipitation changes at higher altitudes.

Variables Analysis: Frost Indices

The third aim of the study was to describe how variables important for plant species, such as frost indices, vary within and between the thermal zones over a 20 year period. To do so, the recorded frost days from three sites (Mokhotlong, Shaleburn, and Giants Castle) were counted from the raw data and categorised. For the purpose of this study, a frost day was defined as any day in which the temperature fell to 0 ºC or below, even though ground level frost may occur when air temperatures are above 0 ºC. For the purpose of this study the frost days were categorised, to better understand the severity of the temperature changes, into three groups: 0 to -2 ºC, -2 to -5 ºC, -5 ºC and below. These categories describe below freezing temperatures from 'mild' (0 to -2 ºC) to 'moderate' (-2 to -5 ºC) to 'extreme' (-5 ºC and below). These categories show not only the frost days over time, but the extent of the frost (mild, moderate or extreme).

Results

Linear regressions of precipitation and temperature data

Linear regressions of annual rainfall across Sani Pass (SP), Giants Castle (GC), and Shaleburn (SH) showed a generally negative relationship of rainfall over the 20 year period (Figure 4; Table 1). SP (2874 m) in the alpine zone showed a negative relationship of annual rainfall over time from 1994 to 2014 (m = -32.568). The average annual rainfall at SP was 903.4 mm. The rainfall at SP decreased by 32.6 mm per annum which is a 3.8% decrease of the total rainfall that had fallen over 20 years from 1994 to 2014 (Table 1). This is an unusually large decrease which might indicate problems in the data. The GC (1759 m; lower montane zone) data also showed a decrease in rainfall from 1994 to 2014 (m = -16.622). The average rainfall was 733.5 mm per annum, with an annual average decrease of 16.6 mm, therefore an overall 20 year decrease of approximately 2% (Table 2). At SH (1614 m; lower montane), the data showed a negative relationship, but a relatively smaller decrease than the other two sites (m = -6.0584). The average rainfall at this site was recorded at 1112.8 mm per annum from 1994 to 2014. This

site showed an annual decrease on average of 6 mm, which was a decrease of 0.5% over the 20 year period, such a low value is not substantially different from a flat slope (Table 1).

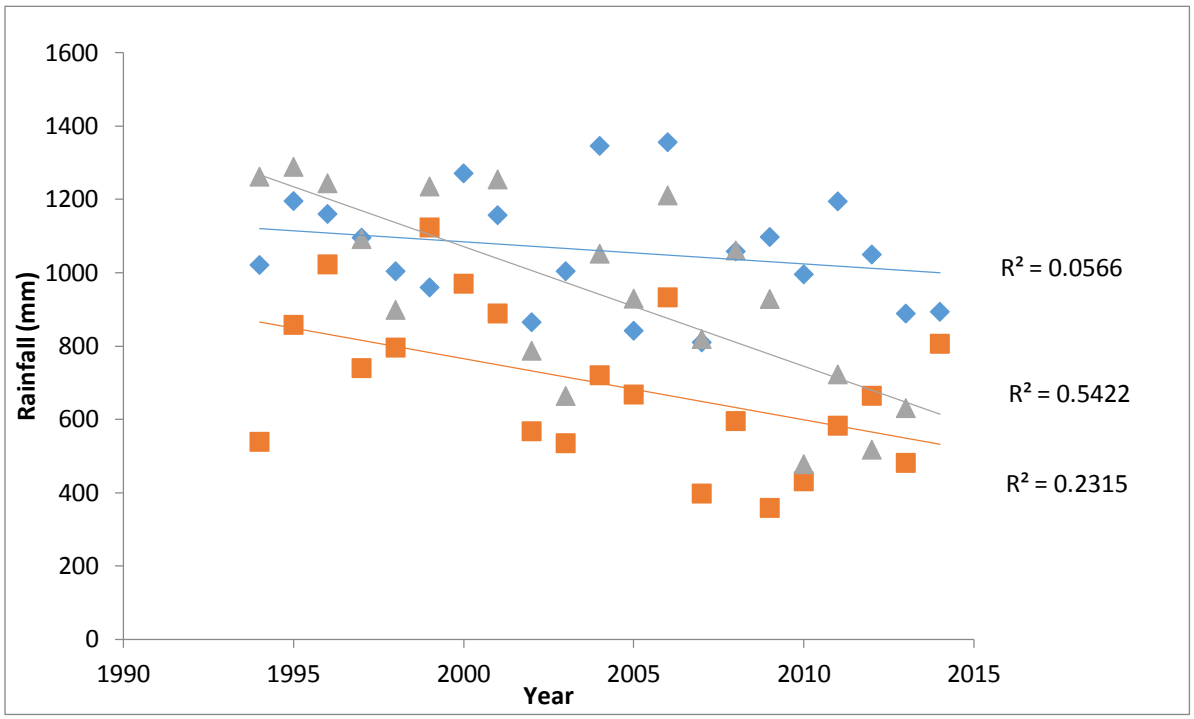

Figure 4. The annual rainfall for Sani Pass (alpine; grey triangles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

Linear regressions of the growing season rainfall showed a negative relationship at all three sites (SP: m = -27.474; GC: m = -14.352; SH: m = -5.6801; Table 1). SP data showed the largest decrease relative to the other two sites with a 3.7 % decrease, compared to the 2.4% and 0.6% of GC and SH, respectively. The average growing season rainfall recorded at SP was 750.5 mm per annum. This site showed a decrease on average of 27.5 mm of rainfall per annum which is approximately 3.7% of the total rainfall (Figure 5, Table 1). The GC site showed the second largest decrease in growing season rainfall. The average growing season rainfall was recorded as 609.4 mm per annum with an annual decrease on average of 14.4 mm (approximately 2.4% decrease; Figure 5, Table 1). SH showed the smallest relative decrease of the three sites. The average growing season rainfall per annum from 1994 to 2014 was 950.7 mm with an annual

decrease on average of 5.6 mm, which is approximately 0.6% of the total rainfall over the 20 year period (Figure 5, Table 1).

Figure 5. The growing season rainfall for Sani Pass (alpine; grey triangles), Giants Castle (lower montane; orange squares) and Shaleburn (lower montane; blue diamonds) data collection sites from 1994 to 2014.

The non-growing season rainfall showed a negative trend, although a much smaller decrease relative to other variables. SH and GC data showed a minimal decrease, whereas SP showed a greater decrease (SH: m = -0.3783; GC: m = -0.6777; SP: m = -2.0826). SP data showed a decrease on average of 2.1 mm per annum which is approximately 1.5% of the total non-growing season rainfall. GC showed an annual decrease, on average, of 0.7 mm per annum which is approximately 0.6% of the total. SH showed a minimal decrease, on average, of 0.4 mm of rainfall per annum, which is approximately 0.2% of the total. (Figure A1, Table 1).

The regression of the number of rain days in the growing season showed a negative relationship for the SP data (m = -1.3538), and a positive relationship for the SH and GC data (SH: m = 0.4519; GC: m = 0.1869). SP showed a decrease, on average, of 1.35 rain days per annum which is approximately 1.9% of the 1400 rain days recorded. The average number of rain days recorded for GC was 82.6 days per annum. GC showed an increase, on average, of 0.18 rain days per annum, approximately 0.2% of the total rain days. SH showed an increase, on average, of 0.45 days per annum which is approximately 0.4% of the total rain days recorded (Figure A2, Table 1). The rain days did not show a significant change over time.

An overall comparison of tends showed that SP data had the largest negative relationship when compared to SH and GC. GC data showed a negative relationship across all rainfall variables except for the number of rain days which showed a slight increase. The SH data have been relatively stable with minimal changes (Table 1). Nonetheless, it should be taken into consideration that the Sani Pass data might be of poorer quality than the other two sites as the readings are taken manually and could include human-induced errors.

Table 1. The total rainfall recorded over 20 years, the actual change (mm and days) and the percentage change (in bold) in the rainfall variables from the Shaleburn (lower montane), Giants Castle (lower montane) and Sani Pass (alpine) data collection sites from 1994 to 2014

	Sani Pass (2874 m)					Giants Castle (1759 m)					Shaleburn (1614 m)				
	Mean annual	Regression Slope	Annual change	Change over 20 years	% change over 20 years	Mean annual	Regression Slope	Annual Change	Change over 20 years	% change over 20 years	Mean annual	Regression Slope	Annual change	Change over 20 years	% change over 20 years
Annual rainfall (mm)	903.4	-32.568*x*	-32.568	-650	**-3.6**	733.5	-16.622*x*	-16.622	-332.4	**-2.3**	1112.8	-6.058*x*	-6.058	-120	**-0.5**
Growing season rainfall (mm)	750.5	-27.474*x*	-27.474	-548	**-3.7**	609.4	-14.352*x*	-14.352	-287	**-2.4**	950.8	-5.6*x*	-5.6	-112	**-0.6**
Non-growing season rainfall (mm)	136.7	-2.08*x*	-2.08	-41	**-1.5**	109.6	-0.67*x*	-0.67	-13.4	**-0.6**	162	-0.37*x*	-0.37	-7.4	**-0.2**
No. of rain days p/a (days)	70	-1.35*x*	-1.35	-27	**-1.9**	82.6	+0.18*x*	+0.18	+3.7	**+0.2**	107.3	+0.45*x*	+0.45	+9	**+0.4**

Temperature variable regressions were done for Mokhotlong (MK; upper montane), Shaleburn (lower montane) and Giants Castle (lower montane) over 20 years for all temperature variables separately. The mean annual temperature showed an increase at all the sites (SH: m = 0.0388; GC: m = 0.0261; MK: m = 0.0286, Figure: 6). SH showed the highest relative increase of 0.6 °C, GC an increase of 0.5 °C, and MK an increase of 0.4 °C over the 20 years. SH also showed unusual oscilation from 2007 onwards where the interannual variability becomes more constrained than at other sites.

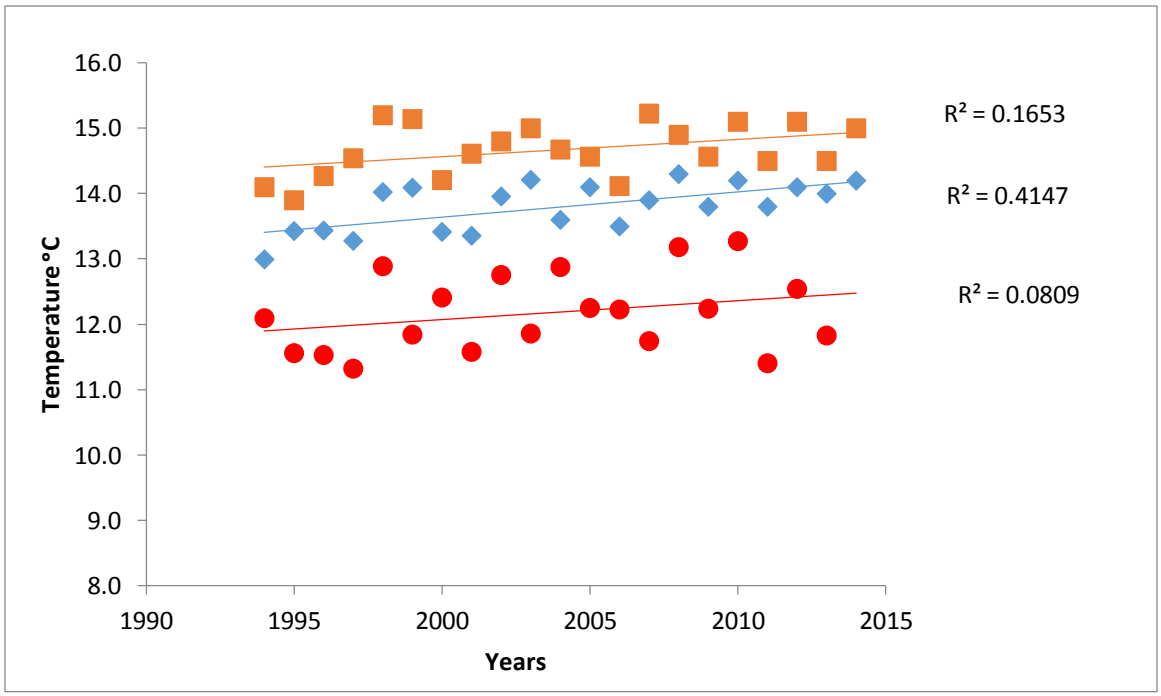

Figure 6. The mean annual temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

The regression of the minimum annual temperature showed no association between temperature and time at the SH site and a relatively small change at the GC site of 0.1 °C. This suggests that there has been little to no change in minimum annual temperature over 20 years within the lower montane sites (SH: m = -0.0014; GC: m = 0.0031). In contrast, MK data showed a positive relationship with an increase of 0.3 °C (m = 0.0196, Figure A3). The annual maximum temperature trend showed a positive relationship at all sites (MK: m = 0.045; SH: m = 0.0748; GC: m = 0.04). SH data showed the highest relative increase of 1.4 °C, while GC and MK data both showed an increase of 0.8 °C over the full period of analysis (Figure A4).

A regression of the mean growing season temperature (October to March) showed that all three sites had a positive relationship between temperature over time with an increase of 0.6 °C at SH, 0.5 °C at both GC and MK over the 20 year period (MK: m = 0.0271; SH: m = 0.0326; GC: m = 0.028; Figure 7). Once again SH has shown unusual oscilation from 2007 onwards with more contrained interannual variability than other sites.

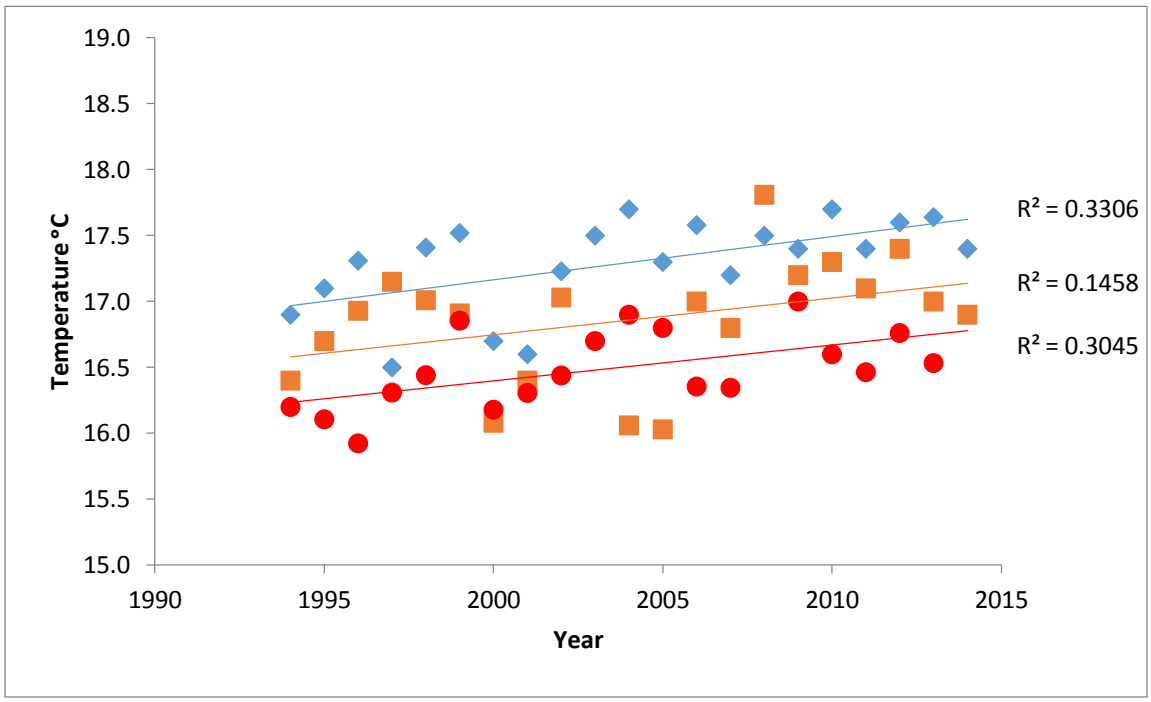

Figure 7. The mean growing season temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

The minimum growing season temperature regression showed an increased trend at two sites: MK and GC. MK had the highest relative increase of 0.4 °C and GC showed an increase of 0.2 °C (MK: m = 0.0199; GC: m = 0.0086). SH showed no change over the 20 year period (SH: m = 0.0038), see figure A5. The maximum growing season temperature regression showed all three sites (MK, SH, and GC) to have a positive trend. SH data showed an increase of 1.2 °C GC data an increase of 0.8 °C and MK an increase of 0.7 °C (MK: m = 0.0367; SH: m = 0.0636; GC: m = 0.0396; Figure 8).

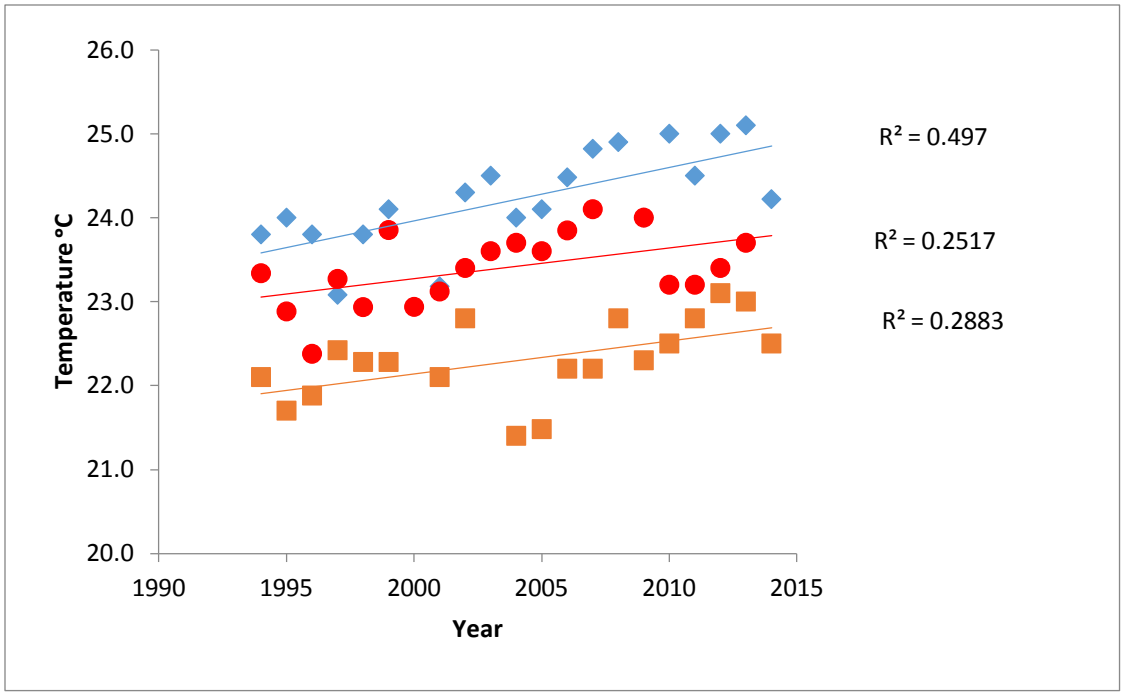

Figure 8. The maximum growing season temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

The regressions of the mean non-growing season temperature (April to September) showed a positive trend for all sites (MK, SH and GC). SH data showed an increase of 0.6 °C, GC and MK an increase of 0.4 °C (MK: m = 0.0198; SH: m = 0.034; GC: m = 0.0191; Figure A6). The minimum non-growing season temperature trend showed an increase in temperature at the MK site by 0.2 °C, a decrease in temperature of 0.2 °C at the GC and SH sites (MK: m = 0.0095; SH: m = -0.0102; GC: m = -0.0124; Figure A7). A regression of the maximum non-growing season temperature showed a positive relationship at all the sites, the two lower montane sites (SH and GC) showed a larger increase relative to the upper montane site (MK). SH data showed an increase of 1.1 °C, GC showed an increase of 0.7 °C and MK showed an increase of 0.4 °C (SH: m = 0.0507; GC: m = 0.035; MK: m = 0.0183; Figure A8).

There was a general positive linear trend for the temperature variables at MK, SH and GC. However, the minimum temperature variables (annual temperature, growing season temperature and non-growing season temperature) showed smaller relative increases than the mean and maximum temperatures and even a decrease (minimum non-growing season

temperature) at GC and SH. SH (lower montane) showed the highest relative increase in temperature in comparison to the other two sites in the mean and maximum temperature variables (Table 2).

Table 2. The change in the temperature (°C) variables from Shaleburn (lower montane), Giants Castle (lower montane) and Mokhotlong (upper montane) from 1994 to 2014, as well as the calculated temperature change per decade; the most prevalent increase in each variable is in bold. Ann = annual; Min = minimum; Max = maximum; T =temperature; GST = growing season temp; NonGST = non-growing season temperature

	Mokhotlong (°C)		Giants Castle (°C)		Shaleburn (°C)	
	1 decade	2 decades	1 decade	2 decades	1 decade	2 decades
Mean Ann T	0.2	0.4	0.3	0.5	0.3	**0.6**
Min Ann T	0.2	**0.3**	0.1	0.1	0	0
Max Ann T	0.4	0.8	0.4	0.8	0.7	**1.4**
Mean GST	0.3	0.5	0.3	0.5	0.3	**0.6**
Min GST	0.2	**0.4**	0.1	0.2	0	0
Max GST	0.4	0.7	0.4	0.8	0.6	**1.2**
Mean NonGST	0.2	0.4	0.2	0.4	0.3	**0.6**
Min NonGST	0.1	**0.2**	-0.1	-0.2	-0.1	-0.2
Max NonGST	0.2	0.4	0.4	0.7	0.6	**1.1**

Statistical Analyses of Trends:

A PCA of precipitation variables (annual rainfall, growing season rainfall, non-growing season rainfall and number of rain days in a growing season) from three sites (SP, SH and GC) indicated that the first three components explained 49.5%, 26.5%, and 12.2% of the variance respectively, with eigenvalues above one. Combined, the first three components explain 88.2% of the variance. The fourth and fifth components had eigenvalues below one and combined explained 11.8% of the variance (Figure A9). All four variables (annual rainfall, growing season rainfall, non-growing season rainfall, and number of rain days in a growing season) loaded in the first component suggesting high variability at all three sites.

The PCA on the temperature variables (annual mean, annual min., annual max., growing season mean, growing min., growing season max., non-growing season mean., non-growing season min., and non-growing season max.) from three sites (MK, SH and GC) over 20 years (1994–2014) showed that the first three components explained 51.6%, 36.2%, and 6.9% of the

variance respectively. Therefore the first three components explained 94.7% of the variance. The fourth and fifth factors had eigenvalues below one and explained 4.4% of the variance (Figure A10). Annual mean, annual minimum, growing season minimum, non-growing season mean and non-growing season minimum variables loaded on the first component. The annual maximum, growing season mean, growing season maximum and non-growing season maximum variables loaded on the second component. Site groupings by similarities were observed — Shaleburn showed a high values for the second component suggesting a high variation in these variables. In contrast, Giants Castle showed high values for the first component suggesting a high variation in these variables. Mokhotlong showed low values for both first and second components suggesting low variability in this thermal zone.

A MANOVA of all the precipitation variables of three sites (Sani Pass, Shaleburn and Giants Castle) over 20 years showed that precipitation variables across three sites were statistically significant (Wilks lambda = 0.32028, $F_{(6,116)} = 14.829$, $P < 0.05$: Figure 9). The Bonferroni Correction (adjusted $\alpha = 0.0166$ per test) showed that three variables (annual rainfall, growing season rainfall and number of rain days in a growing season) showed a significant result or significant difference between the means, and one variable (non-growing season rainfall) showed a non-significant result or no significant difference between means (Table 3).

MANOVA results for comparisons between temperature variables from Mokhotlong, Shaleburn and Giants Castle showed that the annual maximum, growing season maximum and non-growing season maximum temperatures have similar mean values (Figure 9). The annual mean, non-growing season mean and the growing season minimum temperature variables showed similar means. The annual minimum and non-growing season minimum temperature variables also showed similar means. The growing season mean temperatures seemed to not be similar to any other variable. Overall, the results of the MANOVA across three sites showed a statistically sidgnificant difference between temperature variables (Wilks lambda = 0.00129, $F_{(27, 193.4)} = 62.665$, $P < 0.05$: Figure 9).

A Bonferroni correction (adjusted $\alpha = 0.0166$ per test) showed that six variables (annual mean, annual minimum, growing season minimum, growing season maximum, non-growing season mean, and non-growing season maximum temperatures) showed a significant result or a significant difference between the means (Table 4). Three variables (annual maximum, growing

season mean and non-growing season minimum temperatures) showed a non-significant result (Table 4).

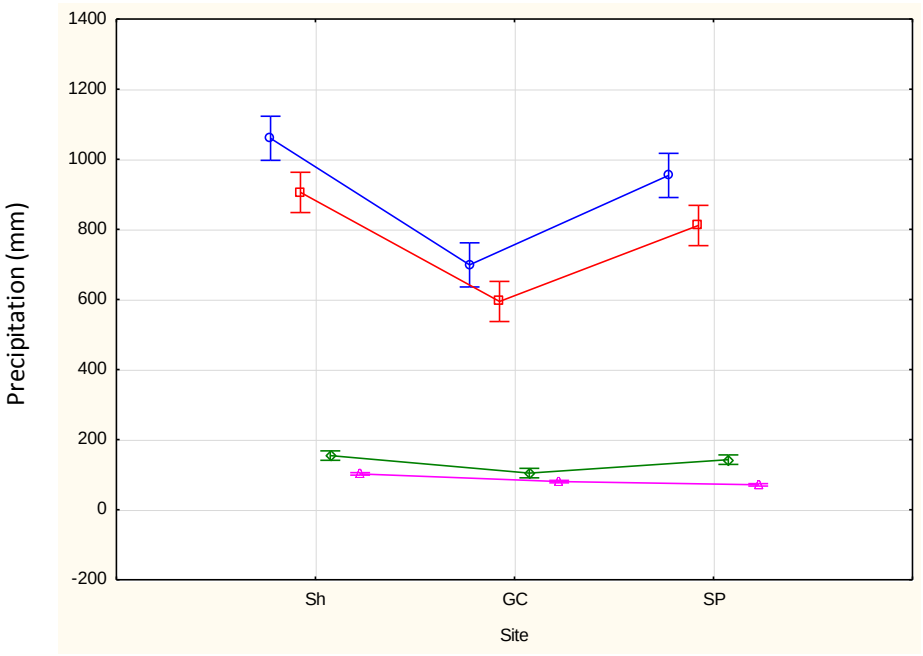

Figure 9. Variable mean vectors from the MANOVA of the precipitation variables (annual rainfall (blue), growing season rainfall (red), non-growing season rainfall (green), number of rain days in a growing season (purple)) for Sani Pass (SP, lower alpine), Shaleburn (lower montane) and Giants Castle (GC, lower montane) data from 1994 – 2014. Vertical bars denote 0.75 confidence intervals.

Table 3. The results for the Bonferroni correction post-hoc test for the precipitation variables (annual rainfall, growing season rainfall, non-growing season rainfall, and number of rain days) for Sani Pass (alpine), Shaleburn (lower montane) and Giants Castle (lower montane) with the significant results in bold.

Precipitation Variable	Mean square	Degrees of freedom	P value
Annual	61890	60	**0.005**
Growing season	51329	60	**0.009**
Non-growing season	2821.9	60	1.00
Number of rain days	189.60	60	**0.00**

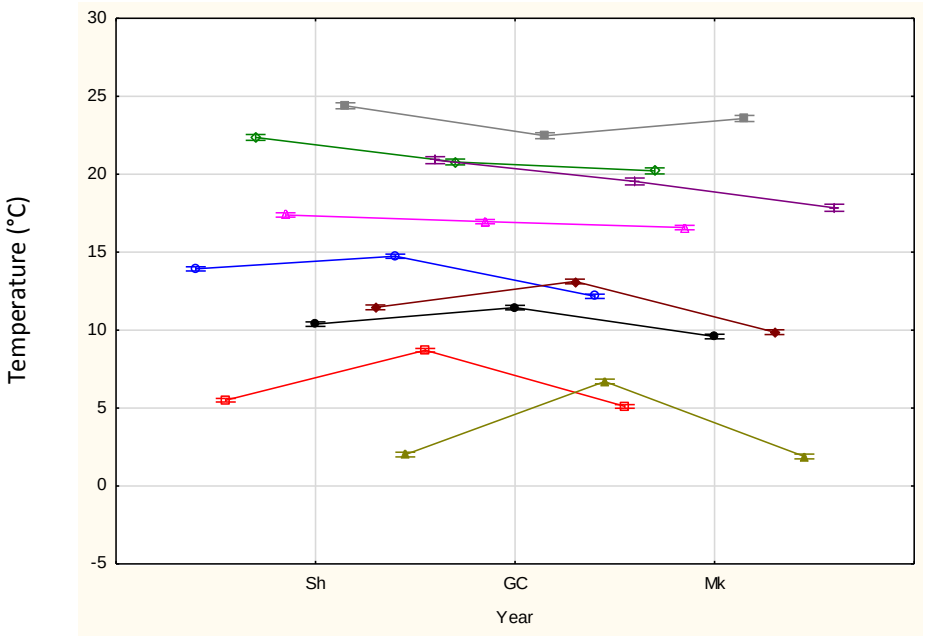

Figure 10. Variable mean vectors from the MANOVA of the temperature variables (growing season maximum (grey), annual maximum (green), non-growing season maximum (purple),

growing season mean (pink), annual mean (blue), non-growing season mean (maroon), growing season minimum (black), annual minimum (red), non-growing season minimum (light green)) for Mokhotlong (upper montane), Shaleburn (lower montane) and Giants Castle (lower montane) data from 1994 – 2014. Vertical bars denote 0.75 confidence intervals.

Table 4. The results for the Bonferroni Correction post-hoc test for the temperature variables for Mokhotlong (upper montane), Shaleburn (lower montane) and Giants Castle (lower montane) with significant results in bold.

Temperature Variable	Mean square	Degrees of freedom	P value
Annual mean	0.280	59	**0.01**
Annual minimum	0.199	59	**0.001**
Annual maximum	0.552	59	0.06
Growing season mean	0.29399	59	0.09
Growing season minimum	0.323	59	**0.002**
Growing season maximum	0.568	59	**0.006**
Non-growing season mean	0.364	59	**0.001**
Non-growing season minimum	0.35445	59	1.00
Non-growing season maximum	0.779	59	**0.001**

Inter-annual Variability:

Results from Levene's test showed that annual rainfall, growing season rainfall and number of rain days indicated a variance that was heterogeneous across Sani Pass, Shaleburn and Giants Castle from 1994 to 2014. One variable, non-growing season rainfall indicated variances

that were homogeneous among sites (Table 5). Results from Levene's test on the temperature variables from three sites (Mokhotlong, Shaleburn and Giants Castle) showed that annual mean, annual minimum, annual maximum, growing season mean, growing season minimum, growing season maximum, non-growing season mean, non-growing season minimum, and non-growing season maximum temperature variables indicated that variances were homogeneous among sites (Table 6).

Table 5. The results for the Levene's test for the precipitation variables for Sani Pass (alpine), Shaleburn (lower montane) and Giants Castle (lower montane) with the significant results in bold.

Precipitation Variable	W	F	P value
Annual	113345.8	5.9	**0.01**
Growing season	127102.9	7.9	**0.01**
Non-growing season	289.8	0.3	0.73
Number of rain days	237.2	3.9	**0.03**

Table 6. The results for the Levene's test for the temperature variables for Mokhotlong (upper montane), Shaleburn (lower montane) and Giants Castle (lower montane).

Temperature Variable	W	F	P value
Annual mean	0.09	1.1	0.33
Annual minimum	0.05	0.6	0.54
Annual maximum	0.25	1.6	0.21
Growing season mean	0.05	0.4	0.67
Growing season minimum	0.07	0.7	0.51
Growing season maximum	0.27	1.3	0.27
Non-growing season mean	0.35	2.9	0.06
Non-growing season minimum	0.41	2.9	0.06
Non-growing season maximum	0.33	1.5	0.23

In addition to the Levene's test, standard deviations were used to compare variances across sites for all variables. The standard deviations plotted for the temperature variables showed that Mokhotlong (upper montane) had a greater deviation (SD = 0.6 °C) (all values are positive) than the mean annual temperature of Shaleburn and Giants Castle (SD = 0.37 °C; SD = 0.4 °C; Table 7; Figure A11). Giants Castle (lower montane) had a greater deviation (SD = 0.5 °C) than the minimum annual temperature of Mokhotlong and Shaleburn (SD = 0.36 °C; SD = 0.4 °C; Figure A11). Shaleburn (lower montane; SD = 0.59 °C) and Mokhotlong (upper montane, SD = 0.58 °C) had the highest deviation from the maximum annual temperature in comparison to Giants Castle with a standard deviation of (SD = 0.46 °C; Figure A11).

Giants Castle had a greater deviation (SD = 0.47 °C) from the mean growing season temperature than Mokhotlong (SD = 0.3 °C) and Shaleburn (SD = 0.4 °C; Figure A14). All of the sites (Mokhotlong, Giants Castle and Shaleburn) showed the same standard deviation from the minimum growing season temperature of 0.5 °C (Figure A11). Shaleburn had a greater deviation (SD = 0.6 °C) from the maximum growing season temperature than Giants Castle (SD = 0.5 °C) and Mokhotlong (SD = 0.4 °C; Figure A11). Giants Castle had a greater deviation (SD = 0.7 °C) from the mean non-growing season temperature, minimum non-growing season temperature and the maximum non-growing season temperature than Mokhotlong and Shaleburn (Figure A11). Mokhotlong and Shaleburn (SD = 0.4 °C and SD = 0.3 °C, respectively) showed similar diviations for the mean non-growing season temperature. Shaleburn and Mokhotlong showed the same deviation for the minimum non-growing season temperature (SD = 0.4 °C) and for the maximum non-growing season temperature (SD = 0.6 °C; Figure A11).

The coefficient of variation plotted for Shaleburn (lower montane), Giants Castle (lower montane) and Sani Pass (alpine) precipitation variables from 1994 to 2014 showed that the Giants Castle and Sani Pass data have shown the most variability, and the Shaleburn data had the lowest variability in each variable group. Giants Castle data had the highest variation (31%) in mean annual rainfall and for mean growing season rainfall (33%; Figure A11; Table 8). The coefficient of variation suggests that the Giants Castle area is likely to deviate from the annual rainfall mean by 31% and deviate from the growing season rainfall mean by 33%. Sani Pass data showed similar deviations in annual rainfall mean and the growing season rainfall mean of 28% for both variables. Shaleburn had the lowest deviations in mean annual rainfall and mean growing season rainfall (15% and 14%, respectively). Giants Castle had the greatest variation in the non-growing season rainfall mean with a coefficient of variance at 48% (Figure A11). However, Shaleburn and Sani Pass had a relatively lower coefficient of variation of 36% and 30%, respectively. Giants Castle and Sani Pass had the highest variation in mean number of rain days in a growing season, with the coefficient of variation being 16% in both sites (Figure A11).

Table 7. Standard deviations (°C) of the temperature variables from Shaleburn (lower montane), Giants Castle (lower montane) and Mokhotlong (upper montane) collection sites between 1994 – 2014, all the values are positive and highest values overall in bold.

	Standard Deviation (°C)		
Temperature variables	Shaleburn	Giants Castle	Mokhotlong
Mean Annual	0.4	0.4	**0.6**
Min. Annual	0.4	**0.5**	0.4
Max. Annual	**0.6**	0.5	**0.6**
Mean Growing season	0.4	**0.5**	0.3
Min. Growing season	0.5	0.5	0.5
Max. Growing season	**0.6**	0.5	0.4
Mean Non-growing season	0.3	**0.7**	0.4
Min. Non-growing season	0.4	**0.7**	0.4
Max. Non-growing season	0.6	**0.7**	0.6

Table 8. Coefficient of variation (%) of the precipitation variables from Shaleburn (lower montane), Giants Castle (lower montane) and Sani Pass (alpine) collection sites from 1994 – 2014, the highest percentage in each variable in bold.

	Coefficient of variation (%)		
	Shaleburn	Giants Castle	Sani Pass
Annual precipitation.	15	**31**	28
Growing season precipitation.	14	**33**	28
Non-growing season precipitation	36	**48**	30
No. of rain days	9	**16**	**16**

Frost Trends

The number of frost days were recorded from three sites, Mokhotlong (upper montane), Shaleburn (lower montane) and Giants Castle (lower montane). The Mokhotlong (MK) and Shaleburn (SH) sites showed a similar mean number of frost days over the time period (Figure 11). At both of these sites the fewest frost days in a year were 66 for MK in 2009 and 67 days for SH in 2007, and the greatest number of frost days in a year was 109 (MK in 1996) and 108 units

(SH in 2001). Both sites oscillated over the period of time and showed a general decrease in the number of frost days from 1994 to 2014 (Figure 10). The Mokhotlong and the Shaleburn data showed a decrease of approximately 11.5 (0.7 %) and 9.1 (0.5 %) days, respectively, over the 20 year period. Giants Castle (GC) data showed a lower number of frost days per year as the temperature is generally higher than at MK or SH. The number of frost days at GC increased by 1.4 days (0.7 %) from 1994 to 2014 (Figure 11). The lowest number of frost days in one year was four (in the years 1999 and 2005) and the highest was 20 days (in 1994).

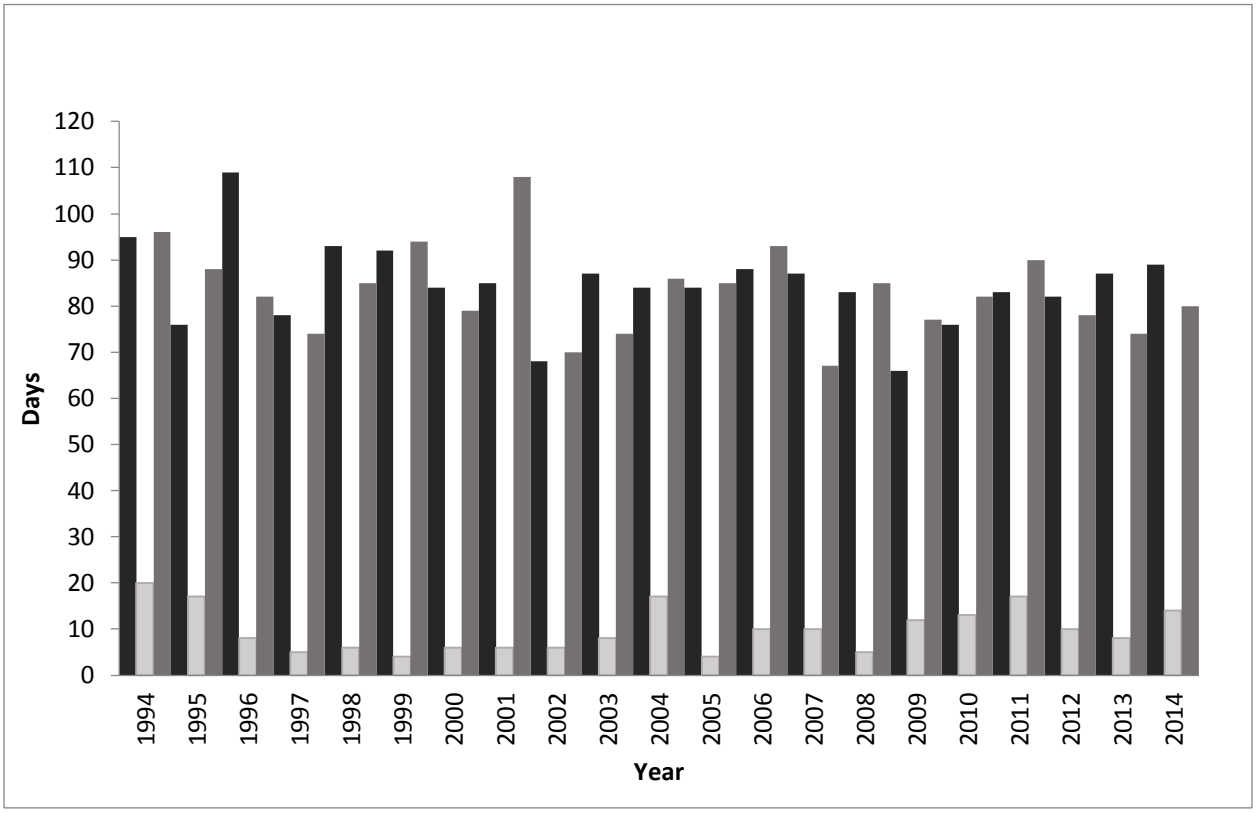

Figure 11. Number of frost days recorded at the Mokhotlong (upper montane; 2209 m; black), and Giants Castle (lower montane; 1759 m; light grey) and Shaleburn (lower montane; 1614m; grey) sites from 1994 – 2014.

Number of frost days were separated into three categories of severity to test if the severity has increased or decreased. Three categories were used: 0 to -2 ^{o}C (Low), -2 to -5 ^{o}C (Medium), and -5 ^{o}C and below (High). Over the 20 year period the Mokhotlong (upper

montane) data showed an overall decrease of 1.2 frost days (0.2%) in the low category (0 to -2 °C; Figure A12), while Shaleburn (lower montane) data showed a decrease of 7.7 frost days (1.6%) in the same category (Figure A13). In contrast, Giants Castle (lower montane) showed an increase of 2.7 days (1.7%) in the low category over the same period with 157 frost days recorded in total (Figure A14). The Mokhotlong data recorded 780 frost days in total, and Shaleburn recorded 491 frost days over the 20 year period. In the medium category, -2 to -5 °C, the Mokhotlong and Giants Castle data showed a decrease of 1.2 frost days (0.2%) and 1.3 frost days (2.7%), respectively (Figure A15 and A17). This showed a relatively larger decrease at the Giants Castle site as there were only 48 recorded frost days in this category over the 20 year period. Mokhotlong had a recorded 680 frost days in this category. Shaleburn showed no change over the 20 year period and 630 frost days were recorded in this category (Figure A16). Mokhotlong (upper montane) had the highest number of frost days in the medium category (-2 to -5 °C) at 51 days in the year 2000 (Figure A15), Shaleburn (lower montane) had the second highest with 42 days in the same year (Figure A16). Giants Castle (lower montane) had the lowest number of frost days in the medium category with the highest being nine days in the year 1994 (Figure A17). In the high category (-5 °C and below) Mokhotlong (upper montane) data recorded a decrease of 5.5 frost days or 1.7% (Figure A18). Shaleburn (lower montane) data in this category also showed a decrease of 2.4 frost days or 0.4% over the 20 years. (Figure A19). Both the Mokhotlong and Shaleburn sites had the highest number of frost days in the high category in the year 1994: Mokhotlong with 42 days and Shaleburn 43 days, however Shaleburn had more frost days in this category (626 frost days) than the Mokhotlong site (322 frost days). The Giants Castle site experienced only one day in the last 20 years where the temperature fell to -5 °C or below in the year 2003 (Figure A20).

Discussion

The trends shown by the data indicate that lower altitudes warmed at a faster rate than the higher altitudes and that higher altitudes had a larger decrease in precipitation than the lower altitudes from 1994–2014. The inter-annual variability results showed that temperature and precipitation were more variable at lower altitudes than higher altitudes, and frost days showed an overall decrease over time with the exception of Giants Castle which remained constant.

Ecological response to climatic changes depends on the local microclimate as well as the complex patterns of interannual variability and can make comparing sites with different topographies a challenge (Bennie *et al.*, 2013). Giants Castle and Shaleburn sites, although in the same thermal zone (montane), had slightly different temperature and precipitation trends. Different temperature and precipitation trends in the same zone may be due to topographical differences (such as an inversion layer of a valley in the case of Giants Castle which may show warmer temperatures than Shaleburn which is situationed on a valley bottom) and should be taken into account when interpreting these trends. The results of this study suggest that plants at lower altitudes in the Drakensberg region will have to adapt to warming temperatures and higher inter-annual variability, while plants at higher altitudes will have to adapt to a decrease in rainfall and frost days.

The upper and lower montane thermal zones showed a greater warming rate than the alpine zone. A similar study of mean annual temperature in the Australian Alps over a 39 year period from 1962–2001 (Hennessy *et al.*, 2008) showed positive trends in all three thermal zones which reveals a different trend to the Drakensberg sites. The alpine zone in the Australian Alps (1380–2000 m a.s.l.) showed the greatest increase in temperature of 0.2ºC/decade; however, the upper montane zone showed the smallest increase in mean annual temperature, this was the opposite to what was found in the Drakensberg alpine site (the upper montane was not included due to missing data). Additionally, in the Swiss, Austrian, and Bavarian Alps from 1951–1980, there was an average increase in annual mean temperature of approximately 1 ºC over a 29 year period, and up to 2 ºC at specific data collection sites (Beniston *et al.*, 1997). The sites were in different altitudinal zones ranging from montane to alpine, but the collective results did not specify which altitudinal zones had the highest increase over that period of time. The increase of between 1 and 2 ºC in these Alps were relatively higher than the results from the Shaleburn, Giants Castle and Mokhotlong data in this study, which show a general increase of between 0.6 ºC and 0.9 ºC over the 20 year period. Results presented in this work contradict previous studies in mountain areas where increased warming was more pronounced at higher altitudes (Körner *et al.*, 2011; Mountain Research Initiative Elevation Dependant Warming Working Group, 2015).

Precipitation in the alpine thermal zone showed a decreasing trend over time. Sani Pass data showed a strong negative trend over the four variables considered (mean annual rainfall,

growing season rainfall, non-growing season rainfall and number of rain days) and showed the largest decrease of all the data in annual rainfall with an overall decrease of 3.6%, and a 3.7% decrease in growing season rainfall. A previous study of rainfall in the Drakensberg recorded that the amount and intensity of rainfall at higher altitudes, in both growing and non-growing seasons, is less than that at lower altitudes (Nel *et al.*, 2010). This trend was not found to be corroborated by this report as the Sani Pass (alpine) data began with higher amounts of rainfall (i.e. above that of the lower montane zone) and ended with similar rainfall figures, but not less than that of the lower altitudes. (However, it should be noted that the data quality issues should also be considered here as Sani Pass data could include some human error). Precipitation in other alpine areas has been projected to decrease in the coming years due to climatic changes, such as in the Australian Alps where precipitation is projected to decrease −24% by 2050, relative to the 1990 average rainfall (Hennessy *et al.*, 2003). This is somewhat greater than what was found in the Drakensberg lower alpine zone, where a 3.6% decrease over 20 years extrapolated would result in an 11% decrease by the year 2050 assuming a constant rate of change. This figure is an estimate as there is no guarantee the rate of change will remain constant. There are many dynamic factors that can affect precipitation in mountain systems such as: air ascent and static instability of clouds, microphysical processes (converting condensation to precipitation in high altitudes), as well as associated feedback mechanisms such as latent heating (Mölg *et al.*, 2009). These factors should be studied in conjunction with the precipitation trends to better understand the cause of the change, as well as the implications the changes could have on local fauna and flora. The trend of decreasing rainfall in the higher altitudes (or alpine thermal zone) might affect plant persistence and community dynamics as rainfall is crucial for survival (Knapp *et al.*, 2002). Previous precipitation studies have shown an increase in rainfall and rain days in the growing season in the southern Drakensberg over a 50 year period from 1960 to 2010 (Mackellar *et al.*, 2014), opposite to what was found in the alpine zone (as well as the upper and lower montane zones) in this study. Engelbrecht *et al.*, (2012) projected an increase in extreme rainfall events over South Africa in years to come. Mackellar *et al.* (2014) and Englebrecht *et al.* (2012) have shown previous increases or projected increases in rainfall in the area which is opposite to what was found in this study. This opposite result suggests that there may be other factors that have influenced the data of this study, such as topography, aspect or data quality issues.

The recorded frost days showed an overall decreasing trend in this study. A study in the central Tibetan Plateau between 1961 and 2003, at an elevation of 2000 m a.s.l., showed a decrease of 4.1 frost days per decade which would equate to 8.2 frost days over 20 years. (Liu *et al.*, 2006). The overall decrease at the Mokhotlong site in the upper montane zone was 11.5 days over the twenty years. The trend presented in this work is slightly greater than what was recorded for the Tibetan Plateau and spanned a shorter time period (i.e. 20 years and not 43), this should be considered when comparing results. However, it is similar to the decrease at the Shaleburn (lower montane) site, which exhibited an overall decrease of 9.1 days over 20 years. Only one data collection site (Giants Castle) showed a slight increase in frost days in the medium frost category (portraying a medium threat to plants).

Inter-annual variability in temperature and precipitation regimes could also result in a change of vegetation structure in mountain systems (Walker *et al.* 1994). A higher inter-annual variability in the lower thermal zones (upper and lower montane) than in the higher zone (alpine) was seen in this study. The high inter-annual variability suggests that the upper and lower montane zones might become tougher environments for flora to inhabit, as high inter-annual variability can act as an environmental filter allowing only the most tolerant species to survive (Brochmann *et al.*, 2013). There is a need for variability estimates in other mountain systems as changes in temperature and the supply of resources such as water and nutrients have a large effect on the functioning of ecosystems (Burkle and Irwin, 2009). Changes in the inter-annual variability may be a potential indicator of changes in future plant composition, and therefore important to consider in biodiversity conservation planning as the change in composition may have a broader effect on the area and eco-system services provided.

Plants may respond to climatic changes through adaptation, migration or extinction (Aitken *et al.* 2008). Some plants have adapted to harsh conditions with specialised life forms, such as geophytes and hemicryptophytes. Geophytes and hemicryotophytes have specialized root systems that protect the storage organ of the plant by storing it below ground, more so for the geophyte (Dafni *et al.*, 1981). These adaptations have allowed plant species to survive the extreme conditions of high mountains (Gutterman, 2002). Plant species that are unable to adapt might migrate to areas with more suitable conditions (Bellard *et al.*, 2014). Warming temperatures in mountain systems create suitable habitat for lower altitudinal species to survive, thus creating a

movement of plant species from low to high altitudes (Beniston, 2003; Gehrig-Fasel, 2007). Increased warming will likely affect the plant species in the Drakensberg. One way that plants may adapt to a warmer environment is to reproduce (develop flowers and seeds) at a faster rate and develop more flowers than in previous years (Ellebjerg *et al.*, 2008). This adaptation may enhance the survival of a species and encourage migration to and growth in areas of higher altitude (Parolo and Rossi, 2008).

Plants migrating to new altitudinal or thermal zones may lead to hybridization with other closely related species (Gomez *et al.,* 2015). Hybridization could cause loss of biodiversity if the hybrid population outcompetes the parent population(s) (Hoffmann and Sgrò, 2011). According to Parolo and Rossi (2008), the opposite effect occurred in the Rhaetian Alps in Northern Italy where migration of species increased species richness at higher altitudes, a survey from 2003 – 2005 compared with the records from the 1950's showed an increase from 153 to 166 species in the alpine zone. This suggests plant biodiversity may benefit from the migration of species into higher altitudinal zones. Therefore the movement of lower altitude species into higher altitude habitats will have an effect on plant community dynamics, and potentially an even greater effect on the biodiversity of an area (Jump and Peñuelas, 2005; Frank *et al.* 2013; Abbot and Brennan, 2014). Hybridization usually occurs on the boundaries of the parent species' range and as plants are migrating to higher altitudes there is greater potential for contact between related species, and therefore a greater potential for hybridization (Vallejo-Marín and Hiscock, 2016). An example of this would be the hybrid between *Circaea alpina* and *C. lutetiana* (*Circaea* x *intermedia*) in northern Britain. The parent species are well adapted to cold climates but have since been displaced by the hybrid, since the ice retreated, which is better adapted to warmer climates (Vallejo-Marín and Hiscock, 2016). Another example of hybridization due to environmental changes is between *Ipomopsis aggregata* (a lower montane species) and *I. tenuituba* (an upper montane species) in western North America (Grant and Wilken, 1988; Abbot and Brennan, 2014). Through environmental change the ecological isolation between these species broke down and hybridization occurred. The hybrid species was very successful as hybrid swarms were reported in northern Arizona, Colorado and Utah (Grant and Wilken, 1988; Abbot and Brennan, 2014). The plant populations in the lower and upper montane thermal zones may experience

similar trends of migration and hybridization due to climatic and environmental change in the Drakenberg.

Hybridization between closely related species within a genus in these two thermal zones in the Drakensberg is a strong possibility as *Rhodohypoxis* and *Glumicalyx*, which occur in the lower montane, upper montane and alpine zones have a history of hybridization between species of the same genus (Hilliard and Burtt, 1977, 1978). Three species of *Glumicalyx* that occur in the upper montane zone (*G. goseloides, G. montanus, and G. apiculatus*) occur close to the edge of the alpine zone, which implies that they may come into contact with the other species occurring on the edges on the alpine zone (viz. *G. nutans, G. flanaganii, and G. lesuticus* Hilliard and Burtt, 1977). The outcome of warming temperatures would therefore potentially result in more contact between the montane and the alpine *Glumicalyx* species as there are temperature overlaps between the two thermal zones and species may be able to move and survive in other zones. Previously recorded hybridization between *Glumicalyx nutans* and *G. goseloides* near the base of the Sentinel in the northern KwaZulu-Natal Drakensberg (Hilliard and Burtt, 1977) shows that hybridization is a distinct possibility if these two species were to come into contact with each other more frequently. These hybrid plants were found in freshly disturbed ground next to a new road where their putative parent plants were also found. These two species do not normally grow in the same place, although they have an overlapping range as *Glumicalyx goseloides* grows between 1600 and 2800 m a.s.l. (upper and lower montane zone) and *G. nutans* is widespread and grows between 1800 and 3000 m a.s.l. (all three thermal zones) they have different habitats which separate the two species. There are no records of hybrids between these two species at any other localities (Hillard and Burtt, 1977), but if climatic conditions were to change, there is the possibility that hybridization would occur more widely. It is not known whether the hybrid between *Glumicalyx goseloides* and *G. nutans* is fertile or if the offspring are viable, which would be necessary for the hybrid to reproduce and establish itself.

It is not certain which other *Glumicalyx* species would be able to cross pollinate and hybridize even if they did come into contact, as there may be reproductive isolating mechanisms. Reproductive isolation is when a species is unable to breed successfully with a related species due to a variety of geographical, physiological, genetic and/or behavioural barriers (Boughman, 2001). Pollinators are one example of these mechanisms as species in the same genus may have

different pollinators. Comparing the length, width and colour of the corolla tube is one way to speciulate that plants have the same or similar pollinators. *Glumicalyx apiclatus* has a corolla length of 3–4 mm with a width of 1.5 mm, similar to that of *G. montanus* with a corolla length of 4–6 mm and width of 1.5 mm (Hilliard and Burtt, 1977). These two species occur at similar altitudes and have similar colours inside (orange to yellow) and outside (pale or creamy) of the corolla; it is therefore likely these two species could share similar pollinators and therefore hybridize. *Glumicalyx flanaganii* and *G. nutans* have a similar corolla length (13–17.5 mm and 12–16 mm respectively), but different widths (2 mm and 1 mm respectively). They have similar colours outside and inside the corolla, *G. flanaganii* being orange inside and creamy outside and *G. nutans* being a dull violet outside and an orange red inside (Hilliard and Burtt, 1977). These species have overlapping altitudes, but different habitats and seem likely to share similar pollinators. Perhaps if these two species migrate closer to each other they will hybridize.

Glumicalyx goseloides and *G. nutans* do not share similar habitat and altitude, as *G. goseloides* occurs at lower altitudes in boulder beds of streams and *G. nutans* at higher elevation on rock sheets (Hilliard and Burtt, 1977). *Glumicalyx goseloides* has a much longer corolla tube (20-29 mm) with a width of 1.25 mm than *G. nutans*. *Glumicalyx goseloides* has a similar corolla colour to *G. nutans* being orange red on the inside and creamy violet on the outside (Hilliard and Burtt, 1977). These two species occur in different habitats and have different corolla lengths, it seems unlikely they will hybridize, although these two species did hybrize at Witsieshoek (near the Senitel) where their co-occurrence was purly by chance (road construction). This highlights that in the future hybridization of these two plants may increase in contact zones as the morphological differences between the species have not prevented hybridization. *Glumicalyx lesuticus* has a unique corolla length of 7–11.5 mm long (and 1.5 mm broad) as no other *Glumicalyx* species has a similar length (Hilliard and Burtt, 1977). This suggests that this species has its own unique pollinators and may not hybridize even when in contact with associated species.

Rhodohypoxis species naturally occur in the three thermal zones in the Drakensberg. *Rhodohypoxis incompta, R. rubella, R. baurii var. confecta* and *R. deflexa* are all found in the alpine zone. *Rhodohypoxis rubella* and *R. baurii var. confecta* are known to hybridize with *R. thodiana* which is found in both lower thermal zones. *Rhodohypoxis baurii var. confecta* is also

known to hybridize with *R. milloides* (occurring in the upper montane zone) and *R. deflexa* (in the alpine zone; Hilliard & Burtt 1978). These taxa are known to hybridize with each other in intermediate zones (a zone between the two preferred habitats of the parent populations), some of these species also may occur in the upper montane zone and are likely to overlap with upper montane species (Hilliard & Burtt 1978). Four species occur in the upper montane zone, *Rhodohypoxis thodiana*, *R. milloides*, *R. baurii* var. *platypetala*, and *R. baurii* var. *baurii*, the latter three species occur in both upper and lower montane zones. *Rhodohypoxis thodiana* has, however, only been recorded in two localities at Giants Castle and Langalibalele at approximately 2000 m a.s.l. There are records of hybridization between *Rhodohypoxis* species and hybrid populations do exist, which implies that there are few genetic barriers between the species (Hilliard and Burtt, 1978). Hybrid plants of *Rhodohypoxis baurii* var. *platypetala* and *R. baurii* var. *baurii* (both occuring in the upper montane zone) have been found in intermediate habitats, as *Rhodohypoxis baurii* var. *platypetala* prefers drier habitats and *Rhodohypoxis baurii* var. *baurii* prefers the wetter habitats. The areas bordering these two microhabitats create an opportunity for hybrid plants to survive, however they have not been seen to introgress with the parent populations (Hilliard and Burtt, 1978). Hybrid plants have also been recorded in the alpine zone between 2800 and 300 m a.s.l. between *R. rubella* in the alpine zone and *R. thodiana* in the upper montane zone. *Rhodohypoxis thodiana* commonly grows in cropped turf on gentle slopes whereas *R. rubella* grows in the damper bare areas (Hilliard and Burtt, 1978). Hybrids were found where these two species came into contact between their preferred habitats (Hilliard and Burtt, 1978). There was also a report of a cross between the alpine taxon *R. baurii* var. *confecta* and the upper montane species *R. thodiana* between 2600 m and 2800 m a.s.l. (Hilliard and Burtt, 1978). These hybrids have all been found in habitats that are intermediate to their parent populations, since 1973 and still exist (E. Uys, pers. comm.). If climatic changes lead to increased proximity of taxa perhaps this will result in more hybrid species forming among the *Rhodohypoxis* species and varieties.

Rhodohypoxis has been shown to hybridize within the genus and have the potential to create different varieties and it is therefore important to further understand if these hybrid species are sterile or fertile. If the hybrid plants are fertile they could outcompete their parent species and lower the biodiversity of an area. Some species of *Rhodohypoxis* have different ploidy levels (Uys and Cron, unpublished data). Ploidy is the number of sets of chromosomes found in a cell,

and if ploidy levels differ between two plant species, the resulting hybrid is likely to be sterile (due to different numbers of chromosome sets). Therefore, even though *Rhodohypoxis* species readily hybridize, the resulting hybrids may be sterile and pose little threat to the existing biodiversity of the area.

While the high mountain plants adapt to climatic changes it is important to discuss the zones in which they survive, and which delineation of these zones most clearly defines their habitat. Previous delineation of mountain zones used an altitudinal scale (altitudinal zones; White, 1978), while the more recent delineation of a thermal zone is based on a temporal scale (thermal life zones; Carbutt and Edwards, 2015) that excludes elevation. The altitudinal zones assist in describing a plant community and its location on a mountain. The thermal life zones describe a plant community by the temperature range in which the community lives and how many days in the growing season (Körner *et al.*, 2011). Altitudinal zones may be a fair description of a particular mountain region but cannot be used on a larger scale as plant communities do not all begin at similar altitudes. Thermal life zones, however, can be used to describe all mountain regions, as they are not based on elevation alone. However, this study has shown that there can be different temperature and precipitation trends within the same thermal zone possibly influenced by topography and position on a slope, e.g. as in the different trends seen at the Giants Castle and Shaleburn sites. This research shows a general increase in temperature occurring in the lower and upper montane zones, which means that these zones have overlapping temperatures and may be merging. It is imperative to mention that when comparing the lower montane sites (Giants Castle and Shaleburn) to the upper montane site (Mokhotlong) the topography of the sites should be taken into consideration. Giants Castle is in an inversion layer in a valley, Shaleburn is in a valley bottom and Mokhotlong on a north facing slope, and this may affect the temperatures of these areas. The growing season temperatures in three of the years studied (1999, 2000 and 2001) showed the same average temperature for Mokhotlong and Giants Castle (16.9 ℃, 16.1 ℃ and 16.3 ℃) respectively. The minimum growing season temperatures, once again, in three of the years studied (2001, 2010 and 2013) showed that Mokhotlong had the same average temperature as Shalburn (9.5 ℃, 10.1 ℃ and 9.3 ℃) respectively. Interestingly, the minimum non-growing season temperatures for Mokhotlong and Shaleburn were similar on every year studied. These similarities are not in every variable for every year but do suggest that temperatures of the upper and lower montane zones may become

more alike. This suggests the upper and lower montane zones may be merging as temperatures are beginning to overlap. Therefore the thermal life zone delineation may be more accurate as they adjust with temporal changes.

There have been some limitations to this research that must be considered when interpreting the data. One of the limitations of this study was the incomplete dataset, where there were only three data sets that recorded precipitation (Sani Pass, Shaleburn and Giants Castle) and three data sets that recorded temperature (Mokhotlong, Shaleburn and Giants Castle). Further data collection is needed to improve estimates of Sani Pass temperature data and the Mokhotlong precipitation data. The Giants Castle data showed much warmer temperatures than any other site, which might be due to the Giants Castle weather station being in an inversion layer on a valley slope as well as on the warm north-facing side of a valley, therefore increasing the air temperature at the site (Werger and Van Bruggen, 2012). North facing slopes do not receive the same moist south-easterly wind from the Indian Ocean as the east facing slopes. The south-easterly wind that blows from the warm Indian Ocean towards the Drakensberg results in rainfall on the eastern slopes, rarely reaching the interior of the mountains as they act as a climatic barrier (Werger and Van Bruggen, 2012). Perhaps a different site in the lower montane zone should be studied that is not situated in an inversion layer as it would be easier to compare to other sites. Wind strength is another aspect to be considered when interpreting the data. The wind strength is much stronger on the escarpment edge (i.e. where the Sani Pass site is situated) and therefore likely to reduce the precipitation captured. These different systems could affect the amount of rainfall recorded at the collection sites and should be considered when comparing rainfall between the thermal zones, as the two other rainfall sites in the lower montane zone might receive more moisture and less wind. The final limitation identified in this study was length and quality of data, the data studied spanned a 20 year period which is not long enough to identify clear trends. An extended data set is needed to better understand the long term trends in the thermal zones. The quality of the data from Sani Pass, Shaleburn and Giants Castle was a concern and data collection methods perhaps can be improved for more accurate studies in future.

Conclusions and Recommendations

The climatic changes in this research generally showed an increased rate of warming at lower elevations and a larger decrease in rainfall at higher elevations, overall a warmer and drier environment in which the flora of the Drakensberg will need to survive (especially endemic flora as they do not occur elsewhere), with increased opportunities for movement of species between thermal zones. The large variation in data from the two lower montane sites, however, may suggest that Körner's thermal zones be critically assessed for practical use in southern African mountains, and specifically the Drakensberg.

Also, further studies on the autecology, genetic barriers and ploidy levels of *Glumicalyx* and *Rhodohypoxis* are needed to give new insights into plant distribution and to see if further hybridization can occur. More surveys of known parent and hybrid populations are needed as these genera may become indicators of merging zones in the future. Further studies on the response of plants to the changing climate in the Drakensberg are needed. Previous studies, in a more tropical climate, have shown that plants may respond to warming in different ways, not only with upslope movement, but also horizontal and downslope movement (Platts *et al.* 2013). Edaphic differences (referring to the structure and composition of the soil), as well as the escarpment itself, being a physical barrier in some areas, may also hinder the expected upslope movement of plants. These factors need to be extensively studied in order to further understand how Drakensberg flora may respond to changing climate, this demonstrations the complexity of eco-systems and that the response of plant species to climatic changes may be varied according to local conditions. Future research on plants in the southern hemisphere should consider using an Austral year (1 June – 30 July) instead of a normal calendar year from January to December, as this will show the entire plant growing season and perhaps lend to a more accurate data analysis.

The study and predictions of high mountain climatic change are imperative to our understanding of these systems and the survival of endemic biodiversity which depend on them. Comprehensive temperature and precipitation data for this research were collected for three out of four sites, and further analysis of the Sani Pass temperature and the Mokhotlong rainfall data is needed for improved comparisons between sites. The data used in this research assessed 20 years of climatic changes, further analysis of long term data is needed to better understand the

long term temperature and precipitation trends in the Drakensberg and the implications for endemic flora.

References

Abbot, R.J. and Brennan, A.C., 2014. Altitudinal gradients, plant hybrid zones and evolutionary novelty. *Philos Trans R Soc Lond B Biol Sci.* 369 (1648): 20130346.

Aitken S.N., Yeaman, S., Holliday, J.A., Wang, T. and Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications.* 1 (1): 95–111.

Bellard, C., Lecleac, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., and Courchamp, F., 2014. Vulnerability of biodiversity hotspots to global change. *Global Ecology and Biogeography.* 23 (12): 1376–1386.

Beniston, M., Diaz, H.F., & Bradley, R.S., 1997. Climate change at high elevation sites: an overview. *Climate Change.* 36: 233–251.

Beniston, M. & Fox, D.G., 2003. Impacts of climate change on mountain regions: a review of possible impacts. *Climate Change.* 59 (1-2): 5–31.

Bennie, J., Hodgson, J.A., Lawson, C.R., Holloway, C.T.R., Roy, D.B., Brereton, T., Thomas, C.D., and Wilson, R.J., 2013. Range expansion through fragmented landscapes under a variable climate. *Ecology Letters.* 16: 921–929.

Bland, J.M. & Altman, D.G., 1994. Regression towards the mean. *British Medical Journal.* (308): 1499.

Boughman, J.W., 2001. Divergent sexual selection enhances reproductive isolation in sicklebacks. *Nature.* 411: 944–948.

Box, G. E. P., 1953. Non-normality and tests on variances. *Biometrika.* 40: 318–335.

Box, G. E. P., 1954. Some theorems on quadratic forms applied in the study of analysis of variance problems, I. Effect of inequality of variance in the one-way classification. *Annals of Mathematical Statistics*. 25: 290–302.

Brochmann, C., Edwards, M.E., and Alsos, G., 2013. The balance of nature and human impact: the dynamic past and future of Arctic vascular plants: climate change, spatial variation and genetic diversity. Cambridge University Press, Cambridge.

Burkle, L. and Irwin, R., 2009. The importance of interannual variation and bottom–up nitrogen enrichment for plant–pollinator networks. *OIKOS*. 118 (12): 1816–1829.

Bussmann, R.W., 2006. Vegetation zonation and nomenclature of African mountains – an overview. *Iyonia-Journal of Ecology and Application.* 11 (1): 41–66.

Carbutt, C. & Edwards, T.J., 2001. Cape elements on high-altitude corridors and edaphic islands: historical aspects and preliminary phytogeography. *Systematics and Geography of Plants*. 71 (2): 1033–1061.

Carbutt, C. & Edwards, T.J., 2004.The flora of the Drakensberg Alpine Centre. *Edinburgh Journal of Botany*. 60 (3): 581–607.

Carbutt, C. & Edwards, T.J., 2006. The endemic and near-endemic angiosperms of the Drakensberg Alpine Centre. *South African Journal of Botany*. (72): 105–132.

Carbutt, C. & Edwards, T.J., 2015. Reconciling ecological and phytogeographical spatial boundaries to clarify the limits of the montane and alpine regions of sub-Sahelian Africa. *South African Journal of Botany*. (98): 64–75.

Chunco, A.J., 2014. Hybridization in a warmer world. *Ecology and Evolution.* 4 (10): 2019–2031.

DEA (Department of Environmental Affairs), 2013. Long-Term Adaptation Scenarios Flagship Research Programme (LTAS) for South Africa. *Climate Trends and Scenarios for South Africa*. Pretoria, South Africa.

Du Toit, J.C.O., and O'Connor, T.G., 2014. Changes in rainfall pattern in the eastern karoo, South Africa, over the past 123 years. *Water SA.* 40 (3): 452–460.

Engelbrecht, C.J., Engelbrecht, F.A., and Dyson, L.L., 2012. High-resolution model-projected changes in mid-tropospheric closed-lows and extreme rainfall events over southern Africa. *International Journal of Climatology.* 33: 173–187.

Fowler, J., Cohen, L., and Jarvis, P., 1998. Practical statistics for field biology, second edition. John Wiley & Sons Ltd, England.

Franks, S.J., Weber, J.J. and Aitken, S.N., 2013. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications.* 7 (1): 123–139.

Frei, C. & Schär, C., 1998. A precipitation climatology of the Alps from high-resolution rain-gauge observations. *International Journal of Climatology.* (18): 873–900.

Dafni, A., Cohen, D. & Noy-Meir, I., 1981. Life-cycle variation in geophytes. *Annals of the Missouri Botanical Garden.* 68 (4): 652–660.

Gale, J., 2004. Plants and altitude – revisited. *Annuals of Botany.* 94 (2): 199

Gallager, R.V., Hughes, L., and Leishman, M.R., 2008. Phenological trends amoung Australian alpine species: using herbarium records to identify climate change indicators. *Australian Journal of Botany.* 57 (1): 1–9.

Galley, C., Bytebier, B., Bellstedt, D.U., & Linder, H.P., 2007. The Cape element in the afrotemperate flora: from Cape to Cairo? *Proceedings of Royal Society B: Biological Sciences.* 274 (1609): 535–543.

Gehrig-Fasel, J., Guisan, A., and Zimmerman, N.E., 2007.Tree line shifts in the Swiss Alps: climate change or land abandonment*? Journal of Vegetation Science*. (18): 571–582.

Gholinejad, B., Farajollah, A., and Pouzesh, H., 2012. Environmental factors affecting on distribution of plant communities in semi-arid area (case study: Kamyaran rangelands, Iran). *Annals of Biological Research.* 3 (8): 3990–3993.

Gomez, J.M., Gonzalez-Megias, A., Lorite, J., Abdelaziz, M., and Perfectti, F., 2015. The silent extinction: climate change and the potential hybridization-mediated extinction of endemic high mountain plants. *Biodiversity Conservation.* (24): 1843–1857.

Gotfried, M., Pauli, H., Reiter, K., and Grabherr, G., 1999. Global change and plant diversity: A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity and Distributions.* (5): 241–251.

Grab, S., 2010. Geomorphic landscapes: Drakensberg escarpment. Springer International Publishing, Switzerland.

Grab, S.W., and Craparo, A., 2011. Advance of apple and pear tree full bloom dates in response to climate change in the southwestern Cape, South Africa: 1973-2009. *Agricultural and Forest Meteorology,* 151: 406–413.

Grab, S., 2013. Fine-scale variations of near-surface-temperature lapse rates in the high Drakensberg escarpment, South Africa: Environmental implications. *Artic, Antarctic and Alpine Research* 45 (4): 500–514.

Grab, S. & Knight, J., 2015. World geomorphological landscapes: landscapes and landforms of southern Africa. Springer International Publishing, Switzerland.

Grant, V., and Wilken, D., 1988. Natural Hybridization between *Ipomopsis aggregata* and *I. tenuituba* (Polemoniaceae). *Botanical Gazette.* 149 (2): 213–221.

Grimshaw, J.M., 2001. What do we really know about afromontane archipelago? *Systematics and Geography of Plants.* 71 (3): 949–957.

Gutterman, Y., 2002. Adaptations of desert organisms: survival strategies of annual desert plants. Springer-Verlag Berlin, Heidelberg.

Ellebjerg, S.M., Tamstorf, M.P., Illeris, L., Michelsen, A. and Hansen, B.U., 2008. Inter-annual variability and controls of plant phenology and productivity at Zackenberg. *Advances in Ecological Research* 40: 249–273.

Halloy, S.R.P. & Mark, A.F., 2003. Climate-change effects on alpine plant biodiversity: a New Zealand perspective on quantifying the threat. *Arctic, Antarctic, and Alpine Research* 35 (2): 248–254.

Harper, C.W., Blair, J.M., Fay, P.A., Knapp, A.K., and Carlisle, J.D., 2005. Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in grassland eco-system. *Global Change Biology.* 11 (2): 322–334.

Hasler, R., 1982. Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. *Oecologia*. (54): 14–22.

Hedberg, O., 1970. Evolution of afroalpine flora. *Biotropica.* 2 (1): 16–23.

Hennessy, K., Whetton, P., Smith, I., Bathols, J., Hutchinson, M., and Sharples, J., 2003. The impact of climate change on snow conditions in mainland Australia. *CSIRO Atmospheric Research,* Aspendale, Victoria, Australia.

Hennessy, K., Whetton, P., Walsh, K., Smith, I.N., Bathols, J.M. Hutchinson, M.and Sharples, J., 2008. Climate change effects on snow conditions in main-land Australia and adaptations at ski resorts through snowmaking. *Climate Research.* (35): 255–270.

Hilliard, O.M. & Burtt, B.L. 1973. Notes on some plants of southern Africa chiefly from Natal III. *Rhodohypoxis*. *Notes from the Royal Botanic Garden, Edinburgh*. 32: 305–314.

Hilliard, O.M. & Burtt, B.L., 1977. Notes on some plants of southern Africa chiefly from Natal: VII. *Notes from the Royal Botanic Gardens Edinburgh.* 43: 201–206.

Hilliard, O.M. & Burtt, B.L., 1977. Notes on some plants of southern Africa chiefly from Natal: VI: 221–227. *Glumicalyx. Notes from the Royal Botanic Gardens Edinburgh.* 35: 155–172.

Hilliard, O.M. & Burtt, B.L. 1978. Notes on some plants of southern Africa chiefly from Natal: VII: 233–244. *Rhodohypoxis*. *Notes from the Royal Botanic Garden, Edinburgh.* 36: 43–76.

Hilliard, O.M. & Burtt., B.L., 1987. Notes on some plants from southern Africa chiefly from Natal. *Notes from the Royal Botanical Gardens Edinburgh*. 1: 233–244.

Hoffmann, A.A. and Sgrò, C.M., 2011. Climate change and evolutionary adaptation. *Nature.* 470: 479–485.

Holland, P.G. & Steyn, D.G., 1975. Vegetational responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography.* 2: 179–183.

Honnay, O., Jacquemyn, H., Bossuyt, B., and Hermy, M., 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist.* 166 (3): 723–736.

Howell, D. C. (2002). Statistical Methods for Psychology (5th ed.). Pacific Grove, CA: Duxbury.

Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution.* 15 (2): 56–61.

Huston, M. & Smith, T., 1987. Plant succession: life history and competition. *The American Naturalist*. 130 (2): 168–198.

Inouye, D.W., 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters.* 3 (5): 457–463.

Johnson, S.D., and Hobbhahn, N., 2010. Generalized pollination, floral scent chemistry, and a possible case of hybridization in the African orchid *Disa fragrans. South African Journal of Botany.* 76 (4): 739–748.

Jolliffe, I.T., 2002. Principle component analysis: second edition. Springer-Verlag New York.

Jones, P.D., Raper, S.C.B, and Wigley, T.M.L., 1986. Southern hemisphere surface air temperature variations: 1851-1984. *American Meteorological Society.* 25: 1213–1230.

Jump, A.S. and Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters.* 8 (9): 1010–1020.

Karl, T.R., and Trenberth, K.E., 2003. Modern global climate change. *Science.* 5651 (302): 1719–1723.

Khan, S.M., Page, S., Ahmad, H., Shaheen, H., and Harper, D., 2012. Vegetation dynamics in the western Himalayas, diversity indices and climate change. *Science, Technology and Development.* 31 (3): 232–243.

Killick, D.J.B., 1963. An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. *Memoirs of the Botanical. Survev of South Africa.* 34: 178.

Killick, D.J.B., 1978. Notes on the vegetation of the Sani Pass area of the southern Drakensberg. *Bothalia* 12: 537 – 542.

Killick, D.J.B., 1978. Further data on the climate of the alpine vegetation belt of eastern Lesotho. *Bothalia,* 12 (3): 567 – 572.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S. and McCarron, J.K., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science.* 298 (5601): 2202–2205.

Körner, C., & Larcher, W., 1988. Plant life in cold climates. *Symposia of the Society for Experimental Biology*. (42): 25–57.

Körner, C., 2003. Alpine plant life, functional plant ecology of high mountain ecosystems. Springer-Verlag Publishers. Berlin, Germany.

Körner, C., Paulsen, J., and Spehn, E.M., 2011. A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. *Alpine Botany.* 121 (2): 73–78.

Larcher, W., Kainmuller, C., & Wagner, J., 2010. Survival types of high mountain plants under extreme temperatures. *Flora – Morphology, Distribution, Functional Ecology of Plants.* 205 (1): 3–18.

Löffler, J., 2007. The influence of micro-climate, snow cover, and soil moisture on eco-system functioning in high mountains. *Journal of Geographical Science.* 17 (1): 3–19.

Lorenzen, T. J., Anderson, V. L., 1993. Design of Experiments: a No-Name Approach. Marcel Dekker, New York.

Liu, X, and Chen, B., 2000. Climatic warming in the Tibetan Plateau during recent decades. *International Journal of Climatology.* (20): 1729–1742.

Liu, X., Yin, Z., Shao, X., and Qin, N., 2006. Temporal trends and variability of daily maximum and minimum, extreme temperature events, and growing season length over the eastern and central Tibetan Plateau during 1961–2003. *J. Geophys. Res.* 111 (D19): 109

Liu, X, Cheng, Z., Yan, L., and Yin, Z., 2009. Elevation dependency of recent and future minimum surface temperature trends in the Tibetan Plateau and its surroundings. *Global and Planetary Change.* 68 (3): 164–174.

MacKellar, N., New, M., and Jack, C., 2014. Observed and modelled trends in rainfall and temperature for South Africa: 1960–2010. *South African Journal of Science.* 110 (7/8): 1–13.

Messerli, B., and Winiger, M., 1992. Climate, environmental change, and resources, of the African mountains from the Mediterranean to the equator. *Mountain Research and Development.* 12 (4): 315–336.

Mishra, S.R., 2004. Photosynthesis in plants. Discovery Publishing House.

Mountain Research Initiative EDW Working Group, 2015. Elevation-dependent warming in mountain regions of the world. *Nature Climate Change.* 5: 424–430.

Mölg, T., Chiang, J.C.H., Gohm, A. & Cullen, N.J., 2009. Temporal precipitation variability versus altitude on a tropical high mountain: observations and mesoscale atmospheric modelling. *Quarterly Journal of the Royal Meterological Society.* (135): 1439–1455.

Nel, W., 2007. On the climate of the Drakensberg: rainfall and surface temperature attributes and associated geomorphic effects (Doctoral dissertation). *Department of Geography, Geoinformatics and Meteorology, University of Pretoria.*

Nel, W., 2008. Short communication: observations on daily rainfall events in Kwa-Zulu Natal Drakensberg. *Water SA.* 34 (2): 271–274.

Nel, W., 2009. Rainfall trends in the KwaZulu-Natal Drakensberg region of South Africa during the twentieth century. *International Journal of Climatology.* (29): 1634–1641.

Nel, W., and Sumner, P.D., 2005. First rainfall data from the KZN escarpment edge (2002 and 2003). *Water SA.* 31 (3): 399–402.

Neukom, R., Nash, D.J., Endfield, G.H., Grab, S.W., Grove, C.A., Kelso, C., Vogel, C.H. and Zinke, J., 2014. Multi-proxy summer and winter precipitation reconstruction for southern Africa over the last 200 years. *Climate dynamics.* 42: 2713–2726.

Nicholsom, S.E., Nash, D.J., Chase, B.M., Grab, S.W., Shanahan, T.M., Verschuren, D., Asrat, A., Lezine, A. and Umer, M., 2013. Temperature variability over Africa during the last 2000 years. *The Holocene.* 23 (8): 1085–1094.

Nordal, I., 1998. The Hypoxidaceae. In Kubitski, K. (ed.) The families and genera of vascular plants: Flowering plants. Volume 3. Monocotyledons, Lilianae (except Orchidaceae) Pp. 286–295.

Ohmura, A., 2012. Enhanced temperature variability in high-altitude climate change. *Theoretical Application of Climatology*. 110. (4): 499–508.

Opler, P.A., Frankie, G.W. and Baker H.G., 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography*. (3): 231–236.

Parolo, G. and Rossi, G., 2008. Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology*. 9 (2): 100–107.

Partridge, T.C., 1992. Warming phases in southern Africa over the last 150 000 years: an overview. *Palaeogeography, Palaeoclimatology, Palaeoecology*. (101): 237–244.

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., Arévalo, J.R., Cavieres, L.A., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C.I., Naylor, B.J., Parks, C.G., Rew, L.J., and Seipel, T., 2009. Ain't no mountain high enough: plant invasions reaching new elevations. *Frontiers in Ecology and the Environment.* 7 (9): 479–486.

Pauli, H., Gottfried, M., and Grabherr, G., 2003. Effects of climate change on the alpine and nival vegetation of the Alps. *Journal of Mountain Ecology.* 7: 9–12.

Platts, P.J., Gereau, R.E., Burgess, N.D., Marchant, R., 2013. Spacial heterogeneity of climate change in an Afromontane centre of endemism. *Ecography, Pattern and Process in Ecology.* 36 (4): 518–530.

Pooley, E., 2003. Mountain flowers: a field guide to the flora of the Drakensberg and Lesotho. Flora Publications Trust, Durban.

Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmerman, N., Pearman, P.B., Vittoz, P., Thuiller, W., and Guisan, A., 2009. Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*. (15): 1557–1569.

Raunkiær, C., 1907. Planterigets livsformer og deres betydning for geografien. *Gyldendalske Boghandel - Nordisk Forlag, København and Kristiania*: Pp. 104–132.

Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics.* 27: 83–109.

Rieseberg, L.H., and Carney, S.E., 1998. Plant hybridization. *New Phytologist.* 140: 599–624.

Rieseberg, L.H., 1997. Hybrid origins of plant species. *Annual Review of Ecology and Systematics.* 28: 359–389.

Rutherford, A., 2001. Introducing ANOVA and ANCOVA: A GLM approach. Thousand Oaks, CA: Sage Publications.

Ruxton, G.D. & Neuhauser, M., 2010. When should we use one-tailed hypothesis testing? *Methods in Ecology and Evolution.* (1): 114–117.

Scherrer, D, and Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography.* 38 (2): 406–416.

Schwinning, S., Sala, O.E., Loik, M.E., and Ehleringer, J.R., 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi arid eco-systems. *Oecologia.* (141): 191–193.

Shongwe, M.E., Van Oldenborgh, G.L., and Van Den Hurk, B.J.J.M., 2009. Projected changes in mean and extreme precipitation in Africa under global warming. Part I: southern Africa. *Journal of Climate.* 22: 3819–3837.

Shuttleworth, M., 2008. "Students t-test" Retrieved from http://www.explorable.com/students-t-test.

Smith, W.G., 2013. Raunkiaer's "Life Forms" and statistical methods. Retrieved from http://www.britishecologicalsociety.org/100papers/100_Ecological_Papers/100_Influential_Papers_026.pdf.

Snijman, D.A., 2013. Plants of the greater Cape floristic region, 2: the extra Cape flora. *Strelitzia 30,* SANBI Pretoria.

Spehn, E.M., Rudmann-Maurer, K., Körner, C., and Maselli, D., 2010. Mountain biodiversity and global change. GMBA-DIVERSITAS, Basel.

StatSoft, Inc., 2013. Electronic statistics textbook: electronic version. *Tulsa, OK*: StatSoft. WEB: http://www.statsoft.com/textbook/.

Stinson, K.A., 2005. Effects of snowmelt timing and neighbour density on the altitudinal distribution of *Potentilla diversifolia* in Western Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research.* 37 (3): 379–386.

Takeishi, H., Hayashi, J., Okazawa, A., Harada, K., Hirata, K., Kobayashi, A., and Akamatsu, F., 2013. Effects of elevated pressure on rate of photosynthesis during plant growth. *Journal of Biotechnology.* 168 (2): 135–141.

Theurillat, J.P. & Guisan, A., 2001. Potential impact of climate change on vegetation in the European Alps: a review. *Climatic change.* 50 (1-2): 77–109.

Thobei, Sutarno and Komariah, 2014. Effects of climate change on crop production in Thaba-Nseka and Mokhotlong districts Lesotho highlands. *IOSR Journal of Agriculture and Veterinary Science.* 7 (1): 37–44 Ver. IV.

Thuiller, W., 2007. Biodiversity: Climate change and the ecologists. *Nature* 448: 550 – 552 Gale, J., 2004. Plants and altitude – revisited. *Annals of Botany.* 94 (2): 199.

Totlan, Ø., and Alatalo, J.M., 2002. Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis. Oecologia.* 133 (2): 168–175.

Tyson, P.D., Preston-Whyte, R.A., and Shulze, R.E., 1976. The climate of the Drakensberg. *Natal town and regional planning commission, Pietermaritzburg.* Pg. 82.

Urban, M.C., 2015.Accelerating extinction risk from climate change. *Science.* 348 (6234): 571–573.

Uys, E., and Cron, G.V., 2013. Relationships and evolution in the Drakensberg near-endemic genus, *Craterocapsa* (Campanulaceae). *South African Journal of Botany.* 86: 79–91.

Vallejo-Marín, M. and Hiscock, S. J., 2016. Hybridization and hybrid speciation under global change. *New Phytol.* 211: 1170–1187.

Van Der Heijden, M.G.A., Bardgett, R.D., and Van Straalen, N.M., 2007. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial eco-systems. *Ecology Letters.* 11 (3): 296–310.

Vera, M.L., 1997. Effects of altitude and seed size on germination and seedling survival of heathland plants in north Spain. *Plant Ecology.* 133: 101–106.

Vuille, M., Bradley, R.S., 2000. Mean annual temperature trends and their vertical structure in the tropical Andes. *Geophysical research letters.* 27 (23): 3885–3888.

Vuille, M., Bradley, R.S., Werner, M., and Keimig, F., 2003. 20th Century climate change in the tropical Andes: observations and model results. *Climatic Change.* (59): 75–99.

Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K., and Poschold, P., 2011. Climate change and plant regeneration from seed. *Global Change Biology.* 17 (6): 2144–2162.

Walker, M.D., Webber, P.J., Arnold, E.H. and Ebert-May, D., 1994. Effects of inter-annual climate variation on aboveground phytomass in Alpine vegetation. *Ecology.* 75 (2): 393–408.

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O., and Bairlein, F., 2002. Ecological responses to recent climate change. *Nature.* 416: 389–395.

Walther, G., Bieβner, S., & Burga, C.A., 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science.* 16: 541–548.

Warren, D.L., Glor, R.E., and Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *The Society for the Study of Evolution.* 62 (11): 2868–2883.

Werger, M.J.A. and Van Bruggen, A.C., 2012. Biogeography and ecology of southern Africa. *Monographiae Biologicae.* 31: 53–69.

White. F., 1978. Biography and ecology of southern Africa: the afromontane region. *Monographiae Biologicae.* (31): 463–513.

White, F., 1981. The history of the afromontane archipelago and the scientific need for its conservation. *African Journal of Ecology.* (19): 33–54.

Whitham, T.G., Martinsen, G.D., Floate, K.D., Dungey, H.S., Potts, B.M. and Keim, P., 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. *Ecology.* 80 (2): 416–428.

Woodward, F.I. & Williams, B.G., 1987. Climate and plant distribution at global and local scales. *Vegetation.* (69): 189–197.

Zogg, G.P., Zak, D.R., Ringelberg, D.B., White, D.C., MacDonald, N.W., and Pregitzer, K.S., 1995. Compositional and functional shifts in microbial communities due to soil warming. *Soil Science Society of America Journal.* 61 (2): 475–481.

Appendices

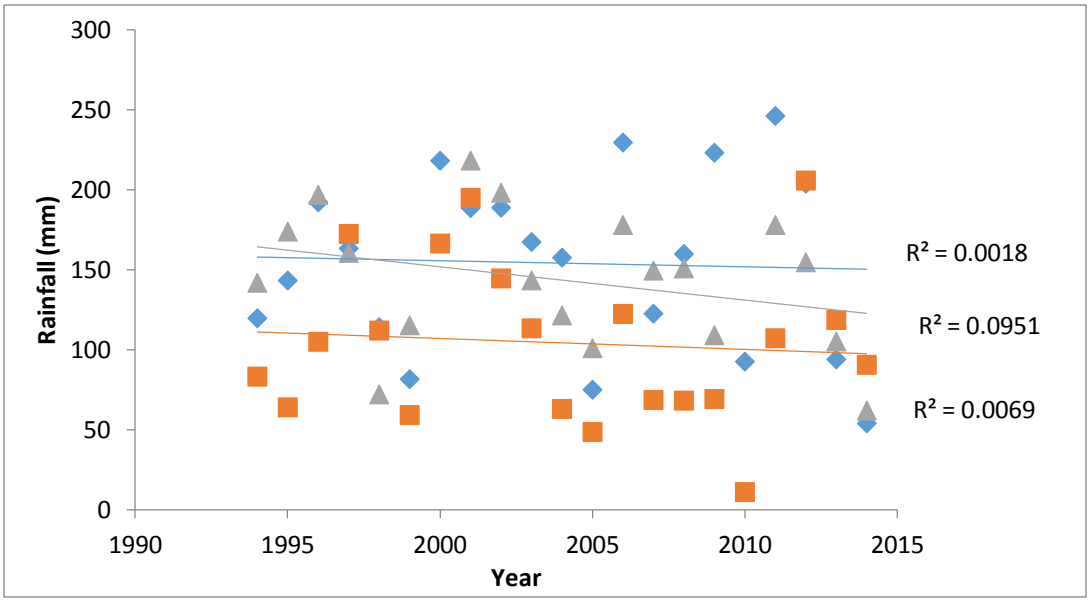

Figure A1. The non-growing season rainfall for Sani Pass (alpine; grey triangles), Giants Castle (lower montane; orange squares) and Shaleburn (lower montane; blue diamonds) data collection sites from 1994 to 2014.

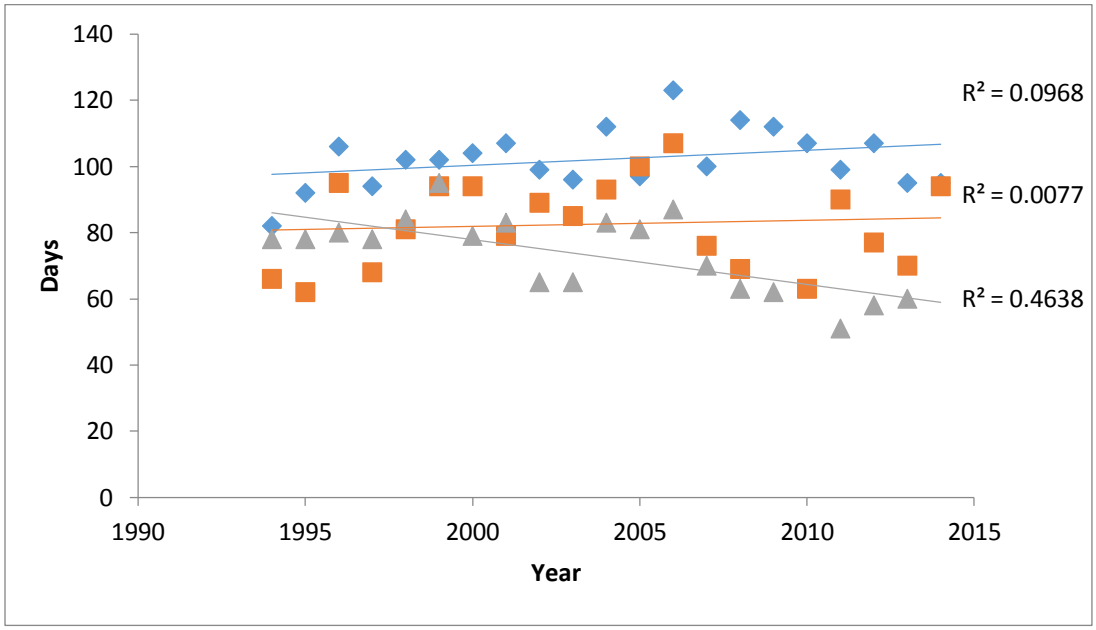

Figure A2. The number of rain days per annum for Sani Pass (alpine; grey triangles), Giants Castle (lower montane; orange squares) and Shaleburn (lower montane; blue diamonds) data collection sites from 1994 to 2014.

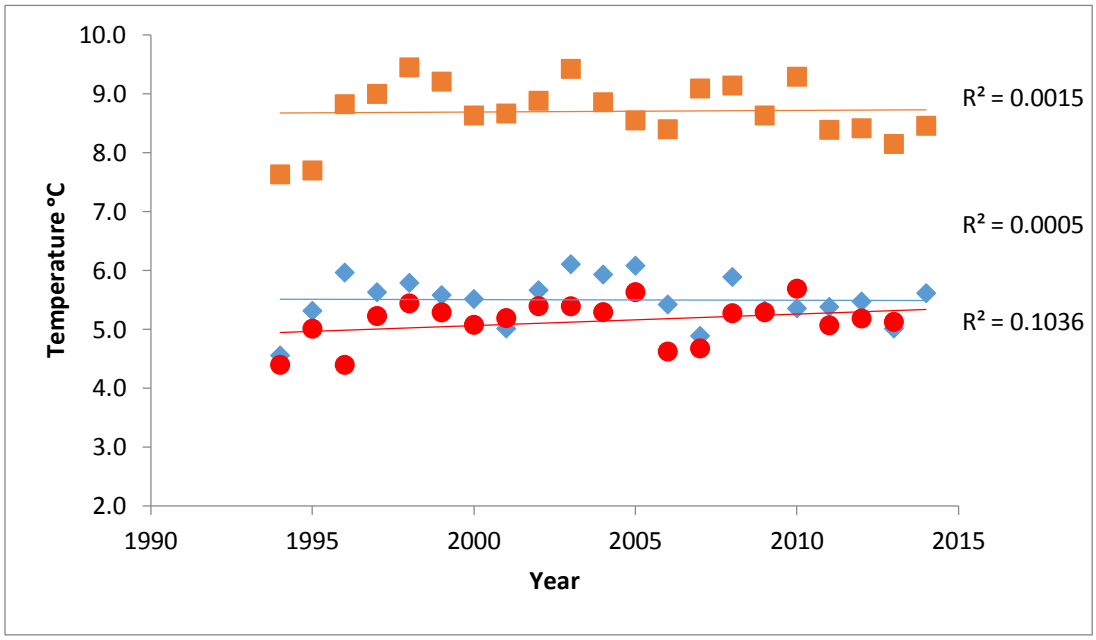

Figure A3. The minimum annual temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

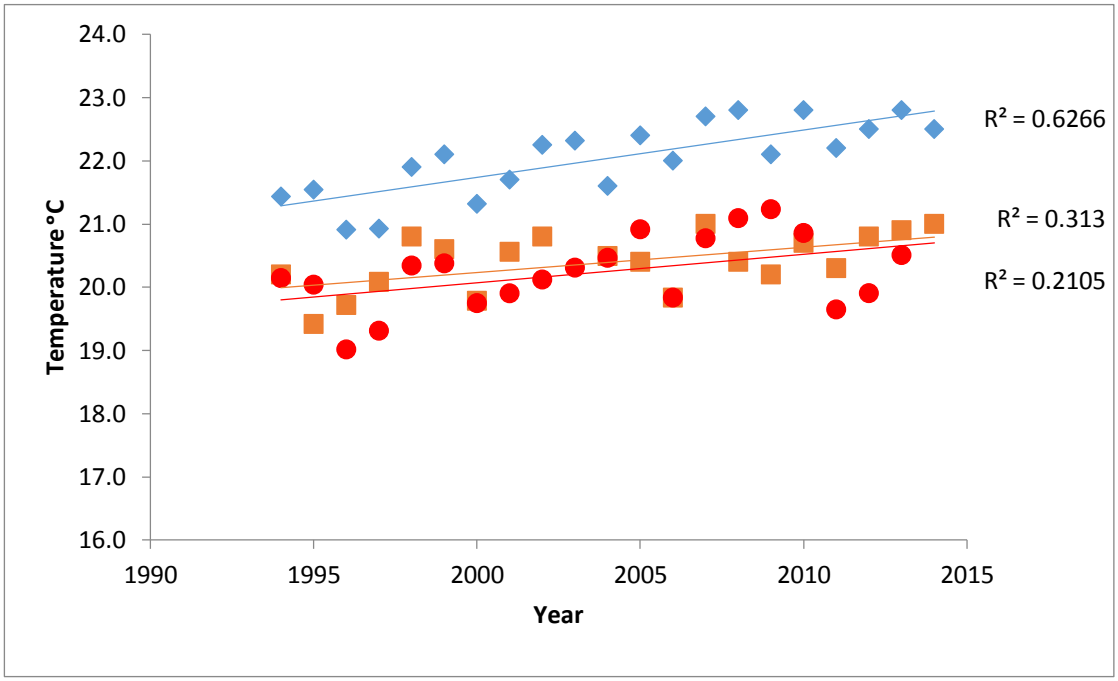

Figure A4. The maximum annual temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

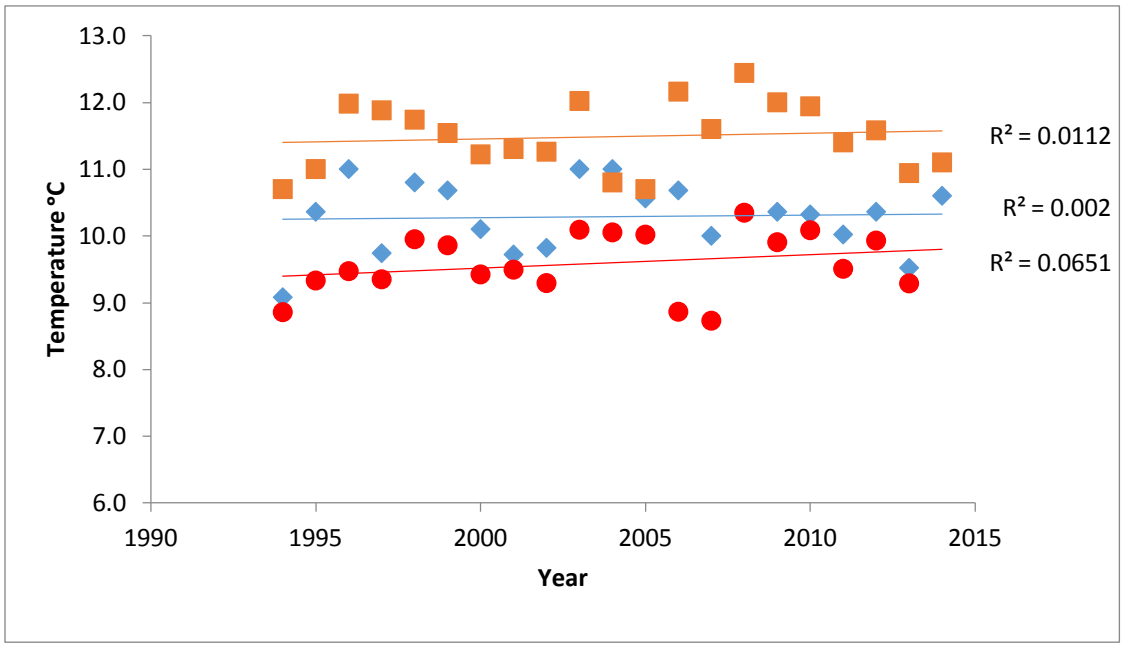

Figure A5. The minimum growing season temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

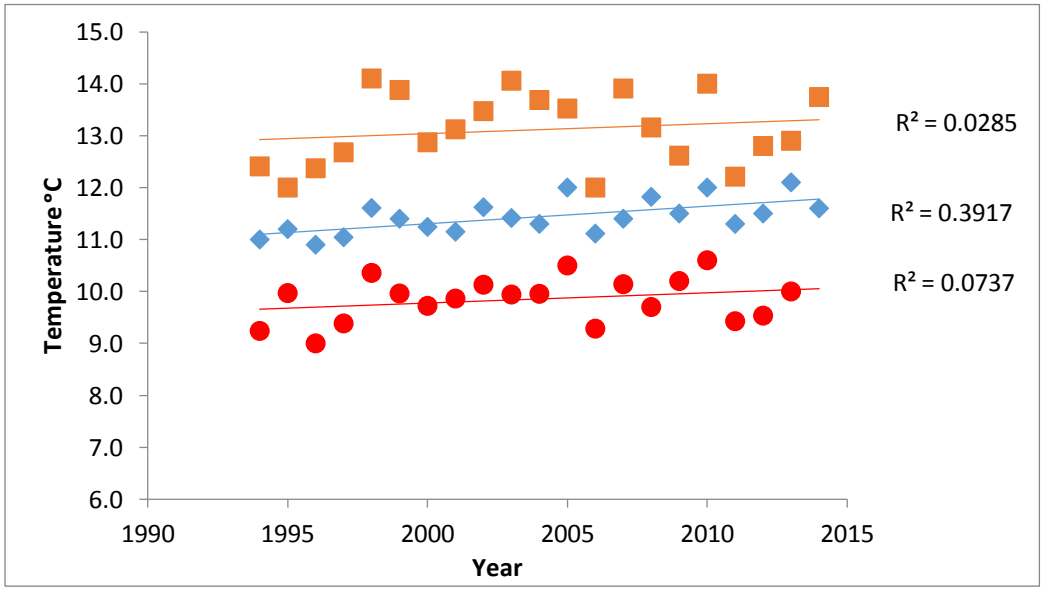

Figure A6. The mean non-growing season temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

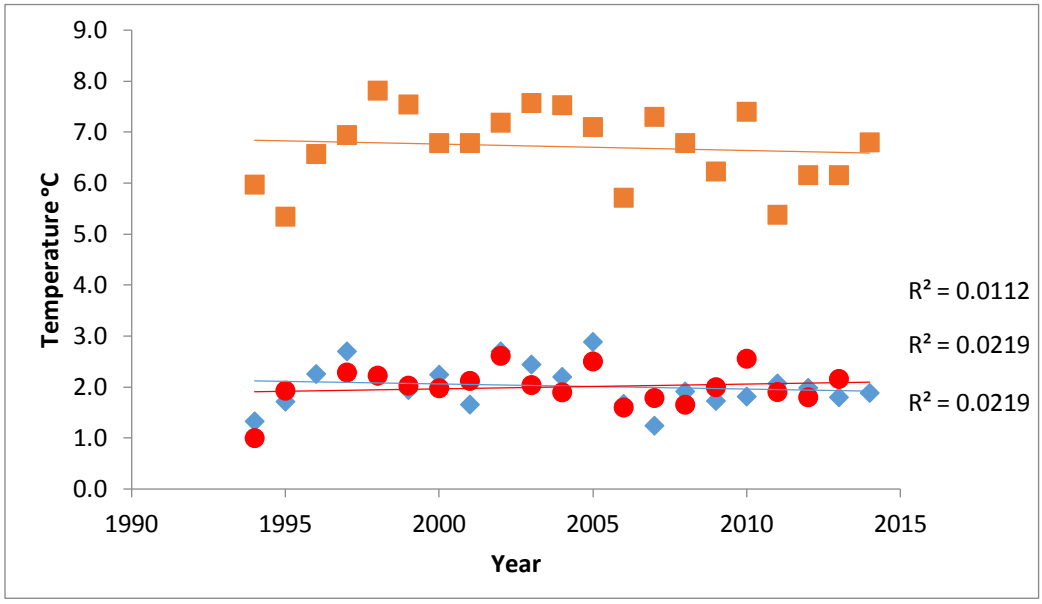

Figure A7. The minimum non-growing season temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

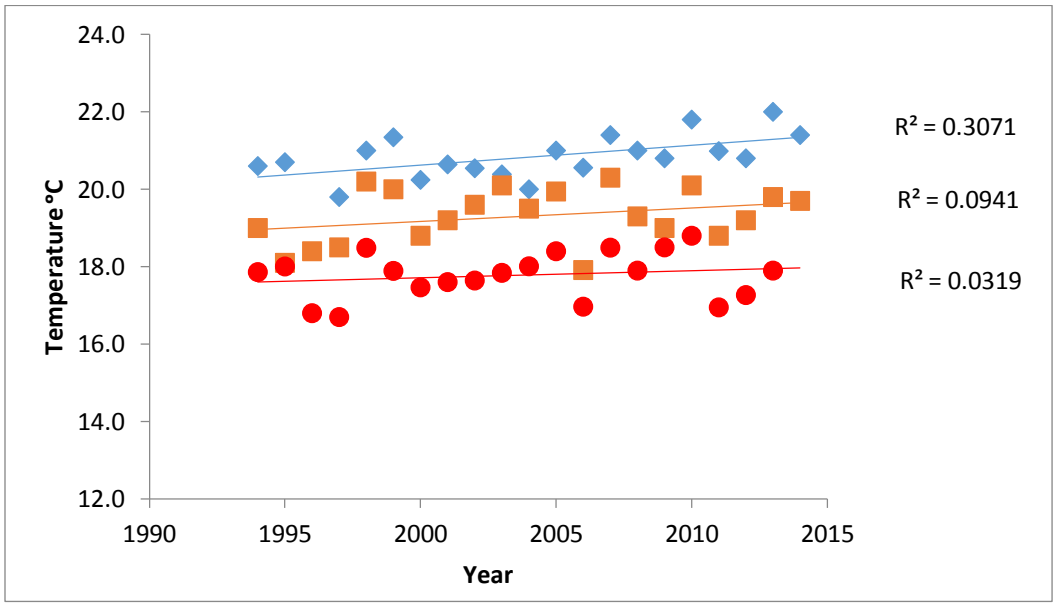

Figure A8. The maximum non-growing season temperature for Mokhotlong (upper montane; red circles), Shaleburn (lower montane; blue diamonds) and Giants Castle (lower montane; orange squares) data collection sites from 1994 to 2014.

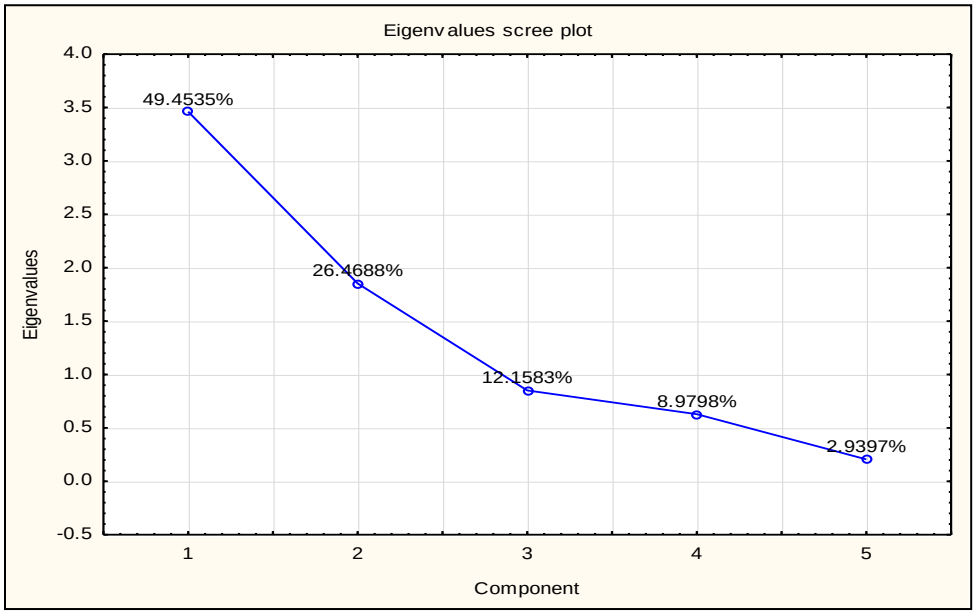

Figure A9. Scree plot showing the percentage of the variance for each component of the PCA on the precipitation variables for Sani Pass (alpine), Shaleburn (lower montane) and Giants Castle (lower montane) data collection sites from 1994 to 2014.

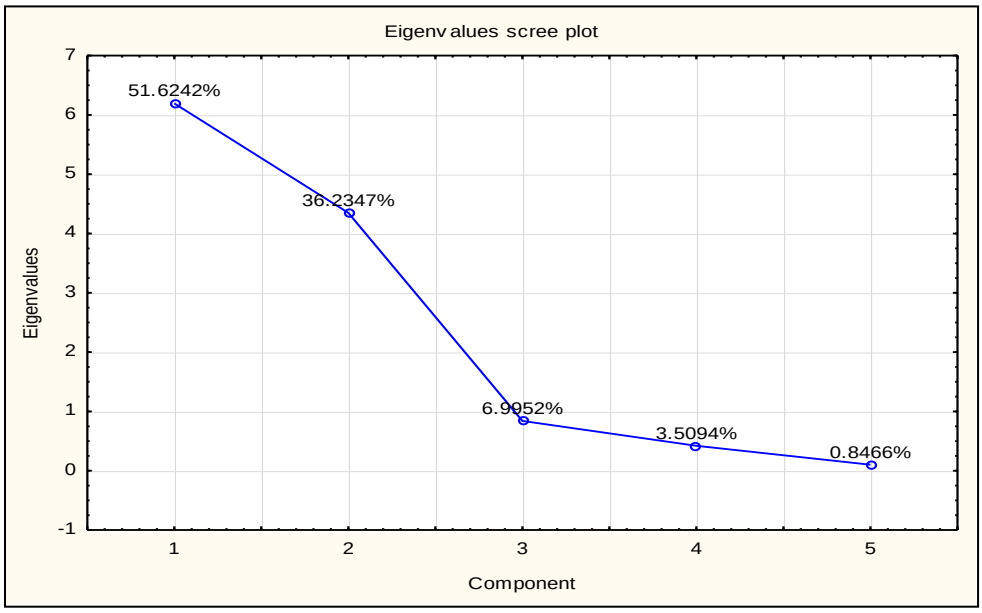

Figure A10. Scree plot showing the percentage of the variance for each component of the PCA on the temperature variables for Mokhotlong (upper montane), Shaleburn (lower montane) and Giants Castle (lower montane) data collection sites from 1994 to 2014.

	Standard Deviation (°C)		
Temperature variables	Shaleburn	Giants Castle	Mokhotlong
Mean annual	0.4	0.4	0.6
Min. annual	0.4	0.5	0.4
Max. annual	0.6	0.5	0.6
Mean growing season	0.4	0.5	0.3
Min. growing season	0.5	0.5	0.5
Max. growing season	0.6	0.5	0.4
Mean non-growing season	0.3	0.7	0.4
Min. non-growing season.	0.4	0.7	0.4
Max. non-growing season	0.6	0.7	0.6
	Coefficient of variation (%)		
Precipitation variables	Shaleburn	Giants Castle	Sani Pass
Annual	15	31	28
Growing season	14	33	28
Non-growing season	36	48	30
No. of rain days	9	16	16

Figure A11. Standard deviation of temperature variables from Shaleburn (lower montane), Giants Castle (lower montane), and Mokhotlong (upper montane), as well as Coefficient of variation precipitation variables from Shaleburn, Giants Castle and Sani Pass (alpine) data collection sites from 1994 to 2014.

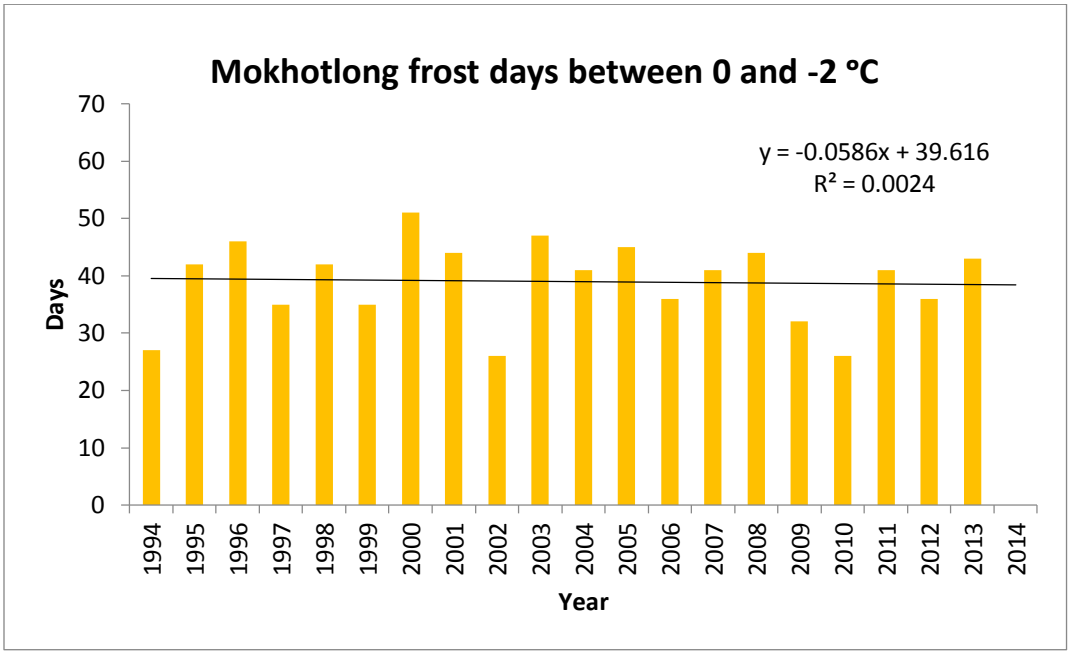

Figure A12. Mokhotlong (upper montane) number of frost days in the first category (0 ˚C to -2 ˚C) from 1994 to 2014.

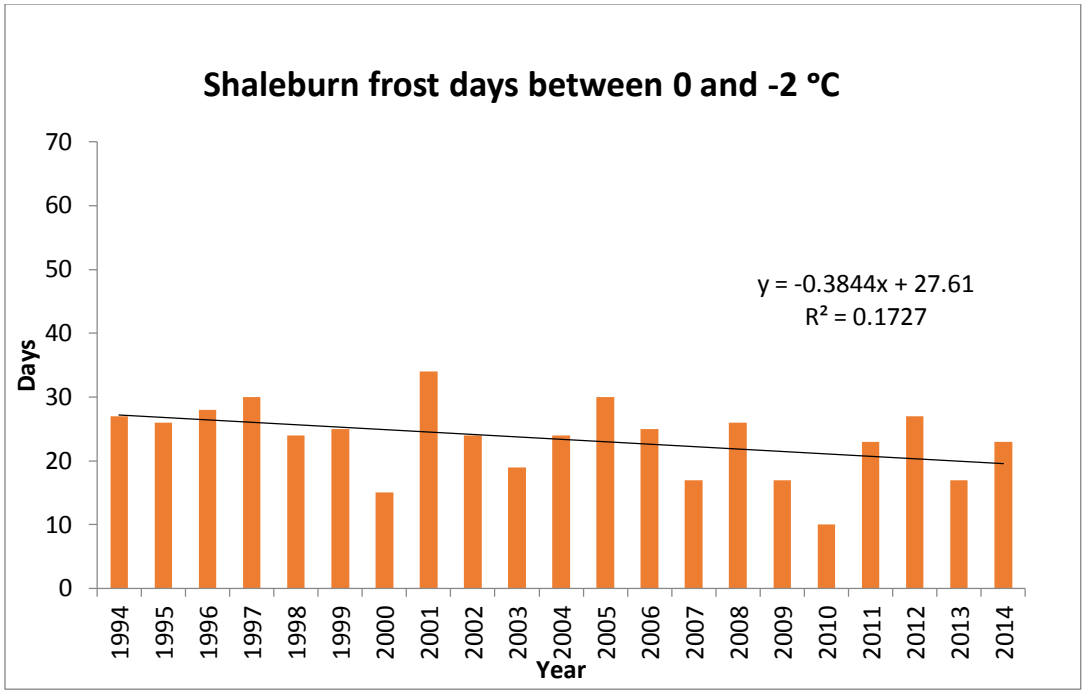

Figure A13. Shaleburn (lower montane) number of frost days in the first category (0 ˚C to -2 ˚C) from 1994 to 2014.

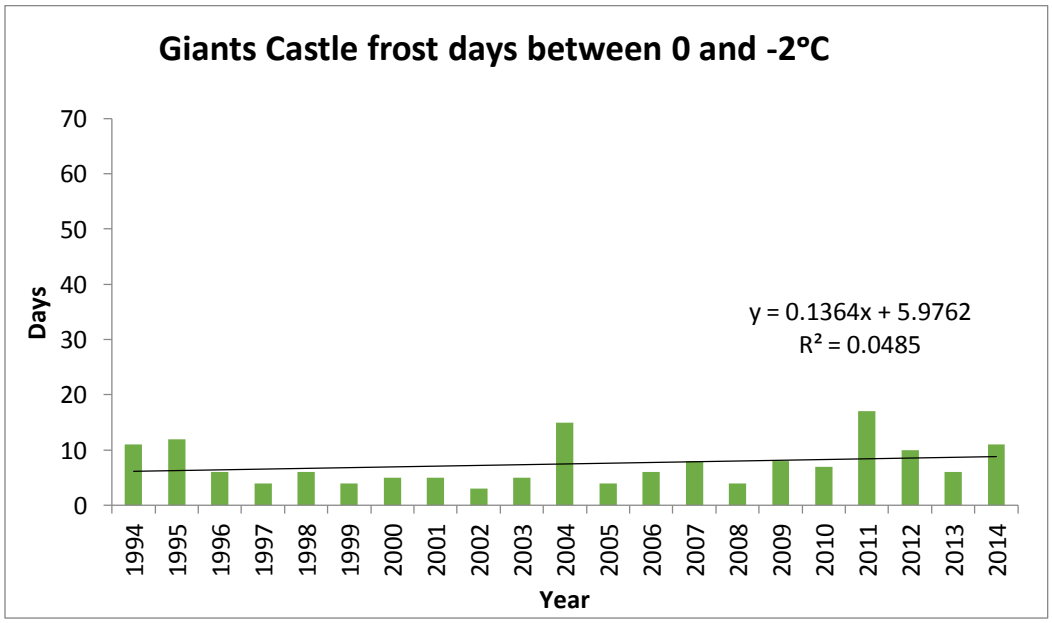

Figure A14. Giants Castle (lower montane) number of frost days in the first category (0 ˚C to -2 ˚C) from 1994 to 2014.

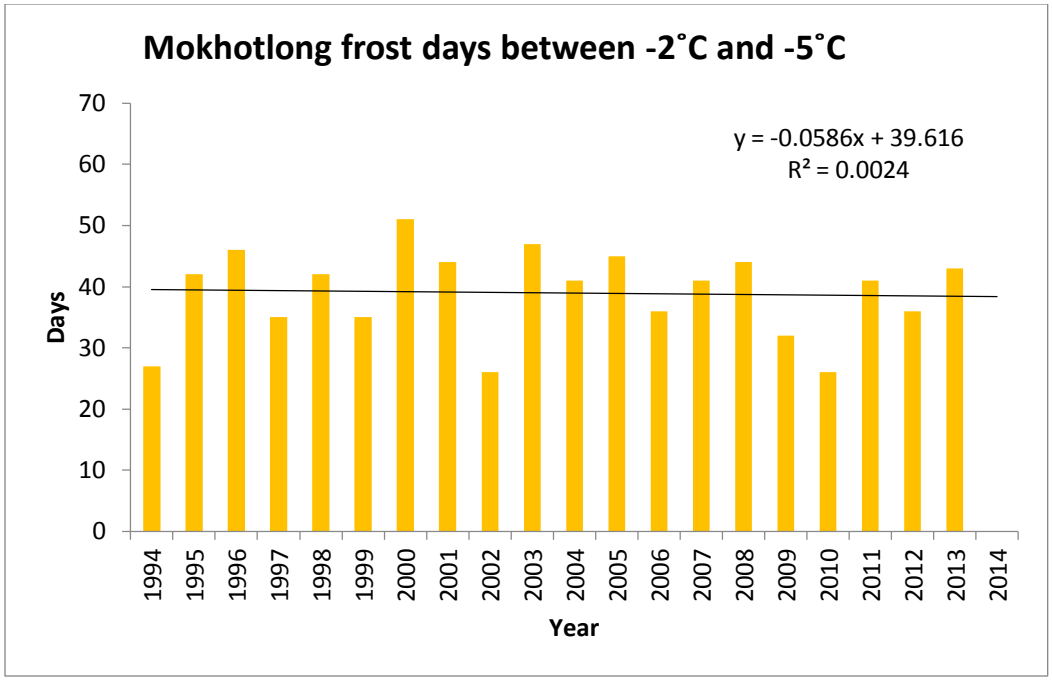

Figure A15. Mokhotlong (upper montane) number of frost days in the second category (-2 ˚C to -5 ˚C) from 1994 to 2014.

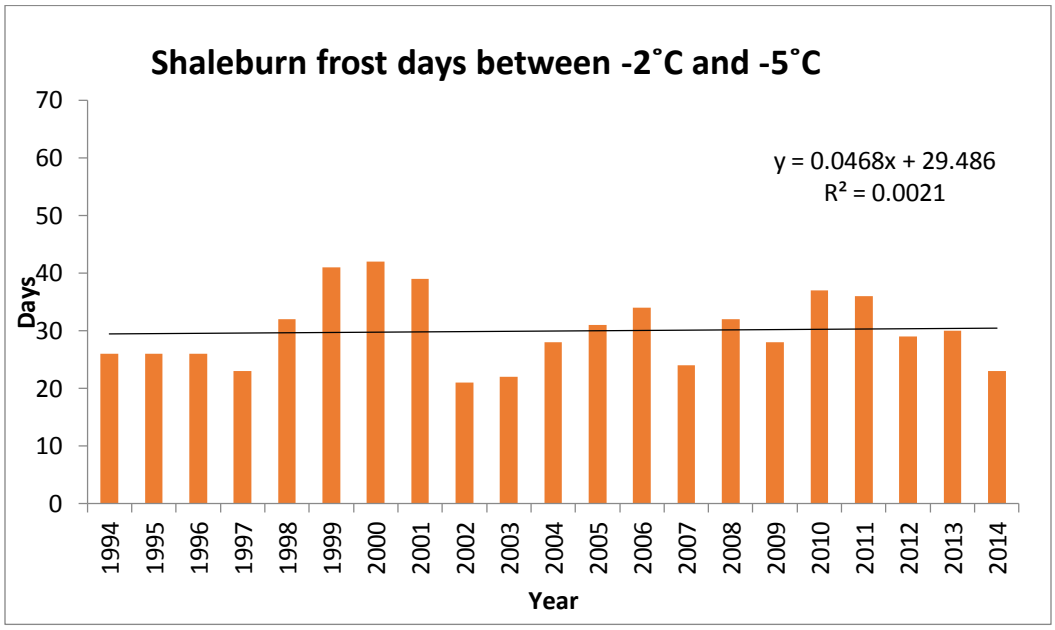

Figure A16. Shaleburn (lower montane) number of frost days in the second category (-2 ˚C to -5 ˚C) from 1994 to 2014.

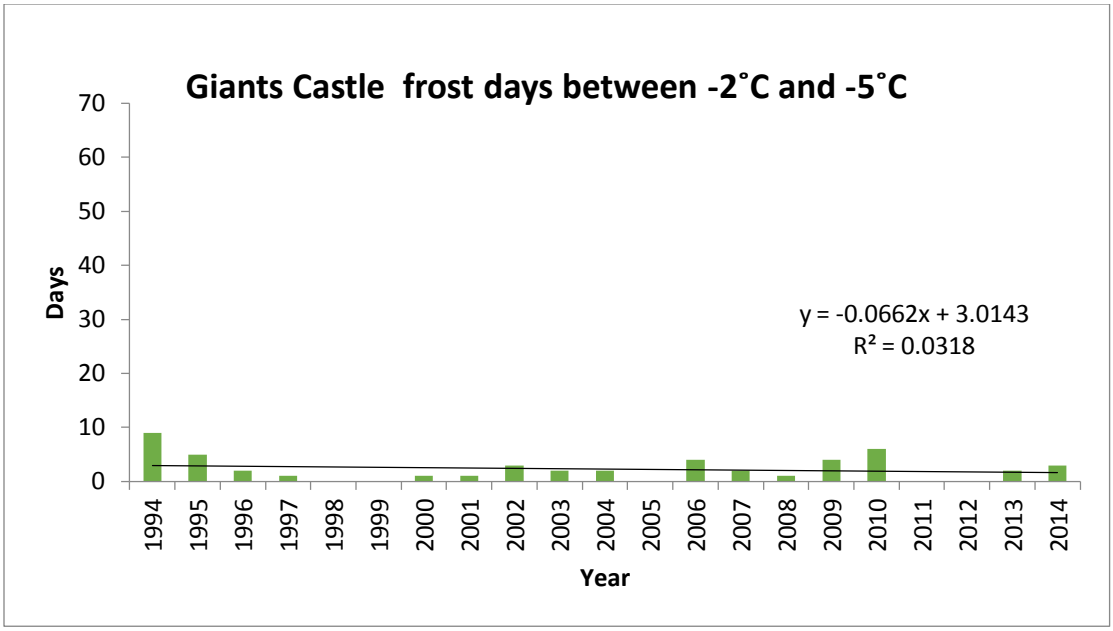

Figure A17. Giants Castle (lower montane) number of frost days in the second category (-2 ˚C to -5 ˚C) from 1994 to 2014.

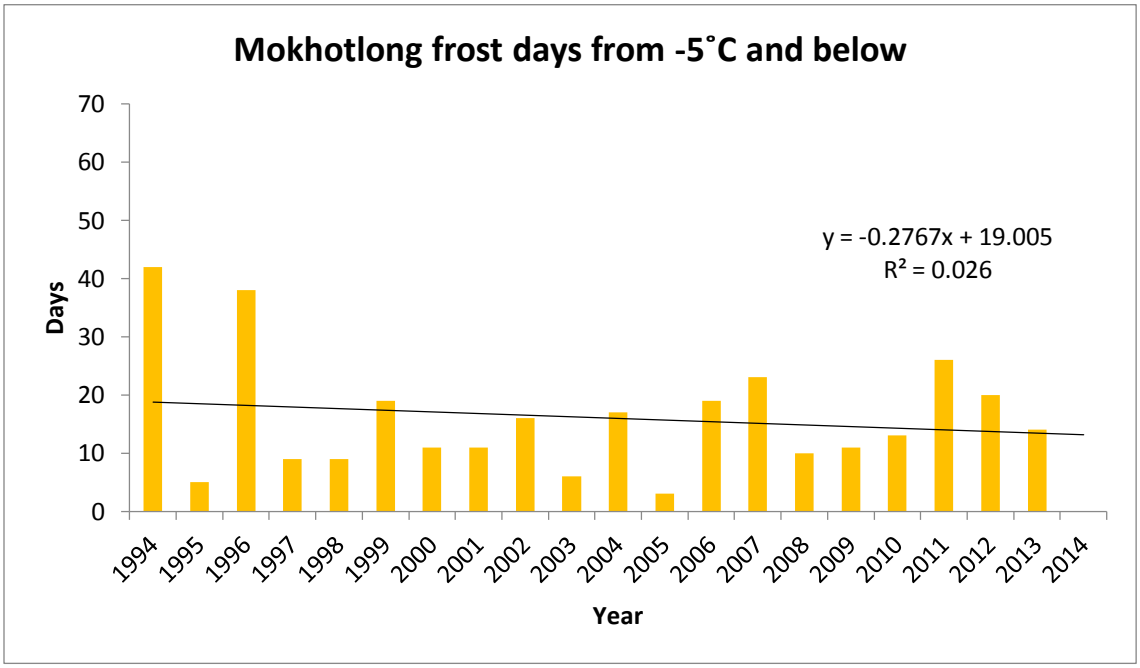

Figure A18. Mokhotlong (upper montane) number of frost days in the third category (-5 ˚C and below) from 1994 to 2014.

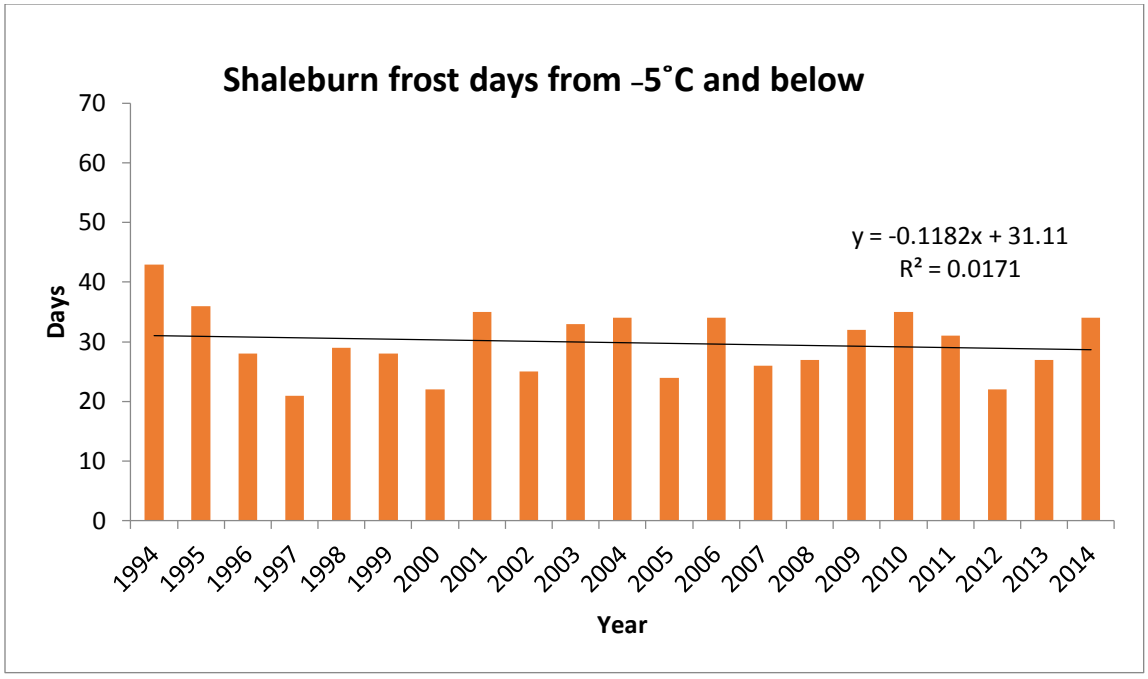

Figure A19. Shaleburn (lower montane) number of frost days in the third category (-5 ˚C and below) from 1994 to 2014.

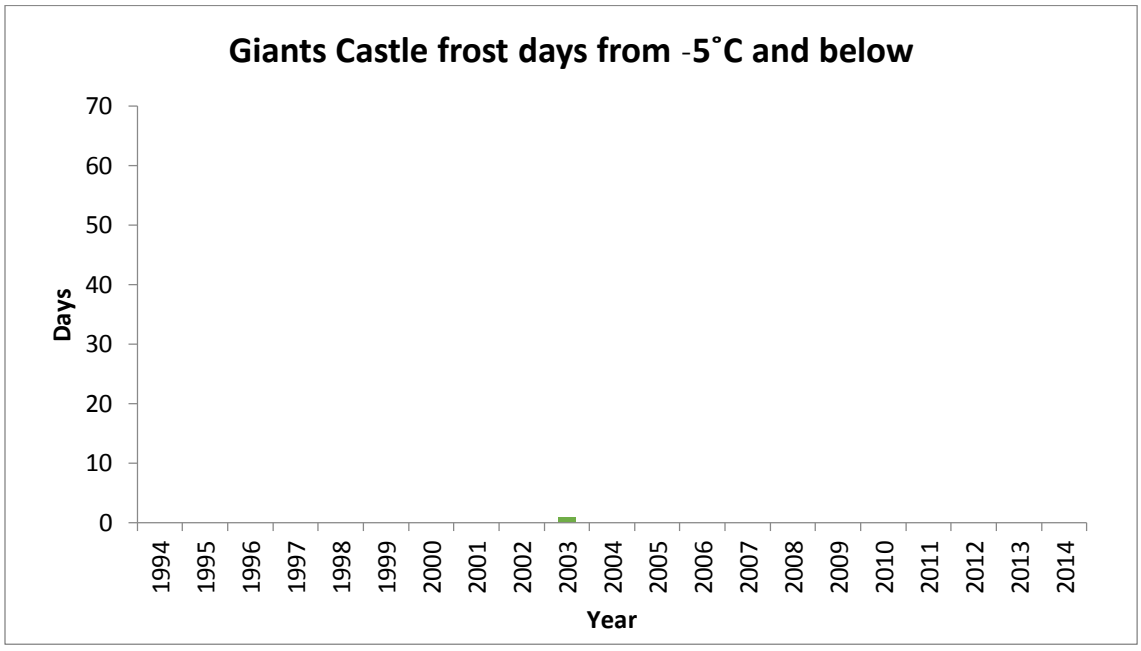

Figure A20. Giants Castle (lower montane) number of frost days in the third category (-5 ˚C and below) from 1994 to 2014.

Figure A21. Precipitation data for Giants Castle (lower montane; 1759 m), Shaleburn (lower montane; 1614 m) and Sani pass (alpine; 2874 m) from 1994 to 2014 (mm).

	Shaleburn				Giants Castle				Sani Pass			
Year	Annual Rainfall	Growing season rainfall	Non-growing season rainfall	No. Of rain days in a growing season	Annual Rainfall	Growing season rainfall	Non-growing season rainfall	No. Of rain days in a growing season	Annual Rainfall	Growing season rainfall	Non-growing season rainfall	No. Of rain days in a growing season
1994	1020.7	900.8	119.9	82	538.4	455	83.4	66	1261.6	1119.5	142.1	78
1995	1195	1051.5	143.5	92	857.4	793.2	64.2	62	1288.4	1114.3	174.1	78
1996	1159.8	967.4	192.4	106	1022.3	917.1	105.2	95	1243.6	1046.5	197.1	80
1997	1095.2	931.6	163.6	94	739.4	566.8	172.6	68	1091.3	930.5	160.8	78
1998	1003.5	889.2	114.3	102	795.4	683.2	112.2	81	898.4	826.1	72.3	84
1999	959.5	877.7	81.8	102	1123	1063.6	59.4	94	1234.8	1119.3	115.5	95
2000	1270.5	1052.1	218.4	104	969.6	803	166.6	94	1169.7	1026.0	143.7	79
2001	1156.5	967.7	188.8	107	888.4	693.2	195.2	79	1254	1035.5	218.5	83
2002	864.6	675.6	189	99	567.2	422.4	144.8	89	786.9	588.5	198.4	65
2003	1003.7	836.1	167.6	96	534.6	421	113.6	85	663.6	520	143.6	65
2004	1345.4	1187.6	157.8	112	720	656.8	63.2	93	1051.5	929.8	121.7	83
2005	841.3	766.1	75.2	97	667.4	618.6	48.8	100	928.9	827.7	101.2	81
2006	1355.4	1125.6	229.8	123	932.4	809.8	122.6	107	1210.5	1032.3	178.2	87
2007	809.6	686.8	122.8	100	397.3	328.5	68.8	76	818.8	669.1	149.7	70
2008	1057.7	897.6	160.1	114	595	526.6	68.4	69	1060.3	909.2	151.1	63
2009	1097	873.6	223.4	112	358.2	650.6	69.4	84	928	818.7	109.3	62
2010	995.2	902.4	92.8	107	430.8	419.6	11.2	63	477.5	452.8	152.4	77
2011	1194.2	947.8	246.4	99	582.4	475	107.4	90	722.5	544.3	178.2	51
2012	1049.2	845.2	204	107	664	458	206	77	517	620	154.9	58
2013	888.2	794	94.2	95	481	362.2	118.8	70	630.4	525	105.4	60
2014	893	838.8	54.2	95	805.8	715	90.8	94	850.0	648.4	62.2	56

Figure A22. Temperature data for Shaleburn (lower montane; 1614 m) from 1994 to 2014 (°C).

	Shaleburn								
Year	Annual Mean	Annual Minimum	Annual Maximum	Growing Season Mean	Growing Season Minimum	Growing Season Maximum	Non-Growing Season Mean	Non-Growing Season Minimum	Non-Growing Season Maximum
1994	13.0	4.6	21.4	16.9	9.1	23.8	11.0	1.3	20.6
1995	13.4	5.3	21.5	17.1	10.4	24.0	11.2	1.7	20.7
1996	13.4	6.0	20.9	17.3	11.0	23.8	10.9	2.3	20.5
1997	13.3	5.6	20.9	16.5	9.7	23.1	11.0	2.7	19.8
1998	14.0	5.8	21.9	17.4	10.8	23.8	11.6	2.2	21.0
1999	14.1	5.6	22.1	17.5	10.7	24.1	11.4	1.9	21.3
2000	13.4	5.5	21.3	16.7	10.1	23.8	11.2	2.2	20.2
2001	13.4	5.0	21.7	16.6	9.7	23.2	11.2	1.7	20.6
2002	14.0	5.7	22.3	17.2	9.8	24.3	11.6	2.7	20.5
2003	14.2	6.1	22.3	17.5	11.0	24.5	11.4	2.4	20.4
2004	13.6	5.9	21.6	17.7	11.0	24.0	11.3	2.2	20.0
2005	14.1	6.1	22.4	17.3	10.6	24.1	12.0	2.9	21.0
2006	13.5	5.4	22.0	17.6	10.7	24.5	11.1	1.7	20.6
2007	13.9	4.9	22.7	17.2	10.0	24.8	11.4	1.2	21.4
2008	14.3	5.9	22.8	17.5	10.3	24.9	11.8	1.9	21.0
2009	13.8	5.3	22.1	17.4	10.4	24.0	11.5	1.7	20.8
2010	14.2	5.4	22.8	17.7	10.3	25.0	12.0	1.8	21.8
2011	13.8	5.4	22.2	17.4	10.0	24.5	11.3	2.1	21.0
2012	14.1	5.5	22.5	17.6	10.4	25.0	11.5	2.0	20.8
2013	14.0	5.0	22.8	17.6	9.5	25.1	12.1	1.8	22.0
2014	14.2	5.6	22.5	17.4	10.6	24.2	11.6	1.9	21.4

Figure A23. Temperature data for Giants Castle (lower montane; 1759 m) from 1994 to 2014 (°C).

	Giants Castle								
Year	Annual Mean	Annual Minimum	Annual Maximum	Growing Season Mean	Growing Season Minimum	Growing Season Maximum	Non-Growing Season Mean	Non-Growing Season Minimum	Non-Growing Season Maximum
1994	14.1	7.6	20.2	16.4	10.7	22.1	12.41	6.0	19.0
1995	13.9	7.7	19.4	16.7	11	21.7	12.00	5.3	18.1
1996	14.3	8.8	19.7	16.9	11.98	21.88	12.37	6.6	18.4
1997	14.5	9.0	20.1	17.2	11.88	22.42	12.68	6.9	18.5
1998	15.2	9.5	20.8	17.0	11.74	22.28	14.10	7.8	20.2
1999	15.1	9.2	20.6	16.9	11.54	22.28	13.88	7.5	20.0
2000	14.2	8.6	19.8	16.1	11.22	22.11	12.87	6.8	18.8
2001	14.6	8.7	20.6	16.4	11.3	22.1	13.12	6.8	19.2
2002	14.8	8.9	20.8	17.0	11.26	22.8	13.47	7.2	19.6
2003	15.0	9.4	20.2	16.7	12.02	22.45	14.06	7.6	20.1
2004	14.7	8.9	20.5	16.1	10.8	21.4	13.69	7.5	19.5
2005	14.6	8.6	20.4	16.0	10.7	21.48	13.52	7.1	19.9
2006	14.1	8.4	19.8	17.0	12.16	22.2	12.00	5.7	17.9
2007	15.2	9.1	21.0	16.8	11.6	22.2	13.91	7.3	20.3
2008	14.9	9.1	20.4	17.8	12.44	22.8	13.16	6.8	19.3
2009	14.6	8.6	20.2	17.2	12	22.3	12.61	6.2	19.0
2010	15.1	9.3	20.7	17.3	11.94	22.5	14.00	7.4	20.1
2011	14.5	8.4	20.3	17.1	11.4	22.8	12.21	5.4	18.8
2012	15.1	8.4	20.8	17.4	11.58	23.1	12.80	6.2	19.2
2013	14.5	8.2	20.9	17.0	10.94	23	12.90	6.2	19.8
2014	15.0	8.5	21.0	16.9	11.1	22.5	13.74	6.8	19.7

Figure A24. Temperature data for Mokhotlong (upper montane; 2209 m) from 1994 to 2014 (°C).

	Mokhotlong								
Year	Annual Mean	Annual Minimum	Annual Maximum	Growing Season Mean	Growing Season Minimum	Growing Season Maximum	Non-Growing Season Mean	Non-Growing Season Minimum	Non-Growing Season Maximum
1994	12.1	4.4	20.1	16.2	8.9	23.3	9.2	1.0	17.9
1995	11.6	5.0	20.0	16.1	9.3	22.9	10.0	1.9	18.0
1996	11.5	4.4	19.0	15.9	9.5	22.4	9.0	1.5	16.8
1997	11.3	5.2	19.3	16.3	9.3	23.3	9.4	2.3	16.7
1998	12.9	5.4	20.3	16.4	9.9	22.9	10.4	2.2	18.5
1999	11.8	5.3	20.4	16.9	9.9	23.9	10.0	2.0	17.9
2000	12.4	5.1	19.7	16.2	9.4	22.9	9.7	2.0	17.5
2001	11.6	5.2	19.9	16.3	9.5	23.1	9.9	2.1	17.6
2002	12.8	5.4	20.1	16.4	9.3	23.4	10.1	2.6	17.6
2003	11.9	5.4	20.3	16.7	10.1	23.6	9.9	2.0	17.8
2004	12.9	5.3	20.5	16.9	10.1	23.7	10.0	1.9	18.0
2005	12.3	5.6	20.9	16.8	10.0	23.6	10.5	2.5	18.4
2006	12.2	4.6	19.8	16.4	8.9	23.8	9.3	1.6	17.0
2007	11.7	4.7	20.8	16.3	8.7	24.1	10.1	1.8	18.5
2008	13.2	5.3	21.1	16.4	10.3	23.4	9.7	1.7	17.9
2009	12.2	5.3	21.2	17.0	9.9	24.0	10.2	2.0	18.5
2010	13.3	5.7	20.9	16.6	10.1	23.2	10.6	2.6	18.8
2011	11.4	5.1	19.6	16.5	9.5	23.2	9.4	1.9	17.0
2012	12.5	5.2	19.9	16.8	9.9	23.4	9.5	1.8	17.3
2013	11.8	5.1	20.5	16.5	9.3	23.7	10.0	2.2	17.9
2014	12.2	5.1	20.2	16.6	9.6	23.5	10.0	2.0	17.8