The relationship between the length of flowering periods and the distribution ranges of plant species in eastern South Africa

By

Nikara Mahadeo

207 511 025

Supervisor: Prof. Ş. Procheş

Co-Supervisor: Dr. S. Ramdhani

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Declaration One

This thesis was conducted at the University of KwaZulu-Natal, College of Agriculture, Engineering and Science, School of Agricultural, Earth and Environmental Sciences (Westville) in fulfilment of the MSc. Degree in Environmental Science 2012. It is representative of my original work and where the works of other authors have been used, they are duly acknowledged.

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Nikara Mahadeo

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Prof. Şerban Procheş

(Supervisor)

…….

Dr. Syd Ramdhani

(Co-Supervisor)

Declaration Two: Plagiarism

I, **Nikara Mahadeo** declare that:

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Abstract

Flowering is one of the most important stages in determining the successful survival and spread in plants. The duration of the flowering period is closely associated with successful reproduction, making it essential to understand the importance and effects of the length of flowering on various macroecological variables across plant species. The effects of the length of flowering periods on the distribution range size of species have seldom been investigated. This project aims to identify any macroecological relationship that may exist between the length of flowering periods and the distribution ranges of plant species endemic to the eastern part of South Africa, a region well known for its floral diversity. Range size and flowering phenology data were collected for several genera that are centred in the region (*Cussonia*, *Gymnosporia*, *Searsia*, *Streptocarpus*, *Pavetta*, *Plectranthus*, *Crinum*, *Eulophia*, *Gladiolus*, *Kniphofia*, *Satyrium*, *Watsonia* and *Zantedeschia*). At genus level, the relationship varied considerably. While significant correlations between the two variables were retrieved in four genera, the meaning of these patterns differed. In some cases, these suggested that a larger range was achieved through successful pollination due to extended flowering periods, whereas in others, it is probably just an effect of different flowering seasons in different areas where the range is large enough to comprise diverse climates. When incorporating variables such as growth form (narrowly and broadly-defined) and genus identity in analyses of co-variance between flowering durations and various measures of distribution, the association of genera was far greater than that of growth form. It can be concluded that both range size and the length of the flowering season are the result of numerous factors acting jointly, which differ across plant groups and are likely to be susceptible to changes in climate and biological invasions. This means that the relationship between range size and flowering period is driven by different factors in different genera, suggesting that the conservation of plant diversity in the face of global change will have to consider the complexity of flowering patterns, and it is likely that lineage-specific approaches for different plant groups will be necessary.

Chapter One
Introduction

1.1. Introduction

The field of biogeography is closely related and linked to the fields of ecology and phylogenetics (Wiens and Donoghue, 2004). However, the exchanges, particularly between biogeography and ecology, have been limited for many years and have only recently started converging (Jenkins and Ricklefs, 2011). Posadas *et al.* (2006) describe biogeography as the study of the geographical distributions of organisms and the possible reasons for these distributions, therefore making it both a descriptive and interpretative field of study. Furthermore, biogeography can be subdivided into historical and ecological biogeography which are closely linked. Ecology, on the other hand, where concerned with spatial aspects, describes the effect of spatial dimensions on the organisms' community and population dynamics (Murrell *et al.*, 2001). The common aspects between these two fields thus have the potential to be linked to understanding the distribution patterns of species and organisms.

These common aspects may be taken into account when considering the length of flowering periods amongst certain endemic and widespread plant species and the distribution ranges of these particular species. The change from vegetative growth to flowering is crucial in the plant life cycle (Amasino, 1996). The flowering stage is therefore one of the most important aspects in the success of plant reproduction, making the timing of flowering essential (Elzinga *et al.*, 2007). Murtas and Millar (2000) refer to this as 'biological rhythms', which incorporates flowering phenology, whereby the organism's keep-time by utilising varied time scales. Biological rhythms, such as the length of a flowering period, are influenced by a number of environmental factors and conditions (Elzinga *et al.*, 2007). A few of these include seasonality, rainfall, temperature, soil fertility and availability of sunlight (photoperiod). Elzinga *et al.* (2007) further state that flowering occurs when the climatic conditions are most favourable for reproduction. Environmental conditions such as temperature and day-length are believed to greatly influence synchronisation in plants, allowing flowering to occur (Reeves and Coupland, 2000).The changes in temperature and day-length generally occur with changes of season, which plant species are sensitive to, and this generally initiates the

flowering period. The rate of response, however, is different amongst various species (Penfield, 2008). In some areas, such as the tropics, where there is relatively little change in climate on an annual basis, plants are sensitive and are able to detect the slight changes in temperature and day-lengths (King and Heide, 2009). The *Arabidopsis* genus has been studied extensively, as it readily responds to changes in the environment, particularly with respect to changes in day-length (Searle and Coupland, 2004).

Conversely, environmental factors or conditions alone, do not entirely determine the time and the length of flowering in plant species. Amasino (1996) studied the controls involved in flowering times, with specific observation of *Arabidopsis thaliana* species. The study revealed that the genetics of plant species also plays an important role in the time and length of flowering. Furthermore, Amasino (1996) found that flowering genes are complex in nature and through development of the plant and interaction with the surrounding environment, genes also regulate flowering time and length. However, the genetic influence on flowering length and time is a result of natural selection in the past, based on the present environmental conditions.

From another perspective, the flowering of plants has been suggested to be a trade-off for various other factors (Johnson, 1992). These include pollinator availability, pollinator competition, moisture availability and conditions for seed germination and seedling establishment (Johnson, 1992), as well as vegetation succession. Schemske *et al.* (1978) examined several woodland herb species, during spring, over a period of three years. Herb species flowered during a period that was suitable for pollinator activity and ended by the time the canopy of the woodland 'closed'. There were slight differences in the flowering period over the three years, which were assumed to be associated with differences in the average seasonal temperatures (Schemske *et al.*, 1978). However, the availability of pollinators plays an important role in determining the flowering period of many species, particularly when pollinators are seasonal or if the pollinators are specialists (Stevenson *et al.*, 2008). On the contrary, the abundance or density of flowers over a period can determine the pollinator abundance and availability, as there is an increase of rewards for the pollinators (Ramírez, 2006).

Some scientists believe that coexisting plant species may compete for pollinators. However, numerous studies have illustrated very little competition amongst pollinators and coexisting

species (Ollerton and Lack, 1992). This is also supported by Kochmer and Handel (1986), who suggest that competition amongst pollinators is avoided because flowering times have been adapted by natural selection. However, Ollerton and Lack (1992) suggest that co-occurrence of plant species could increase pollination activity, through attracting more pollinators, as there is a larger source of reward.

The relationship between plant species and geographic range has been studied over a long period of time and the general understanding of geographic range is explained by Rapoport's Rule, which states that species range size tends to decrease with decreasing latitude and elevation (Stevens, 1989). There are many determinants of a species geographic range size, such as altitude, latitude, climate, resource availability and numerous intrinsic factors. However, the extent and range of flowering times and lengths may also vary geographically. Variation may be found across vegetation types, latitudes and altitudes, amongst others. Thórhallsdóttir (1998) states that flowering seasons in the tropics may not be distinguished at a community level, due to little variation in climatic conditions and seasonality. However, plant communities in areas with polar climates or in deserts tend to have flowering periods that are recognisably compressed and timed, due to cooler or shorter growing periods (Thórhallsdóttir, 1998). Similarly, Godoy *et al.* (2009) looked at flowering phenology of native and alien plants species in the Mediterranean-type ecosystems. Their main finding was that alien plant species had different flowering times across three Mediterranean-type ecosystems, in comparison to the native species. The flowering time of these alien plant species was dependent on the climatic regimes across the ecosystems and the proportion of invasive plants originating from different regions.

It is evident that there have been many studies which have focused on flowering phenology and the response of flowering to the physical environment and other biotic and abiotic interactions. However, there is limited support for the association of the length of flowering periods and the geographical distribution of plant species.

1.2. Motivation

The plant kingdom is amongst one of the most diverse kingdoms in terms of evolutionary history and species diversity, therefore enabling scientists to carry out various comparative studies across a number of specialised fields (Silvertown and Dodd, 1996). The key to the

success of many plant species is successful reproduction, which is closely associated with flowering and the length of flowering periods. Flowering periods are, in turn, associated with the success of pollination, which, in many cases, determines seed production (Johnson, 1992). Therefore, the length of the flowering period may be linked to the distribution range size of numerous plant species. The relationship between the length of flowering periods and distribution range size has not yet been identified as a major macroecological pattern. Consequently, it is interesting to determine if there are any possible linkages between these two variables.

Goodwin *et al.* (1999), however, carried out a study which focused on predicting the invasiveness of plants by looking at specific biological information. Three biological characteristics of plants, one being the flowering period, were taken into consideration. Information from numerous species was used for various statistical tests to determine if any significance exists between invading species. However, together with these tests, each characteristic was tested against geographic range. Despite this not being the aim of the study, Goodwin *et al.* (1999) briefly mentioned that a significance existed between flowering period and geographic range size, which suggests that this relationship may exist in different flora.

This research could also be useful in the current climatic variation that is occurring. There have been several studies which have focused on the effect of climate change on flowering phenology. Fitter and Fitter (2002) focused on the rapid changes observed across numerous British plant species, as a result of a changing climate. This study found that the average start-of-flowering time of 385 plant species had advanced by 4.5 days over a decade. Likewise, Fitter and Fitter (2002) also believe that annuals are likely to start flowering earlier than perennials, as well as insect-pollinated earlier than wind-pollinated species, if average temperatures continue to rise. This is also supported by Franks *et al.* (2007), who state that flowering phenology has shifted in many species as a result of climate change. This shift may disrupt ecosystem structure (Fitter and Fitter, 2002).

Another concern which poses a threat to altering the length of flowering periods is biological plant invasions, which can be either an intentional or accidental introduction. A vast body of published literature suggests that alien invasive plant species, as well as other biological invasions, can drastically change ecosystems' processes and dynamics, of which flowering phenology is a part of (Goodwin *et al.*, 1999; Lloret *et al.*, 2005; Ward and Masters, 2007 and

Castro-Díez *et al.*, 2011). The flowering dynamics of alien invasive plant species may be completely different to the native flora, therefore having the potential to change the utilisation of available resources, as well as pollinator availability, which essentially may affect flowering dynamics of the native flora (Davis *et al.*, 2000).

The alteration of the flowering time of plants has the potential to effect important ecosystem events in plants, animals and insects and as mentioned previously, timing of flowering is a key event (Fitter and Fitter, 2002). If flowering time is significantly shortened, it may affect the overall reproduction of the species (i.e. pollination and dispersal). Similarly, if flowering lengths are shorter or longer, this could change the distribution ranges of many plant species. The data gathered from this study may be able to determine this change in distribution, due to the change of flowering periods as a result of climate change or alien plant invasions. Furthermore, the information can be used in the conservation of threatened or endangered species, which are vulnerable to rapid changes in the environment.

1.3. Hypothesis

The length of flowering periods does affect the geographic range size of plant species. Therefore the longer or shorter the duration of flowering the larger or smaller the geographic extent of a species, respectively.

1.4. Aim

To identify patterns in the length of flowering periods in selected endemic South African plant species from a selected geographic region and their effect on distribution range size.

1.5. Objectives

- To determine the length of flowering periods of endemic South African plant species across a number of plant genera
- To determine the distribution range of the various species within each genera
- To establish if there is any significant correlation between the length of flowering periods and distribution range size in each genera

1.6. Dissertation outline

In the following chapters the various aspects that make up this study are reviewed in detail. In Chapter Two, relevant literature on determinants of geographic range and its influence on flowering periods are discussed, together with the determinants of the length of flowering periods. These two sections are the main focus of the chapter and are jointly considered in the final section, where the potential effects of biological invasions and climate change on both distribution range and the length of flowering periods are taken into account.

Chapter Three focuses on the eastern South African region and the main methodologies employed. The first section of the chapter comprehensively describes the climatic, geomorphic and vegetational characteristics of the area covered by the study, as these are likely to have a significant influence on the length of flowering periods and the distribution range of endemic species found in the region. The methodology section explains the approaches used in the collation of relevant flowering and distribution data from various publications and other sources. The details of the data analysis process, using different programmes to carry out Factor Analyses, ANCOVAs (Analyses of Co-variance) and Correlation Analyses are also found in this chapter.

The main outcomes obtained from the series of statistical analyses that are described in Chapter Three, are found in Chapter Four. Patterns that appeared among the chosen genera in various sets of analyses are identified in this chapter.

The interpretation of these patterns is then discussed in depth in Chapter Five. Suggested reasons for the observed patterns are explained and supported with relevant literature, including studies looking at similar data. The length of flowering time is discussed, followed by distribution range size. Thereafter the relationship that seems likely to exist, from the results, between these two variables is then discussed, highlighting relevance to biological invasions and climate change. Finally, all these views are brought together in the conclusions drawn in Chapter Six.

Chapter Two
Literature Review

2.1. Introduction

Plants are known to respond to seasonal changes in the environment, which are referred to as phenological responses. The processes of germination and reproduction, associated with such responses, of which flowering is one, are a set of life history traits that have a significant influence on the reproductive success of any given plant species (Bishop and Schemske, 1998). According to Bishop and Schemske (1998) flowering phenology in particular plays a significant role in determining reproductive synchrony with potential mates, pollinators and the utilisation of available resources, which often also vary on a seasonal basis. Similarly, Bawa *et al*. (2003) also affirms that timing, duration and frequency of flowering are important in the reproductive success of plant species and often defines observed flowering patterns. It is therefore important to understand how different aspects of the environment influence the distribution and reproduction processes of flowering plant species.

This chapter reviews the factors that may determine either the distribution of plant species across geographic ranges, or the onset and duration of flowering species, or both. These factors are discussed under the broader context of the principles of macroecology. The timing, duration and frequency of flowering are seldom determined by a single factor, but rather a group of factors that act jointly. Therefore it is important to note that the aspects covered in this chapter are all inter-linked to one another. Furthermore, the effects of the changes in climate and increased biological plant invasions are also considered, by discussing the possible responses of flowering plant species to these changes.

2.2. Macroecology

Macroecology forms the meeting point of the fields of ecology, biogeography, palaeontology and macroevolution, where it is used to answer a broad range of ecologically related questions (Blackburn and Gaston, 2006). This field of research may be described simply as a way of studying the relationships between organisms and how these organisms interact with the

immediate and surrounding environments on a large spatial and temporal scale (McGill and Collins, 2003). These interactions give rise to statistical patterns of abundance, distribution and diversity of these organisms (Blackburn and Gaston, 2006). Additionally, Marquet (2002) states that macroecology considers the principles which underlie the diversity and variability of ecological systems. Macroecology investigates the empirical and mechanistic processes which complex ecological systems produce (Brown, 1999).

According to Kent (2005), macroecology may be considered similar to biogeography, as it also identifies and aims to explain patterns of species distributions, but at different scales. The two most important patterns that are studied in both macroecology and biogeography are species abundance distributions and the species-area relationships (McGill and Collins, 2003). These patterns may be identified in individual organisms within species, or for species within communities or biogeographical regions (Blackburn and Gaston, 2006). The large scales that are often considered in such studies correspond to national, regional, continental and global scales (Kent, 2005). However, Blackburn and Gaston (2002) argue that biogeography looks at finding and understanding patterns of biodiversity, whereas macroecology focuses on the interactions between organisms and the environment.

McGill and Collins (2003) suggest using a unified theory of macroecology, whereby the numerous macroecological patterns that are identified on a statistical level are explained by the presence of common, large-scale processes that occur in nature. Ecology, however, is more complex, as there is generally more than one process, therefore giving rise to a number of unified theories, which may apply to different spatial scales (McGill and Collins, 2003).

The variables often considered are abundances, geographic range sizes, and body size values characteristic of species. These variables are rarely independent, and usually have interspecific correlations (Gaston and Blackburn, 1996a). Various relationships have been identified. For example, the more abundant a species is, the broader its geographic range. Other relationships include that large-bodied animals are less abundant than medium- or small-bodied species, and that large-bodied species have greater geographic range sizes than smaller species (Gaston and Blackburn, 1996a). Some of the macroecological studies that have observed these patterns cover a small spatial scale. However, as Gaston and Blackburn (1996a) state, using these relationships and dynamics seen between local and regional structures and species assemblages, it is also important to develop an understanding at

moderate to larger spatial scales. The understanding of such structures, of which species abundances, spatial distributions and body sizes are fundamental, will provide evidence that scale does have a significant effect on the different types of interactions (Gaston and Blackburn, 1996a).

2.3. Geographic range size determinants

Geographic range size is the area where individual species are described or known to exist and may be quantified as the sum of the areas or regions in which the species is defined (Gaston, 1991). In the fields of biogeography and ecology, geographical range size is a fundamental concept that forms the basis of many research questions (Brown *et al.*, 1996). Numerous studies investigate the spatial patterns and associated relationships, processes and shifts over time, relevant to geographic ranges, as well as the size of the ranges, for individual or multiple species. According to Brown *et al.* (1996), species' range sizes vary by orders of magnitude. Many studies which have aimed to determine the variation of plant distributions compare widespread and rare species (Lowry and Lester, 2006).

There are a number of ecological and evolutionary processes which can be invoked to explain variation in range size, including dispersal and establishment abilities, climatic and environmental tolerances, habitat availability, niche breadth, population abundance and colonisation-extinction dynamics, amongst others (Gaston 1996; Brown *et al.*, 1996). According to Gaston (1994), range size can also be viewed as a measure of rarity, which is used and applied in areas of high conservation priority. This makes range size of an individual species and the variation of range sizes and distributions amongst various species critical (Gaston, 1994). There are a number of extrinsic and intrinsic factors that determine geographic range size. Factors such as latitude, altitude, climate and resource availability are all considered extrinsic factors, whereas factors that are intrinsic include dispersal ability, body size (which, in the case of plants, can be either stature, or, more relevant to dispersal, seed size), niche breadth and genetic and phenotypic plasticity. These factors never work independently in determining the geographic range size of a species. Therefore; understanding processes that determine the distribution of species across spatial scales, and particularly the way they interact, are important as they may be used to effectively conserve plant species or ecosystems that are under threat (Kolb *et al.*, 2006).

2.3.1. Latitude and altitude

The spatial distribution of species across latitude and altitude is well known in biogeography. More particularly, species richness is known to increase with decreasing latitude and altitude (Stevens, 1989). According to Stevens (1989) however, in terrestrial environments, species range size tends to decrease with decreasing latitude and elevation. This is known as Rapoport's Rule, which more precisely states that there is a positive correlation when the 'latitudinal extent of the geographical range of an organism occurring at a given latitude is plotted against latitude' (Stevens, 1989: 240). Patterns identified by Rapoport's Rule are those where the range size of a species is measured as the latitudinal, elevational or depth range of the species' distribution (Brown *et al.*, 1996). These patterns may be a result of the climatic conditions organisms encounter along a particular geographical gradient (Stevens, 1992).

Elevation and latitude have also shown to have an effect on flowering phenology, particularly with rapid changes in climate. Crimmins *et al.* (2008) looked at the changes in blooming time of various plant species, across an elevation gradient. Their study focused on the range shifts and phenological changes of numerous plant species across an elevation gradient of 1200m over a period of 20 years. Almost a quarter of the species studied displayed a significant change in the elevation at which they flowered and shifts in range size, particularly at higher elevations (Crimmins *et al.*, 2008). However, no indications relevant to changes in flowering period were made.

Similarly Cornelius *et al.* (2012) considered the sensitivity of species due to climatic changes over an altitudinal gradient, with a focus on shift in flowering phenology. Data were collected annually for a number of years, at the same time, in the alpine ecosystem (Bavarian Alps). An average change of 3.8 days for every 100m in altitude for the onset of flowering was reported (Cornelius *et al.*, 2012). This would ultimately result in there being a six day delay for a 1ºC increase in temperature. The length of flowering had therefore also shifted across the altitudes. Flowering of very-early and very-late season flowering species was shorter, but species flowering in mid-season had a longer flowering period, particularly at higher altitudes. However, Cornelius *et al.* (2012) found that temperature was not a significant factor in the shift in the flowering length.

On the contrary, Ranjitkar *et al.* (2012) examined the flowering duration and synchrony of three *Rhododendron* species, across elevation at two sites in the Eastern Himalayas. This study was also carried out over a number of flowering seasons. The data showed a high synchrony in flowering across the elevation gradient, particularly during peak flowering. Ranjitkar *et al.* (2012) suggest that these *Rhododendron* species are likely to favour increases in global temperature, as this aided flowering onset and peak flowerings. This could result in the increase of the geographic ranges of these species across various elevation gradients. It is evident from these studies that latitude and elevation, together with other factors such as climate can have a significant effect on changes of range size and phenological events in some plant species.

2.3.2 Climate

The climatic conditions have a great influence on the range that the species occupy, particularly in plant species. Conditions such as humidity, precipitation, evapotranspiration and temperature are amongst the most important climatic factors that determine range size (Stevens, 1992). Amongst these, temperature may be considered to have the most significant influence. According to Woodward (1990), lower temperatures control the life cycle of plants by means of three mechanisms. The first is by limiting the rate of a particular process occurring within the plant, the second by cooling the plant below a non-lethal threshold temperature of a process and lastly, by cooling the plant into the lethal temperature range (Woodward, 1990). These mechanisms are believed to limit the distribution of plant species or particular vegetation types, therefore affecting the distribution ranges within which the species occurs (Woodward, 1990).

Changes in temperature or climate can result in a variation of a species' geographic range. However, this may not necessarily change the size of a geographical range, but instead shift it to an area which was previously not occupied by the species. Davis and Shaw (2001) who investigated the response and range shift of woody species during the Quaternary found that trees began to occupy higher latitudes, which they previously did not occupy, towards the end of the last glacial interval. This extension or range shift occurs through passive seed dispersal, whereby seedlings establish in new regions where suitable conditions occur (Davis and Shaw, 2001).

The effect of climate and the recent interest in response to climate change is far more detailed than mentioned, and will be discussed further on in a separate section.

2.3.3 Resource availability

In plant ecology, the observed patterns of species richness and distribution are influenced by various environmental gradients. These include the resources available for utilisation by the plant in order to establish, grow, reproduce and disperse. The variation of such resources, known as resource gradients, can also define the geographic ranges of plant species (Gaston, 2009). Resource gradients also determine the spatial distribution and diversity of species growing in a particular area (John *et al.*, 2007). Range expansion as a result of resource availability may be seen amongst invasive species. Alien species that are introduced into new environments may be able to rapidly spread across a geographic range due to the niche availability, but also due to the availability of abundant or suitable resources (Blumenthal *et al*., 2009). Blumenthal *et al.* (2009), further state that many introduced species are likely to adapt to higher resource availability, whether it be increased water availability or soil nutrients, such as nitrogen. The range size expansion of these species is also due to some alien species not having any natural enemies in the introduced environment. However, when introduced species adapt to higher resource availability, the metabolic rates of the species increases, allowing it to reach reproduction maturity more rapidly, which can make the overall plant tissues become weaker, than what it may be in its native range (Blumenthal, 2005). This can increase the species susceptibility to pathogens or herbivory, which may eventually curb the rapid range size expansion of species. This strategy is therefore being employed as an effective tool to reduce the impacts of invasive alien species in many environments.

On a similar basis, resource limitations may also determine the geographic range of species. According to Gaston (2009) and Price and Kirkpatrick (2009), the limitation of resources generally leads to interspecific competition amongst species which results in the limitations of geographic range sizes. Furthermore, the interaction of species amongst different trophic levels also influences the geographic ranges of species, as certain species serve as resources to others in terms of predation (Gaston, 2009). Therefore the distribution range of the enemy or consumer is assumed to fall within or around the species on which it depends and hence limits the range of both the consumed species and the dependent (Gaston, 2009). On the other hand,

the consumer may only limit the distribution of the species which it feeds on (i.e. the resource), as predation is also known to limit the extent of a geographic range (Price and Kirkpatrick, 2009). However, competition and predation might be considered to be intrinsic factors that determine the geographic extent of a species.

2.3.4. Intrinsic determinants

As previously mentioned, latitude; altitude; climate and resource availability are all considered extrinsic factors or environmental tolerances that determine geographic range. Additionally, there are many intrinsic factors that also explain the geographic range size of many species. These include niche breadth, body size, dispersal ability, population abundance, genetic diversity and phenotypic plasticity (Lester *et al.*, 2007).

2.3.4.1. Dispersal ability

Dispersal ability is commonly associated with a species' range size. This has been illustrated amongst insects, plants and other terrestrial and marine organisms (Lester *et al.*, 2007). Furthermore, Lester *et al.* (2007) suggests that there is both an ecological and evolutionary perspective to understanding why dispersal ability has an effect on range size. From an ecological perspective, it may be considered as a life-history trait, which determines population dynamics and colonisation, whereas the evolutionary viewpoint may be that dispersal affects the rate of local adaptation, speciation and extinction, through the flow of genes (Lester *et al.*, 2007). According to Nathan and Muller-Landau (2000), the dispersal of seeds in plants species is one of the key processes that determine the spatial structure of plant populations, therefore also determining the range size occupied by a plant species.

Thompson *et al.* (1999) and Lester *et al.* (2007) hypothesise that there are three different reasons for a positive correlation between dispersal ability and range size. The first is that species may have low dispersal ability or are geographically restricted, and therefore cannot expand over a greater range of suitable areas. Secondly, species may have small geographic ranges because the cost of dispersal is too high or that it is not beneficial to the survival of the species. Lastly, species that have low dispersal ability may have lower gene flow due to geographic isolation, therefore increasing chances of speciation; species with low dispersal

ability may have smaller ranges because there is insufficient time to expand; therefore temporal issues need also be considered important.

Morin and Chuine (2006) studied 234 temperate/boreal tree species and showed that dispersal ability may not be correlated to the geographic range size of species on a global scale, but rather only at regional and local scales. This is supported by a study done by Seidler and Plotkin (2006), where seed dispersal and spatial patterns of numerous tree species were considered in Panama. A significant relationship was found between dispersal and spatial patterns. However, when considering the dispersal ability of plant species, dispersal is also dependent on seed size and dispersal mode, as most plants have multiple dispersal agents (Seidler and Plotkin, 2006; Nathan and Muller-Landau, 2000). These dispersal agents may either be biotic or abiotic. Biotic agents range from insects, birds, mammals or other animals and abiotic agents include wind or water.

2.3.4.2. Body and seed size

Seed size with regard to most plants is also vital in determining how far a species may be dispersed. In the case of animals, the relationship between body size and geographic range size is generally a positive one (Gaston and Blackburn, 1996b). Therefore, the larger the body size of the animal the larger the range the animal species covers. Furthermore, Gaston and Blackburn (1996b) state that the range size occupied by a species tends to increase with body size, therefore suggesting that smaller species can be found in a variation of range sizes, whereas larger species only have large ranges.

In plants, the size of the plant and the geographic range are not necessarily positively correlated. Some ecologists take into consideration the seed size or seed mass and its relationship to the geographic range size. The size and the mass of seeds determine how far the seeds may travel during a dispersal event, depending on the dispersal agent (Westoby *et al.*, 1996). Jakobsson and Eriksson (2000) state that smaller seeds have a greater chance of being dispersed, as lighter, smaller seeds tend to disperse readily by wind. Westoby *et al.* (1996) found that seeds with a mass below 0.1mg tend to be unassisted during dispersal, but seeds above 100mg are dispersed by vertebrates. In many cases, plant species with smaller seeds are more likely to be dispersed over a greater distance, as lighter seeds would travel further, therefore allowing the species to occupy a greater range size (Westoby *et al.*, 1996).

Smaller mass may also allow for both unassisted and vertebrate assisted dispersal to take place.

Furthermore, Moles and Westoby (2006) suggest that seed size may also determine the resilience and success of establishment of the species once it has been dispersed. Larger seed may not be dispersed as readily as smaller seeds, but may be able to withstand hostile conditions, such as shade, drought and competition, therefore increasing the chances of establishment, whereas smaller seeds stand less chance of success (Moles and Westoby, 2006). However, due to the trade-off between seed size and seed quantity, smaller seeds tend to be associated with higher fecundities. Thus, the relationship between seed size and the geographic range size is dependent on various biotic and abiotic factors.

2.3.4.3. Niche breadth

The niche breadth of a species also determines geographic range size. A niche is a set of environmental conditions in which an organism, whether animal or plant, is able to persist. Williams *et al.* (2006) note that the broader the species ecological niche, the more widespread and locally abundant the species is, due to the fact that the species is able to adapt to a number of different (micro) environments and habitats. This therefore gives rise to a larger geographic range, in comparison to a species with a smaller niche breadth, which has specific requirements to establish itself. Furthermore, Williams *et al.* (2006) identify two reasons for the positive relationship between niche breadth and geographical range size. The first is that geographically restricted species produce specialised traits as an adaptation to local conditions, and consequently cannot have a broad niche. Secondly, species with a broader geographic range have access to a variety of resources, therefore allowing more generalised traits to occur, and a broader niche to be occupied.

This is supported by Köckemann *et al.* (2009). This study examined the relationship of range size and niche breadth, based on previous studies showing a positive correlation. Köckemann *et al.* (2009) looked specifically at the range of 25 tree species in central Europe. Using variables related to the soil and temperature across a variety of niches, Köckemann *et al.* (2009) found a significant relationship to the range size of the tree species. The relationship between abundance and niche breath, however, did not yield any significance.

2.3.4.4. Genetic diversity and phenotypic plasticity

Genetic diversity and phenotypic plasticity may also be considered determinants of geographic range size in plants. In most cases these relationships are highly complex, being mediated by life-history traits. Gitzendanner and Soltis (2000) studied the associated patterns between rare and widespread congeneric plants. It has been suggested that rare species, which are known to have limited range sizes, have little or limited genetic variation, in comparison to widespread plant species. On the other hand, it has been argued that rare species which have large localised populations may have high levels of genetic variation (Gitzendanner and Soltis, 2000). Studies which have focused on the correlation between genetic diversity and geographic range have identified significant relationships at both species and population levels. However, in some cases phylogenetics is not taken into account (Gitzendanner and Soltis, 2000). Despite this, results from studies which did use phylogenetic data have not yet disputed that there is a correlation between geographic range and genetic variation (Silvertown and Dodd, 1996 and Gitzendanner and Soltis, 2000).

Similarly, Pohlman *et al.* (2005) examined the phenotypic plasticity of narrowly and widespread distributed *Acacia* species in eastern Australia. Plant species which have a greater phenotypic plasticity range have genotypes that tend to respond more efficiently to changes in environmental conditions, allowing for these species to successfully adapt to a wide range of habitats and environments (Pohlman *et al.*, 2005). Therefore it is hypothesised that widespread species have far greater phenotypic plasticity than narrowly distributed species, as widespread species are more likely to occupy a range of different environments. Results from Pohlman *et al.* (2005) indicated that physiological traits of the *Acacia* species studied had greater phenotypic plasticity than allocated traits. The results also supported the hypothesis that widespread species have greater phenotypic plasticity than narrowly distributed species.

2.4. Determinants of flowering period length

Like most living organisms, plants transition through different phases in a life cycle. One of the most important transitions in plants is from vegetative growth to flowering (Amasino, 1996). The processes that initiate flower development and timing of flowering are critically important for the plants success in reproduction, seed development and dispersal (Amasino, 1996). The timing and length of flowering, known as flowering phenology, varies greatly

amongst species and only occurs in the optimal environmental conditions in which the plant grows and adapts to (Amasino, 1996 and Reeves and Coupland, 2000). There have been many studies carried out which have aimed to determine and explain the different aspects of flowering phenology. Many intrinsic and extrinsic environmental factors initiate flowering, which essentially determine the length of a flowering period.

2.4.1 Seasonality and physiology of flowering

Plants have evolved to flower during a particular time of the year or during a particular season (Amasino and Micheals, 2010). The timing or onset of flowering is crucial to the reproductive success of most plant species and is considered a life-history trait. The seasonality of flowering allows the plant to take maximum advantage of favourable environmental conditions, which results in a chance of higher reproductive success (Amasino and Micheals, 2010). According to Amasino (2010) there are two different types of processes that operate independently to determine the initiation of flowering. The first being environmental cues, such as changes in temperature, and the second being endogenous cues, which include the shift from juvenile to adult stages. Murtas and Millar (2000) also refer to the biological rhythms that allow nature to keep time. Plants, like many other organisms have adapted to follow a circadian clock, which covers a period of one day (Murtas and Millar, 2000). These rhythms are also associated with temperature and light.

2.4.1.1 Temperature

The most widely discussed and understood environmental cues that are known to regulate the seasonality of flowering are the change in temperatures and the shift in the daily light period or day-length, across the different seasons (King and Heide, 2009). According to Penfield (2008), a slight change in temperature can result in a range of significant responses in plants. However, the rate of response varies amongst plant species. Response time may be a few hours to a few weeks. Furthermore, the variation of both high and low temperatures are important in the survival and development of plants (Penfield, 2008). Many species are exposed to extended periods of cold temperatures, known as vernalization, which facilitates flowering in many plant species (Amasino, 2010). One of the most widely studied plant genera, with regard to flowering physiology, is *Arabidopsis*. Vernalization is important in the

flowering process of *Arabidopsis* species and is identified to prevent flowering in autumn, but permits flowering to occur during the spring season (Amasino, 2010).

However, uncharacteristic variation of temperatures during autumn can occur. In this case, it is important that plants which required vernalization do not experience a short period of low temperatures at the beginning of autumn and then a period of warm temperatures, as this may result in these plants flowering at the start of winter (Amasino, 2010). Vernalization ultimately relies on plants detecting the period for which temperatures are lower than usual.

Kang and Jang (2004) found that flowering duration is highly dependent on flowering season of a species. Kang and Jang (2004) studied numerous Korean angiosperms, specifically collecting data on the flowering patterns of these species. The results reflected that flowering duration was not correlated to temperature and precipitation but rather to season and taxonomic influences of the species. Furthermore, the majority of the angiosperm species had longer flowering periods in summer and autumn, not spring (Kang and Jang, 2004). Therefore temperature is likely to only have a significant influence on the initiation of flowering, rather than on the duration.

Additionally, variations in temperature may trigger other responses in addition to flowering (Penfield, 2008). One of these is bud dormancy, which according to Battey (2000), is significant to flowering time in some species. Battey (2000) focused his study on temperate trees in the Northern Hemisphere, and identified that bud-dormancy occurs once flowering has been initiated. The process of flowering is typically halted due to a decrease in photoperiod together with nutrient stress, changes in light intensity and temperature and other endogenous factors (Battey, 2000). Buds are formed prior to the harsh environmental conditions, and continue to form and flower once environmental conditions, such as photoperiod, are favourable once again.

2.4.1.2 Photoperiod

Fluctuations in the period or length of time that the plant is exposed to light, together with changes in temperature, trigger flowering responses (Searle and Coupland, 2004). This was first discovered by Garner and Allard (1920). The daily light period or photoperiod that plants are exposed to has also been studied extensively. The changes in day-length are experienced

over the majority of the surface of the earth, and are therefore recognised as a reliable cue for the onset of flowering (Amasino and Micheals, 2010). The response to the changes in the length of the day is more recognised amongst plants in temperate regions, as seasonal changes are more distinct (Mouradov *et al.*, 2002; Tooke and Battey, 2010). The fluctuations of the photoperiod are detected by the leaves, whereby a stimulus moves from the leaves to area the where flowers are initiated (meristem; Öpik and Rolfe, 2005). However, Öpik and Rolfe (2005) state that the stimulus given by the leaves and the response to this signal can vary from species to species.

Garner and Allard (1920) recognised a range of responses to different photoperiods, including short-day plants (SDPs) and long-day plants (LDPs). Short-day plants flower when the night length exceeds a certain period, and long-day plants flower as the day-length increases (Amasino, 2010). *Arabidopsis* has again been the focus of many studies, as it has been found to have one of the greatest responses to the changes in day-length (Searle and Coupland, 2004). *Arabidopsis* is a long-day plant, as it is more likely to flower when the critical photoperiod has been reached (Amasino and Micheals, 2010). However, *Arabidopsis* is known to flower earlier when 16 hour day-lengths are experienced in comparison to day-lengths of approximately 8 hours (Reeves and Coupland, 2000).

King and Heide (2009) studied the flowering times of Australian perennial grasses at different latitudes over an extended period using previously collected data. Results showed that species either flowered when day-lengths were either shorter or longer than a critical length (which is the period of daylight measured by the daylight time required for a given species to initiate flowering; Öpik and Rolfe, 2005). Species in high latitudes tend to be long-day plants, whereas in low latitudes species displayed short-day plant characteristics (King and Heide, 2009). In low latitude (tropical) regions, there is little seasonal difference in day-length. However, King and Heide (2009) found that perennial grasses in tropical areas in Australia were very precise in detecting day-length and hence flowered in response to shorter days.

Another interesting aspect of variations in flowering times is between annual and perennial plants (described by Battey, 2000). In annuals, the initiation of flowering is followed directly by the appearance of the flower. However, in perennials there is a lapse (lag) in time between the initiation of flowering and the appearance of flowers.

Photoperiod is largely influential on the initiation of flowering and little is understood about the role it has in the flowering duration. However, Amaducci *et al.* (2008) investigated flowering durations of monoecious and dioecious varieties of hemp. Amaducci *et al.* (2008) concluded that flowering duration was dependant on both genotype and sowing time, but it also suggests the importance of photoperiods in the initiation of flowering as it may affect flowering durations.

The timing of flowering is evidently influenced by seasonality and physiological changes within a plant. However, the variations of flowering times amongst plant populations are not thoroughly explained through endogenous and environmental factors. Ollerton and Lack (1992) suggest that flowering variations amongst individuals in a population are a result of natural selection. However, pollinator activity and availability also plays an important role in determining flowering time and duration.

2.4.2. Pollinator availability

The success of reproduction in plants is not entirely the result of genetic background and abiotic environmental factors, but also the interactions between plants and pollinators. Pollination occurs during the flowering period of a plant, when pollen is transferred from the anther of one individual to the stigma of another (or the same) individual of the same species (Öpik and Rolfe, 2005). There are a numerous modes for pollen to be transferred. These include the wind and living vectors, such as vertebrates and insects, known as pollinators (Öpik and Rolfe, 2005). The floral traits of a plant species are important in attracting the right pollinator or pollinators. The relationship between plants and pollinators has been studied extensively from population to community level (Kearns and Inouye, 1997).The process of pollination plays an important role in flowering patterns, as the activity of pollinating agents, such as bees, may have seasonal variations, much like flowering (Stevenson *et al.*, 2008). However, the effect of pollinator availability on the duration of flowering is somewhat poorly understood.

Ramírez (2006) notes that factors such as climate; life form; flowering time and habitat structure, determine the distribution of both flowering plant species and pollinators. This suggests that flowering phenology may potentially determine the abundance of pollinators, particularly in areas where seasonality is easily distinguishable. However, according to

Elzinga *et al.* (2007), pollinators are only attracted to flowering plants once certain densities of flowers are in bloom. Elzinga *et al.* (2007) suggests that the onset of flowering is likely to depend on the synchronicity of an individual plant and its neighbours, when the pollination process is dependent on flowering density. In plant populations of lower flowering densities, greater variation in flowering phenology may be seen (Elzinga *et al.*, 2007). Similarly, many studies have identified the increase and decrease of pollinators according to the abundance of flowers in a given population that has varied plant species (Stevenson *et al.*, 2008). Elzinga *et al.* (2007) therefore suggest that the variation of the onset of flowering or peak flowering times does not only depend on a phenotypic variation, but also on the length of the flowering period.

Waser (1979) specifically examined the correlation between pollinator (hummingbirds) availability and the initiation of flowering of a perennial shrub *Fouquieria splendens* in Arizona. Waser (1979) stated that if through evolutionary history, plants are able to detect changes in temperature and photoperiods to induce flowering, then surely natural selection has allowed for plants which are animal-pollinated, to flower during a period when the respective pollinators are abundantly available. Furthermore, Waser (1979) notes that this type of occurrence is more noticeable when specific pollinators appear at a certain time during a season in order to visit an individual plant species which experiences little or no competition, as this can alter the flowering time. The hummingbird migration to southern Arizona is relatively short, lasting no more than a few weeks. During this time the hummingbird population forage predominantly across the entire range of *F. splendens*. Hummingbirds, together with bees are the primary pollinators of *F. splendens* in southern Arizona. However, in some cases flowering did not coincide with the hummingbird migration. Despite this, Waser (1979) believes that there it is possible for flowering periods and pollinator abundance hummingbirds to synchronize.

In most plant communities, a relationship between flowering period and pollinator abundance may not be evident, due to the variation of species occurring in one area. In this circumstance, different plant species may be flowering at the same time during the season, therefore competing for available pollinators, or may flower asynchronously to avoid the competition (Brown *et al.*, 2002).

Levin and Anderson (1970) considered how plants compete for the same pollinators when flowering simultaneously. In most cases when plants compete for resources such as light, moisture or nutrients, the weaker species is excluded. The competition for pollinators amongst plants determines the reproductive success of the species. Many plants can have the same flowering period and be pollinated by the same animals or insects, resulting in competition, therefore making floral signals and the availability of pollen and nectar significant in the success of the species (Levin and Anderson, 1970). It is advantageous for plants to meet the preferences of the pollinator, as this allows the pollinator to reduce the energy spent on searching for food sources (Levin and Anderson, 1970). However, these preferences are subject to change according to the abundance of the pollen or nectar reward, as well as the abundance of the flowering species. On a similar basis, O'Neil (1999) suggested that pollinator visits may increase in a specific area where the number of flowering plants increases, resulting in pollinator competition and possibly fewer visits by pollinators to individual plants. Levin and Anderson (1970) suggested that flowering plant species that compete for pollinators may be closely related or taxonomically remote, and may have similar floral structure or very distinct and different structures.

Competition for pollinators may also be seen between invasive and native plant species and this has frequently been studied. Brown *et al.* (2002) found that the invasive species *Lythrum salicaria* reduced both pollinator visitation and seed set of the native species *Lythrum alatum*. The possible explanation for the shift in pollinator visitation was that, *Lythrum salicaria* had larger floral structures with more flowers on displays. The pollinators were also found to move regularly between the invasive and native species, which may have also reduced the quantity and quality of the pollen in the native species (Brown *et al.*, 2002).

The correlation between pollinator availability and competition, in influencing the onset and duration of flowering is not frequently studied and hence is poorly understood. Kochmer and Handel (1986) make brief reference to the influence that phylogenetics may have in determining flowering phenology at a community level in comparison to competition between pollinators. In addition, Kochmer and Handel (1986) proposed that if pollinator competition occurs in flowering plant communities, it may assist in fine-tuning the flowering time and length within the phylogenetic constraints of various plant species.

2.5. Effects of plant invasion and climate change on flowering period

Recently, biological invasions and climate change have become the focus of many ecological studies (Ward and Masters, 2007). There is evidence that both biological invasions and changes in climate can alter the dynamics of complex ecological systems (Thuiller, 2007). The smaller changes at community levels are likely to cause greater global changes, which is of particular interest to many scientists. However, it may be important to understand the changes at the community levels first, before understanding the changes that may be seen on a global level. One of the aspects that are known to be altered due to biological plant invasions and climate changes is flowering phenology, therefore having an effect on both flowering time and the flowering period.

2.5.1. Biological plant invasions and flowering periods

Biological plant invasions in terrestrial ecosystems by non-native plants has been of growing concern, as these invasions may have significant impacts on native species composition, by altering ecosystem properties, processes and overall functioning (Goodwin *et al.*, 1999; Lloret *et al.*, 2005 and Castro-Díez *et al.*, 2011). Humans have broken down geographical barriers, therefore allowing long-distance dispersal to take place (Dukes and Mooney, 1999). These dispersal events, if not monitored, assist the invasion process, whether the introductions of the non-native species are accidental or intentional. Many introduced alien plants are kept under cultivation by humans, therefore aliens which survive outside cultivation are termed 'casual aliens', but when an alien species maintains a population outside of cultivation it is termed as a 'naturalised alien' (Prinzig *et al.*, 2002). However, 'invasive aliens' are those species which are able to spread across the region in which it was introduced (Prinzig *et al.*, 2002).

Many scientists have looked at identifying the traits of many successfully naturalised and invasive alien plant species (e.g. Pyšek *et al.*, 2009; Küster *et al.*, 2008), flowering period being of special interest here, as invasion, is in fact a form of range expansion. An example of this is a study by Goodwin *et al.* (1999), who compared the traits of species which came from Europe, that were now invasive in Canada, to congeneric species in Europe which have not invaded Canada. Both woody and herbaceous species were considered, as well as accidentally and intentionally introduced species (Goodwin *et al.*, 1999). Congeneric species, one being invasive and the other non-invasive, were paired and traits compared. The three main

characteristics that were looked at were life-form, stem height, and flowering period (Goodwin *et al.*, 1999). The geographic range of all the invasive and non-invasive species in Europe was also taken into account. Results showed a significant difference in stem height and flowering period between the majority of invasive and non-invasive congeneric pairs. However, these were viewed as poor indicators of invasive ability (Goodwin *et al.*, 1999). Life form showed no significant effect on invasibility between invasive and non-invasive congeneric species. However, indigenous geographic range showed significantly influenced invasiveness. This study suggested that species which have a greater geographic range size or wider distribution across different habitats have a greater chance of invading new environments, due to having better environmental tolerance. Therefore it is important that other ecosystems properties need to be considered when identifying species traits. Furthermore, Goodwin *et al.* (1999) found that geographic range was significantly correlated to flowering period, suggesting that flowering period may affect invasiveness. There have been many studies similar to this, which have focused on the successful invasive plant traits and in many cases flowering period was taken into consideration (Lloret *et al.*, 2005; Pyšek and Richardson, 2007 and Pyšek *et al.*, 2009).

As briefly mentioned previously, one of the main concerns that have arisen from continuous successful invasion events is how alien invaders alter ecosystem properties and processes, and how it can potentially change the overall functioning of an ecosystem (Ward and Masters, 2007). Some changes that may be observed, include changes in vegetation composition and structure, species richness, soil nutrients, water availability, fire regimes, as well as the timing and duration of flowering, which is often found to be longer for the successful invasive species than the native congener (Davis *et al.*, 2000; Barrett *et al.*, 2007). Alternatively, alien species may adapt their flowering times, which allows invasions to be more successful. For example Godoy *et al.* (2009) studied the flowering phenology of invasive alien species and congeneric native species in three Mediterranean-type ecosystems, namely Spain, California and South Africa's Cape region. Similar to Goodwin *et al.* (1999), pairs of alien invasive species and related indigenous species were compared based on several characteristic flowering traits. Results showed that the invasive alien species had different flowering phenologies to native species across the three regions (Godoy *et al.*, 2009). Flowering times of the alien species were dependent on both the climatic regimes in the native range and the species composition in the invasive range. Godoy *et al.* (2009) found that invasive species that were native to temperate climates flowered earlier than native species, in the Cape region.

In Spain the majority of invasive species were originally from tropical climates, flowered later than the native species. In California the invasive species were predominantly from Mediterranean-type climatic regions and this resulted in flowering to take place at a similar time to the native species (Godoy *et al.*, 2009). These authors concluded that these results showed that flowering is a conservative trait that evolves according to climatic regimes. However, these data may be used to determine the duration of flowering of alien species according to the type of habitat that is being invaded.

2.5.2. Climate change and flowering periods

Plants are generally known to be responsive to changes in seasonality across the respective environments. Changes in climate have resulted in shifts in behaviour and development of birds, plants, amphibians and insects, and there is growing evidence that there have been major shifts in plant activity, due to the global environmental changes (Fitter and Fitter, 2002; Cleland *et al.*, 2007). Phenological responses, particularly in plants at community level, are the most detectable and widely covered in terms of available data (Miller-Rushing and Primack, 2008). However, changes in animal behaviour may also have an effect on flowering time and period, as pollinator activity and dispersal agent activity is altered, specifically with regard to seasonal pollinators and dispersers (Fitter and Fitter, 2002). In some cases, changes may only be observed in a single species, which can have an effect on many other species (Miller-Rushing and Primack, 2008). The changes that an ecosystem may undergo are often a result of the shifts in temperatures on a global level and changes in precipitation patterns, which are likely to modify flowering phenology, especially in arid regions (Franks *et al.*, 2007).

Many studies have illustrated shifts in flowering phenology, due to climatic changes. Fitter and Fitter (2002) observed rapid changes in the British flora over a short period of time. Fitter and Fitter (2002) looked at available data from a single locality in south-central England, over a period of 47 years. Over the last decade of the collected data, on average, flowering has advanced by 4.5 days in comparison to the previous decades (Fitter and Fitter, 2002). Approximately 16% of the species studied flowered earlier than previously recorded and only 3% flowered later than earlier records. Fitter and Fitter (2002) suggest that climatic changes are one of the predominant biological response signals, as flowering responses are extremely sensitive to temperature in the months prior to the onset of flowering, particularly in spring-

flowering species. Furthermore, Fitter and Fitter (2002) found that annuals and insect-pollinated species are likely to flower earlier than perennials and wind-pollinated species, respectively, as a result of climate change.

Similarly, Miller-Rushing and Primack (2008) studied changes in flowering time in Concord, Massachusetts, USA. These changes were examined over a greater period of time, and additional data collected by two other naturalists were utilised. Miller-Rushing and Primack (2008) deduced that the mean annual temperature in the region had increased by 2.4ºC due to global climate change and urbanisation. Common species found in the area, on average began flowering seven days earlier than the first recorded data used. In addition, Miller-Rushing and Primack (2008) mentioned that summer-flowering species in comparison to spring-flowering species displayed more variation on an inter-annual basis. However, the flowering time of spring-flowering species showed a greater correlation to the mean monthly temperatures. Similarly Giménez-Benavides *et al.* (2011) investigated the changes in the onset of flowering and duration of flowering in some Mediterranean high-mountain plants. The summer droughts experienced made the flowering patterns observed amongst these plants different from other high altitude plants. Two high mountain species were used and it was assumed that the late-flowering species was likely to have a more successful flowering and reproduction stages. However, the outcomes Giménez-Benavides *et al.* (2011) found were unexpected, as the species with an early onset of flowering, flowered for a longer duration than the late onset flowering species. The early onset flowering species was also found to be linked to the plant fitness (Giménez-Benavides *et al.*, 2011). Thus, late onset flowering species are at risk as temperatures get warmer and there are seasonal shifts.

One of the many fears of global climate change is the loss of biodiversity. There is evidence that rapid change in climate may result in a decline in the number of species and possibly phylogenetic diversity. In this light, Davis *et al.* (2010) examined the phenological responses of plants as a result of climate change. Additionally, the phylogenetic relatedness of the species studied was taken into account. The results indicated that the phenological responses to climate changes amongst closely related species are similar, even in communities that are geographically separated from one another (Davis *et al.*, 2010). Analyses such as this illustrate that by incorporating a phylogenetic perspective in studies, it can provide important information and insight to predict the responses of various plant and animal species to climate change, in future studies, especially those focused on phenology (Davis *et al.*, 2010).

Another suggested reason for the decline in plant species relates to the changes in pollinator-plant interactions, which are also altered by climate change. Burkle and Alarcón (2011) indicate that, together with plants predominantly flowering earlier, rising temperatures are also correlated with earlier activity amongst insects, which act as pollinators for many plant species. Furthermore, the changes in activity experienced amongst these pollinators seems to be greater in comparison to plants, which may potentially result in mismatches in pollinator-plant interactions. This may create competition, but more importantly, reduce the success of reproduction in plant species, therefore resulting in a decline in species numbers (Burkle and Alarcón, 2011). Climate change can evidently have dire effects on ecosystems at various levels, therefore making the use of model predictions an essential tool in preventing species decline and loss (Wolkovich *et al.*, 2012).

2.6. Flowering phenology in South Africa

There is high diversity of flowering plant species in South Africa, with many studies concentrating on the highly rich Cape Floristic Region (Linder *et al*., 2010). Flowering phenology studies in southern Africa have either concentrated on specific genera or species (Dreyer *et al*., 2005; Botes *et al*., 2008) or in specific areas in South Africa, such as Namaqualand (Steyn *et al*., 1996; Cowling *et al.*, 1999) and the Cape Floristic Region (Johnson, 1992). However, no studies in South Africa have identified links between the flowering duration and the distribution of endemic species. This study is therefore innovative in the context of plant biology and macroecology in South Africa.

It is also worth mentioning that recently there has been significant advancement made in pollination biology (Johnson, 2010; Pauw, 2012; Van der Niet and Johnson, 2012) and invasive plant biology (Pyšek and Richardson, 2007; Gibson *et al*., 2012). Both these fields of study are important in the context of this study, as both are linked to flowering patterns. Additionally, these aspects will become increasing important under a climate change scenario.

2.7. Conclusion

Numerous factors determine the length of flowering across various geographic range sizes. Whether it is the availability of resources, climate, pollinator availability or alien species, all the factors discussed above are interdependent and give rise to various flowering patterns and

changes in the geographic range sizes. Understanding how these elements act together is essential in identifying any relationships that may exist between the length of flowering periods and the distribution ranges of various plants species, and hence forms the basis of this study.

Chapter Three

Study Region and Methodology

3.1. Study region

Southern Africa is a vast region with a complex physical environment, comprising a number of countries. There is a remarkably high percentage of endemic plant species in southern Africa. According to Van Wyk and Smith (2001) the species-area ratio in southern Africa is notably high in comparison to other regions in the world, with numerous centres of endemism. The present study focuses on the delineated south-eastern African region, 22ºS-24ºE (Figure 3.1.). Other biodiversity studies which have concentrated on areas of interest, within this south-eastern African region, include Steenkamp *et al.* (2004), which concentrated on the Maputaland-Pondoland-Albany Biodiversity Hotspot, and Carbutt and Edwards (2003; 2006) who studied the endemic flora of the Drakensberg Alpine Centre. Furthermore a study by Perera *et al.* (2011) also focused on this region.

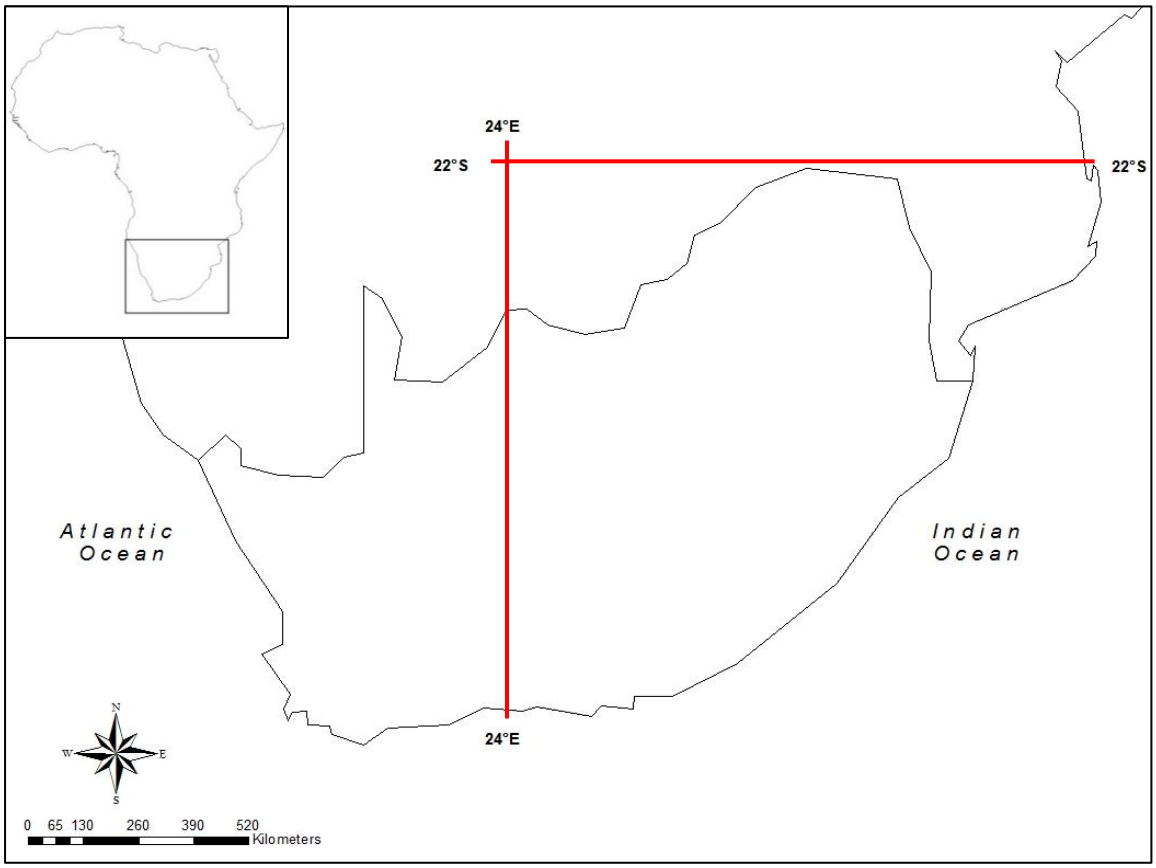

Figure 3. 1. Map depicting the 22ºS-24ºE region of southern Africa (also used by Perera *et al.*, 2011)

The northernmost boundary of this area, at about 22ºS is the Limpopo Valley and the western boundary of the region is characterised by the Nelspoort Interval at approximately 24ºE, which forms part of the southern Great Escarpment (Clark *et al.*, 2009; Perera *et al.*, 2011). The eastern and southern boundaries of the region fall along the Indian Ocean seaboard. The 22ºS-24ºE area consists of various vegetation types and encompasses a number of centres of endemism as described by Van Wyk and Smith (2001), as well as one of the 34 biodiversity hotspots defined by Mittermeier *et al.* (2004). Furthermore, climate, topography and geology vary from the upper reaches of the interior plateau, down towards the low-lying areas of the coast. The physical and environmental variations found in this 22ºS-24ºE region of South Africa are described in more detail further on in this chapter.

3.1.1. Climate

Climate is probably the most important single factor that shapes the distribution of vegetation (Schulze, 1997). The climate of the south-eastern Africa varies from the interior plateau in the north, to the coastal areas in the east and south. The general climate may be described as temperate to subtropical. The Great Escarpment of southern Africa has a marked influence on the climate in this region and is the reason why the temperate climate of the interior plateau is separated from the subtropical climates experienced in the lower-lying coastal areas (Vogel, 2008). Furthermore, the presence of the Great Escarpment results in there being varying altitudes, which contributes to the various temperature and rainfall patterns seen in South Africa (Vogel, 2008). The variation between the seasons is predominantly between summer and winter in this region. Spring and autumn are sometimes considered extended parts of summer and winter, respectively. According to Critical Ecosystem Partnership Fund (CEPF, 2010), September to April constitutes the summer months and May to August constitute the winter months. Rainfall in south-eastern Africa is received primarily in the summer months. Along the western boundaries of south-eastern Africa, rainfall is experienced during the late and very late summer months, whereas areas in the north and along the eastern coastline receive rainfall in early or mid-summer (Schulze, 1997). All-year rainfall only occurs in the south-western parts along the coast. Mean annual rainfall at higher altitudes above the Great Escarpment are between 250-750mm, in comparison to 750-1250mm received in areas below the escarpment. The presence of the warm Agulhas current which flows from the tropics along the east coast, brings moist air (CEPF, 2010). Therefore average rainfall decreases from east to west in South Africa.

Temperatures in south-eastern Africa also vary during the winter and summer months. During summer, maximum temperatures in most places can rise well above 30ºC. However, humidity along the eastern seaboard is far higher than the interior of south-eastern Africa (Vogel, 2008). Further northwards, along the coast the humidity is higher. During the warm summer months, humidity may peak at 90% (CEPF, 2010). This warmer climate results in the maximum winter temperatures along the eastern seaboard being above 20ºC, whereas temperatures in the interior areas can be as low as ~12ºC (Schulze, 1997). Daily maximum temperatures closer to the Great Escarpment, during winter, can be <12ºC. The mean annual temperatures therefore range from 12-25ºC for this entire region (Schulze, 1997). Frost may also occur during early winter mornings, after a clear and cloudless night in the Low- and Highveld areas and if temperatures drop sufficiently (Vogel, 2008).

3.1.2. Topography and geology

The topography of southern Africa varies from east to west and north to south. The most significant factor that contributes to the modern topography is the presence of the Great Escarpment. As mentioned before, this separates the elevated interior plateau from the low-lying coastal plains (Van Wyk and Smith, 2001). The present topography began with the break-up of Gondwanaland, together with a series of uplift and erosion cycles (Eriksson, 2008). This has also given rise to numerous mountain ranges in this 22ºS-24ºE region. The most infamous being the Drakensberg Mountains, which is approximately 1000km in length, where altitudes extend beyond 3000m (Van Wyk and Smith, 2001). This mountain range also extends across into Lesotho, where the highest peak in southern Africa is 3484m. Other mountain ranges that are found in this region, which form part of the Great Escarpment, are the Sneeuberg, Winterberg, Stormberge Amatola Mountains, which are south of the Drakensberg, while the Waterberg, Strydpoortberge and Soutpansberg ranges to the north (Van Wyk and Smith, 2001). The Lebombo Mountains fall east of the Drakensberg and run along the border between South Africa, Swaziland and Mozambique.

The general geology of south-eastern Africa is fairly complex, as is the rest of southern Africa. Some of the formations seen in the South African regions include the Natal, Beaufort, Lebombo, and Dwyka and Ecca Groups, as well as the Cape, Transvaal and Karoo Supergroups, to name a few (Van Wyk and Smith, 2001). This geology together with climate, gives rise to various soil formations, which may favour the growth of a variety of plants.

According to Laker (2008), most soils in South Africa are poorly developed. The majority of the soils in this 22ºS-24ºE region are moderate to highly weathered; moderately deep to deep soils (Laker, 2008). Other soil types found here include sandy soils, moderately deep to deep; solonetzic soils; shallow soils and black and/or red clays (Laker, 2008). The features of some of these soils are conducive to plant growth, as well as crop production, therefore creating a potential threat to endemic plants species.

3.1.3. Vegetation

The vegetation of south-eastern Africa is probably best described by the various biomes found here. The Grassland and Savanna are the two major biomes that cover the majority of the delineated 22ºS-24ºE area. The Indian Ocean Coastal Belt, Forest and Albany Thicket biomes are significantly smaller, but are also found in this region. In addition, small portions of the Nama-Karoo, Succulent Karoo and Fynbos biomes extend into the 22ºS-24ºE region on the western boundary.

The vegetation structure of the grassland biomes is dominated by grasses. Grasslands are considered species-rich. However, woody plant species are only found here in specialised habitats. Forbs form a significant part of the biome, but do not dominate (Mucina and Rutherford, 2006). In comparison, the Savanna biome characteristically has a discontinuous tree layer with a herbaceous layer, consisting predominantly of grasses. The density of trees in savanna can vary significantly, thereby giving rise to many forms of Savanna (Scholes, 1997). Furthermore, the occurrence of fire under different soil and climatic conditions can significantly influence the composition of grasslands and savanna (Bond, 1997; Bond *et al.*, 2003). Fires occur more frequently in grasslands, as this prevents succession in vegetation. In both grassland and savanna, there are distinct wet and dry seasons. During the dry season, usually winter, the drier vegetation allows for fires to occur. Fire therefore plays a vital role in the rejuvenation and maintenance of grasslands and in the structural vegetation seen in savanna (Bond, 1997; Bond *et al.*, 2003). Species diversity within savanna, particularly with relation to trees and shrubs, decreases from east to west within the biome due to temperature and rainfall gradients (Scholes, 1997).

The Indian Coastal Belt biome and the Albany Thicket biome are found within the 22ºS-24ºE region. The Albany Thicket, formerly known as Valley Bushveld, is centred along the

southern coast of South Africa, between Port Elizabeth and Kei Mouth, but also extends inland towards Middelburg (Van Wyk and Smith, 2001). Structurally, Thicket consists of trees and shrubs that have a dense woody, semi-succulent and thorny character (Mucina and Rutherford, 2006). A few of the diverse growth forms found in Albany Thicket are leaf and stem succulents, shrubs, geophytes and grasses, therefore giving rise to a high species richness (Mucina and Rutherford, 2006). There are an estimated 200 endemic plant species found here (Van Wyk and Smith, 2001). Unreliable rainfall in this area and herbivory are believed to have shaped the distinct characteristics of this biome (Mucina and Rutherford, 2006). Despite this, Albany Thicket is considered the dominant vegetation type in the Albany centre of endemism which forms part of the Maputaland-Pondoland-Albany Biodiversity Hotspot.

Similarly, The Indian Ocean Coastal Belt, which is confined to the narrow coastal belt of KwaZulu-Natal and part of the Eastern Cape provinces and extends north into Mozambique, also forms part of the Maputaland-Pondoland-Albany Biodiversity Hotspot. This biome is under major threat from development, due to dense populations and developments along the east coast of South Africa (Mucina and Rutherford, 2006). There are several vegetation units found in the Indian Ocean Coastal Belt, due to the variation in geology and topography along the coastline. These include Maputaland Coastal Belt matrix, Maputaland Wooded Grassland, KwaZulu-Natal Coastal Belt matrix, Pondoland-Ugu Sandstone Coastal Sourveld and Transkei Coastal Belt matrix (Mucina and Rutherford, 2006). Therefore giving rise to a mosaic of different vegetation-types, consisting mainly of forest, grassland and savanna. Additionally, this biome has a relatively high concentration of endemics, which are constantly under threat.

Lastly the Nama-Karoo, Succulent Karoo and Fynbos biomes extend from the west, partially into the 22ºS-24ºE region. Nama-Karoo and Succulent Karoo are considered arid biomes. The Succulent Karoo has a wide range of plant lineages, of which not all are succulents (Mucina and Rutherford, 2006). The Succulent Karoo is distinguished from the Nama-Karoo as it receives a portion winter rainfall, whereas the Nama-Karoo receives unpredictable summer rainfall (Milton *et al.*, 1997). Furthermore, Van Wyk and Smith (2001) also state that the Nama-Karoo does not contain a high diversity and is one of the few biomes which do not contain any centres of endemism, suggesting it is a relatively young biome. However, there is a high diversity of life forms (Mucina and Rutherford, 2006). Both the Nama-Karoo and

Succulent Karoo, border marginally with the Fynbos Biome. This biome is one of the most floristically diverse areas in the world and forms part of the Cape Floristic Biodiversity Hotspot (Mittermeier *et al.*, 2004) The biome is home to some 9000 plant species, of which approximately 69% are endemic (Mucina and Rutherford, 2006). The small part also extends into south-eastern Africa, bordered by Albany Thicket (Van Wyk and Smith, 2001). This boundary is determined by the geomorphology, with characteristic Thicket type vegetation found amongst the fynbos. On a floristic level, the Fynbos and Succulent Karoo Biomes are among the more exceptional biomes in the world, but, as indicated, these are only marginally relevant to this study.

3.1.4. Centres of endemism

There are several centres of plant endemism found in the 22ºS-24ºE region. These areas have been identified by Van Wyk and Smith (2001). These include the Drakensberg Alpine, Barberton, Wolkberg, Sekhukhuneland and the Soutpansberg centres. However, the most notable centre of endemism is the Maputaland-Pondoland-Albany Biodiversity Hotspot, which is one of the 34 international biodiversity hotspots, and is a combination of the Maputaland, Pondoland and Albany centres. All these centres collectively give rise to a number of endemic species.

Three centres of endemism overlap the boundary of the Grassland and Savanna biomes, which are characterised by areas of woody savanna species amongst open areas of grassland (Van Wyk and Smith, 2001). These are the Barberton, Sekhukhuneland and Soutpansberg centres. Mucina and Rutherford (2006) refer to this area as the "tension zone", where elevated islands of rich endemic grasslands are surrounded by subtropical savanna vegetation. The Drakensberg Alpine and Wolkberg centres are found completely within the Grassland biome and are found at high altitudes which has influenced the endemics found in these centres (Mucina and Rutherford, 2006). In comparison the Maputaland, Pondoland and Albany centres (as mentioned previously) form part of the greater Maputaland-Pondoland-Albany (MPA) Hotspot. The Maputaland centre extends into southern Mozambique, whereas the Pondoland and Albany centres fall completely within South Africa. The endemics in Maputaland are generally widespread, but some are restricted to certain parts of the region, such as the Lebombo mountains (Van Wyk and Smith, 2001). Similarly, various endemics in the Pondoland centre are restricted to northern and southern parts of the region (Van Wyk and

Smith, 2001). Approximately 200 endemic species are found in the Albany centre, of which a large percentage are succulents, associated with the thicket vegetation (Van Wyk and Smith, 2001). It is therefore essential that these centres are well conserved, in order to maintain high diversity of endemic species.

3.2. Methodology

The methodology of this study involved three stages. The first stage of this meta-analysis study consisted of setting a number of criteria in terms of the type of data that would need to be sourced. Thereafter the data set was collated and recorded according to specific requirements, and lastly it was analysed statistically.

3.2.1. Criteria

Before any genera were chosen and any data collected from the primary sources, a number of criteria had to be set out in order to avoid any biases in the preliminary choice of genera. It was vital to choose a variety of genera that represented different growths forms, as flowering times and distributions are likely to vary. Seven monocotyledon and six dicotyledon genera were considered, representing a variety of growth forms (refer to Tables 3.2.1a. and 3.2.1b. below). These genera were also chosen because they are known to have a high diversity of endemics in eastern South Africa, and because relevant distribution and phenology data for these genera have been published and were readily available. It must be noted that the majority of the *Searsia* taxa were previously classified under the Rhus genus, which is no longer used.

Table 3.2.1a. Dicotyledon genera used in this study

Genus	Family	Growth From
Cussonia Thunb.	Araliaceae	Tree
Gymnosporia (Wright & Arn.) Hook.f.	Celastraceae	Shrub/Tree
Pavetta L.	Rubiaceae	Shrub/Tree
Plectranthus L'Hér.	Lamiaceae	Herb
Searsia F.A. Barkley	Anacardiaceae	Shrub/Tree
Streptocarpus Lindl.	Gesneriaceae	Herb

Table 3.2.1b. Monocotyledon genera used in this study

Genus	Family	Growth From
Crinum L.	Amaryllidaceae	Geophytic herb
Eulophia R.Br. ex Lindl.	Orchidaceae	Herb
Gladiolus L.	Iridaceae	Geophytic herb
Kniphofia Moench	Asphodelaceae	Geophytic herb
Satyrium Sw.	Orchidaceae	Herb
Watsonia Mill.	Iridaceae	Geophytic herb
Zantedeschia Spreng.	Araceae	Geophytic herb

Once these genera had been selected, the endemic taxa in each genus were established from the Plants of southern Africa (POSA) website (http://posa.sanbi.org), which lists endemic taxa according to Germishuizen *et al.* (2006). 'Taxa' in this case refer primarily to species; but endemic subspecies were also included in this study, due to the possibility of differing flowering times amongst subspecies. Subspecies that did not meet endemism criterion (see Section 3.2.1.1.) were excluded. The varieties and forms of a taxon were considered as a single species, as long as all varieties and forms were endemic according to the endemism criterion seen in Section 3.2.1.1.

3.2.1.1. Distribution criteria

As mentioned in the previous chapter, this study concentrated on the area that falls between 22ºS and 24ºE of South Africa (as seen in Figure 3.1., 3.2.1. and 3.2.2.). These are the same cut-off boundaries of Perera *et al.* (2011). When collecting the relevant data on the various taxa, it was essential that each taxon selected followed the set distribution criteria. The distribution range, in the Quarter Degree Square (QDS) format, of each endemic taxon had to have more than 50% of the total distribution range (i.e. 50% of total QDS) within the 22ºS-24ºE limits. Taxa that did not fit this criterion were excluded, such as those taxa that are centred in the Cape Floristic Region.

Distribution range was quantified using three measures, the most obvious of which is the number of QDS where a taxon has been recorded. However, given the incompleteness of data

at this fine scale, we also considered two coarser units, one based on species endemism patterns and one based on rainfall seasonality.

For species endemism patterns, the geographical units established by Perera *et al.* (2011) in this 22ºS-24ºE region were employed (Appendix A). This unique classification of 37 geographical units are drawn to fit quarter-degree squares that represent endemic vertebrate distributions and boundaries of bioregions or biomes in the 22ºS-24ºE area (see Figure 3.2.1.). These units were therefore used as another measure of distribution.

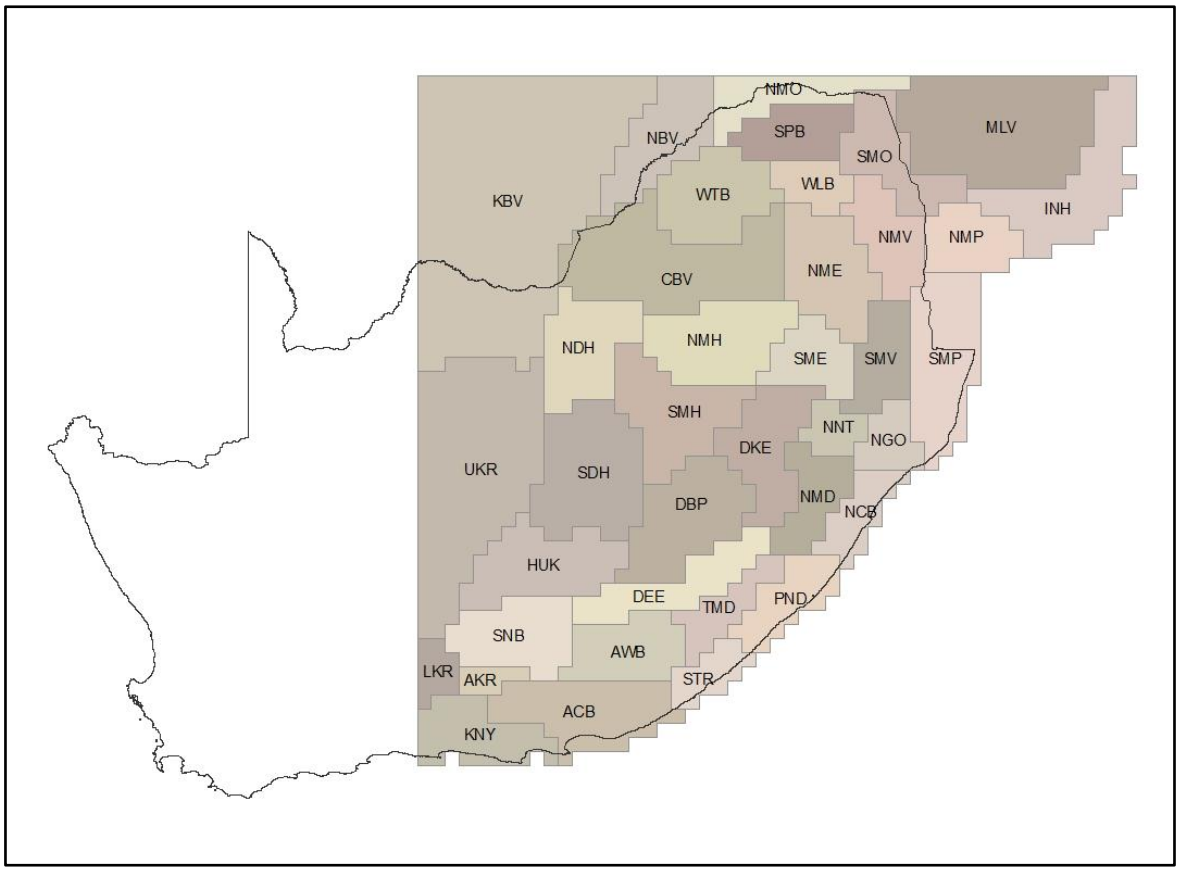

Figure 3.2.1. A QDS based map of the units of Perera *et al.* (2011). Each unit is given a three letter codes, which can be found in Appendix A. It must be noted that units on the 22ºS-24ºE boundary extend beyond these geographic confines.

Furthermore, rainfall regions of South Africa, according to seasonality, as described by Schulze (1997), were also used as a measure of distribution, as this is likely to be a determinant of flowering times as well as distributions of endemic plant taxa (see Figure 3.2.2. below).

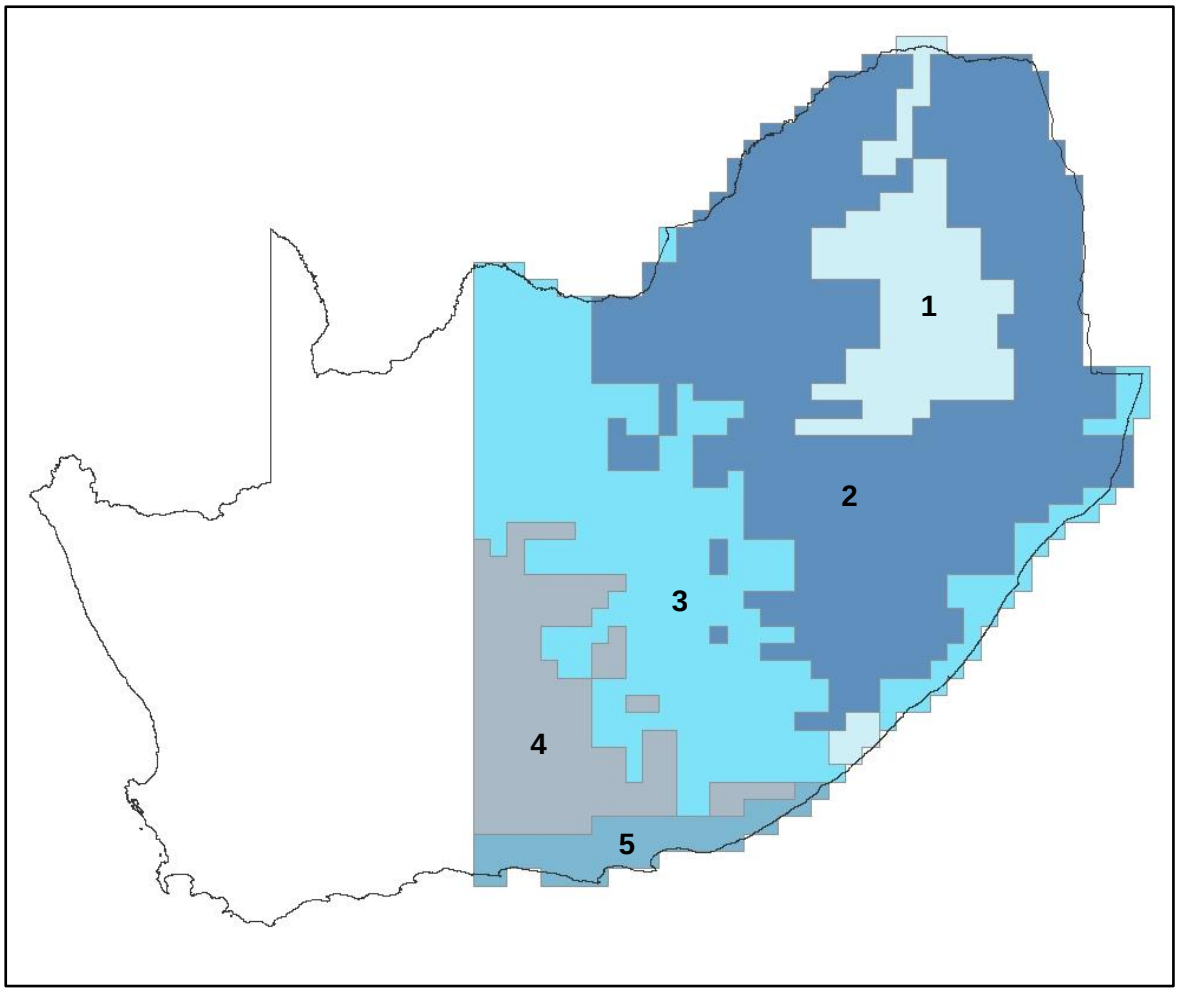

Figure 3.2.2. A QDS based map of the Rainfall Seasonality Zones of the 22ºS-24ºE region of South Africa according to Schulze *et al.* (1997) (1=Early Summer; 2=Mid-Summer; 3= Late Summer; 4=Very Late Summer and 5= All Year)

Once all these criteria were taken into account, suitable and relevant data was sourced from various data sources in order to start data compilation.

3.2.2. Data collection

Data was collected from various sources, depending on the nature of the data required. Specific data, such as flowering months were gathered from a series of published books. The majority of the books used were revisions on the various genera. The books that were used for each genus are listed in Table 3.2.2a. and 3.2.2b.

Table 3.2.2a. List of publications used to gather data on Dicotyledon genera

Genus	Title of Publication	Author/s	Year
Cussonia *Gymnosporia* *Pavetta*	Pooley's Trees of eastern South Africa	R. Boon	2010
Plectranthus	The southern African *Plectranthus* and the art of turning shade into glade	E. van Jaarsveld	2006
Searsia	*Rhus*, Flora of southern Africa Vol. 19, Part 3, Fascicle 1	R.O. Moffett	1993
Streptocarpus	*Streptocarpus*: An African plant study	O.M. Hilliard & B.L. Burtt	1972

Table 3.2.2b. List of publications used to gather data on Monocotyledon genera

Genus	Title of Publication	Author/s	Year
Crinum	The genus *Crinum* in southern Africa, Bothalia, Vol. 11, No. 1 & 2	I.C. Verdooorn	1973
Eulophia *Satyrium*	Orchids of southern Africa	H.P. Linder & H. Kurzweil	1999
Gladiolus	A revision of the South African species of *Gladiolus*	G.J. Lewis A.A. Obermeyer & T.T. Barnard	1972
Kniphofia	The South African Species of *Kniphofia*, Bothalia, Vol. 9, Part 3 & 4	L.E. Codd	1968
Watsonia	The genus *Watsonia*	P. Goldblatt	1989
Zantedeschia	Contributions to the systematics of the genus *Zantedeschia* Spreng. (Araceae) – MSc.	Y. Singh	1996

The flowering time data consisted of the start and end flowering months, and the total number of flowering months of each endemic taxon. This was captured into a Microsoft Excel 2010. Distribution data was gathered from the South African National Biodiversity Institute (SANBI) website (http://sibis.sanbi.org). The distribution data were freely available and was therefore downloaded from the SANBI website (http://sibis.sanbi.org) in shapefile (.shp) format. This allowed the data to be geographically referenced and projected in the Geographic Information System (GIS) programme, ArcMap™ 9.3. (ESRI Inc., 2008). Using this, the total number of QDS's of each taxon in the 22ºS-24ºE region was established. Similarly, distribution data was also used to determine in which rainfall seasonality region/s (Figure 3.2.2.) each taxon occurs in. Both the rainfall seasonality and endemism units' data were captured in Microsoft Excel. In the cases of data deficiency, specimens in the KwaZulu-Natal Herbarium (Durban) were consulted, particularly in the case of flowering times (refer to Appendix B for raw data).

3.2.3. Data analysis

The data analyses that were used were selected according to the type of data that were collected and to fulfil the objectives of this study. Therefore there were various ways employed to evaluate different aspects of the data. Once data collection was completed, all the data that had been collected were consolidated into a single larger database with all relevant data. The data was then transferred into IBM SPSS 19.0 software for Windows in order to carry out more in-depth statistical analyses (IBM Corp., 2010).

Additional, categorical variables were then added to the consolidated data for further statistical analyses. These included coding of each genus (i.e. each genus was allocated a number/code- see Appendix B1) and categorising the species into broad and narrow growth forms. There were three broad growth form categories, which were split further to create six narrow growth form categories (see Table 3.2.3a. below). There were seven variables in the database, including the categorised genera, broad and narrow growth form variables. Other variables comprised of the three measures of distribution (QDS, Perera Units and Rainfall Zones) and the number of flowering months (i.e. length of flowering).

Table 3.2.3a. Broad and narrow growth form categories used in the data analysis

Broad Growth Form Categories (categorical code)	Narrow Growth Form Categories (categorical code)
Monocotyledonous Geophytic Herb (1)	*Zantedeschia* and *Kniphofia* (1)
	Other Monocotyledon Geophytic Herbs (2)
Dicotyledonous Herb (2)	*Streptocarpus (*3)
	All other Dicotyledon Herbs (4)
Dicotyledonous Woody (3)	Tree (5)
	Shrub (6)

In the data analysis it was first necessary to focus solely on the flowering duration of each species in all the genera. Therefore using flowering data that was collected depicting the exact flowering months of each species, a Factor Analysis (Principal Component Analysis) was completed in IBM SPSS 19.0 using the Dimension Reduction-Factor function (IBM Corp., 2010). The values of the two components derived from this were graphed in scatterplots according to the three broad growth forms classified before. The first factor values were plotted along the x-axis and the second factor values against the y-axis. On each graph the genera associated with the broad growth form category were depicted using various symbols. These graphs illustrate if there are any potential flowering patterns within each broad growth form or genera. Then, the categorical variables (genus, broad and narrow growth forms) were graphed in box-and-whisker plots, in order to determine the variation in range size (QDS) in each category. These graphs illustrated the variation of the range sizes amongst the different growth forms and the different genera, as well as depicting the variation within each category. Reisch and Poschlod (2003) also used a similar analysis approach to determine the phenologic and morphometric differentiation of *Sesleria albicans* across different habitat types.

Thereafter data analysis consisted of simple correlations and regressions between the three measures of distribution (QDS, Perera Units and Rainfall Zones) and the number of flowering months of each species. Correlations were first carried out within each genus that had five or more species, in order to establish if there were any significant relationships and to determine how to statistically analyse the data further. The correlations were carried out in IBM SPSS

19.0 (IBM Corp., 2010). All the Pearson's correlation coefficients were recorded accordingly. The correlation and regression tests were then also run for the entire database using IBM SPSS 19.0 (IBM Corp., 2010).

Additionally, when considering the nature of the data, an Analysis of Covariance (ANCOVA) proved to be a suitable statistical test, as this allowed the effect of the categorical variables to be considered in the relationship between the measures of distribution and the length of flowering. ANCOVA analyses have also been used widely in various ecologically-based and flowering phenology studies (Lozano and Schwartz, 2005; Bustamante and Búrquez, 2008; Godoy *et al.*, 2009; Forrest *et al.*, 2010). The ANCOVA analyses therefore formed a large part of the statistical analyses. The measures of distribution were used as dependent variables and the fixed factors were the categorical variables. The length of flowering (number of flowering months) was therefore the covariate in the test.

Prior to the actual ANCOVA model implementation, it is necessary to test the underlying assumptions of the ANCOVA. The tests for the homogeneity-of-regression (slopes) assumption were conducted on nine different combinations of the variables (see table 3.2.3b. below).

Table 3.2.3b. Variables used for the Homogeneity-of-Regression Assumption and ANCOVA analysis.

Set	Test	Dependent Variable (measures of distribution)	Fixed Factor (categorical variables)	Covariate (flowering length)
A	1	QDS	Broad Growth Form	Flowering Months
	2		Narrow Growth Form	
	3		Genus	
B	4	Perera Units	Broad Growth Form	Flowering Months
	5		Narrow Growth Form	
	6		Genus	
C	7	Rainfall Zones	Broad Growth Form	Flowering Months
	8		Narrow Growth Form	
	9		Genus	

The nine tests were divided into three sets of three tests each, relevant on the dependent variable that was used. The homogeneity-of-regressions assumption tests if the slopes of the regression lines in the model are the same or similar enough to be compared further in the ANCOVA test.

This test of assumption was run in IBM SPSS 19.0, using the General Linear Model-Univariate function (IBM Corp., 2010). In order to continue with running the ANCOVA tests, the results of the interaction between the fixed factor and the covariate of the homogeneity-of-regression assumption had to have a non-significant value ($p > 0.05$). The non-significance means that the slopes of the regression lines are not statistically different and can therefore be compared further. All nine tests met the homogeneity-of-regression assumption, and therefore ANCOVAs were carried out (Appendix C). However, it is important to note that the interaction between the fixed factor and covariate was removed when running an ANCOVA, as this would add in greater complexity to the outcomes of the tests. Once the analyses were done, the results of the ANCOVA were then recorded and analysed further.

The various graphs and tables showing the outcomes of all the data analysis may be found in Chapter 5. However, all the detailed data and tables can be found in the Appendix sections (Appendix B and C, with authorships of taxa found in Appendix B1).

Chapter Four
Results

4.1. Patterns in flowering (Factor Analysis)

The factor analysis was conducted in order to ascertain how variability within each genus (intra-generic) compares to variability amongst genera of the same broad growth forms (inter-generic) with regard to flowering. The following graphs show the factor analysis for all species belonging to the relevant broad growth forms and any potential flowering patterns that may exist.

In the scatterplot (Figure 4.1a.), seven monocotyledonous geophytic herb genera were taken into to account (*Crinum*, *Eulophia*, *Gladiolus*, *Kniphofia*, *Satyrium*, *Watsonia* and *Zantedeschia*). There is large variability in these genera and, in some cases, some species overlap – even species belonging to different genera. This is a product of them having the same flowering period; therefore the factor analysis values were the same. However, there is no evident flowering pattern amongst the majority of the genera, on an intra-generic level, particularly in genera, such as *Watsonia*, with numerous species. There is large variability in flowering patterns amongst the species. This is suggested by the small groups of loose clusters in different parts of the scatterplot. This is also observed in *Kniphofia* and *Gladiolus*. Genera with fewer species, such as *Satyrium*, *Crinum* and *Zantedeschia*, have widely distributed points, therefore not showing any sort of flowering patterns. The only possible intra-generic pattern that may be evident is in *Eulophia*, but there are only a few species clustered in the scatterplot. From an inter-generic perspective, there is no obvious pattern with regard to flowering seasons either. However, *Eulophia*, *Watsonia* and *Zantedeschia* are loosely clustered together, suggesting that these species may occur in similar areas and therefore have a similar flowering season. Similarly, *Gladiolus* and *Kniphofia* share similar flowering patterns.

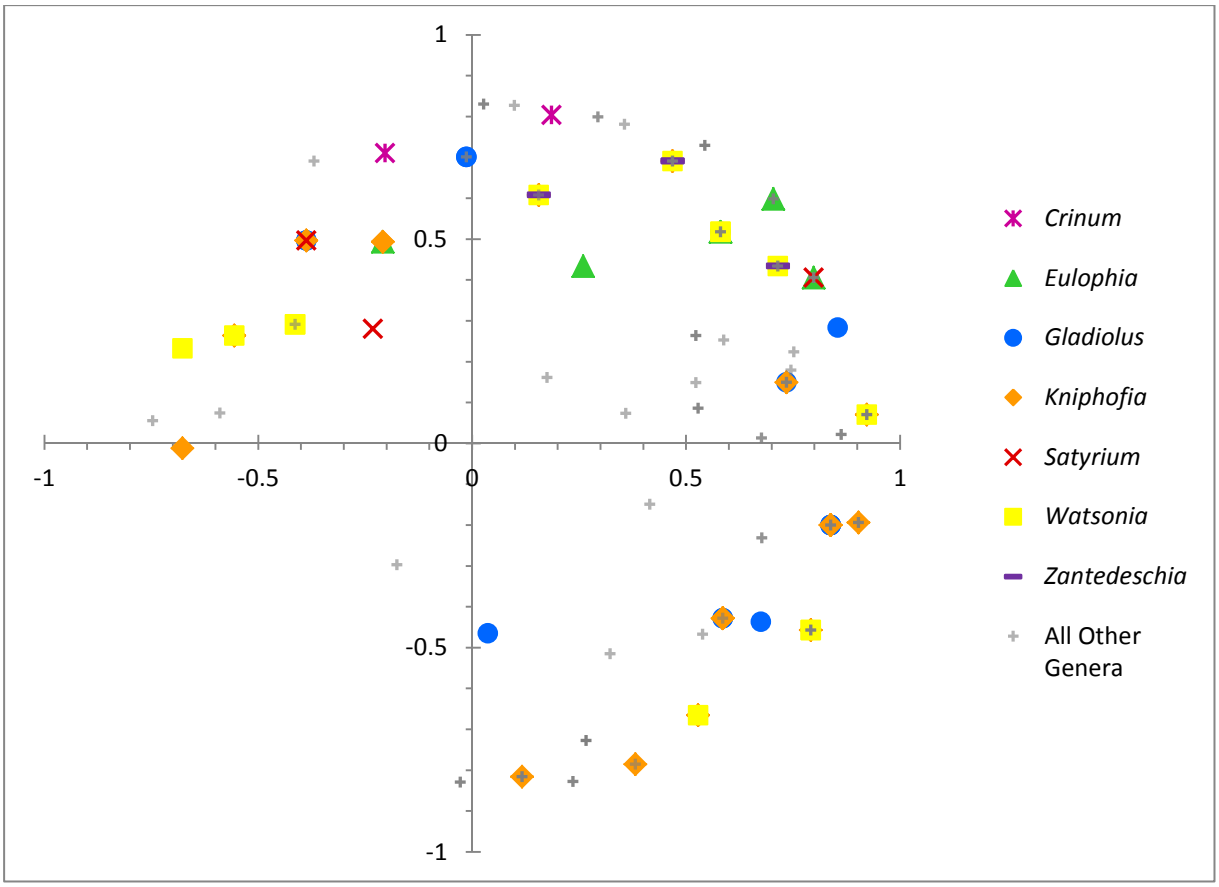

Figure 4.1a. Scatterplot of the factor analysis on the flowering of monocotyledonous geophytic herb genera (Broad Growth Form 1)

The flowering patterns amongst *Streptocarpus* and *Plectranthus* are more apparent in the scatterplot of the dicotyledonous herb species (Figure 4.1b.). The majority of the *Streptocarpus* species are stretched into an elongated cluster on the scatterplot, *Streptocarpus* species thus presenting a continuum in terms of flowering seasons. In the case of *Plectranthus*, there are two distinct clusters observed. This may indicate that within the genus there are two separate flowering seasons, which may be due to the distribution of the species in two different environments that influence the duration of flowering. In addition, one of the *Plectranthus* clusters overlaps with the cluster of *Streptocarpus*, implying that certain species in both *Plectranthus* and *Streptocarpus* have similar flowering seasons. On this plot, the intra-generic variation is far more visible. If more genera of this growth form are included, it may justify that these trends could partially be a result of the dicotyledonous herbaceous growth form of these genera.

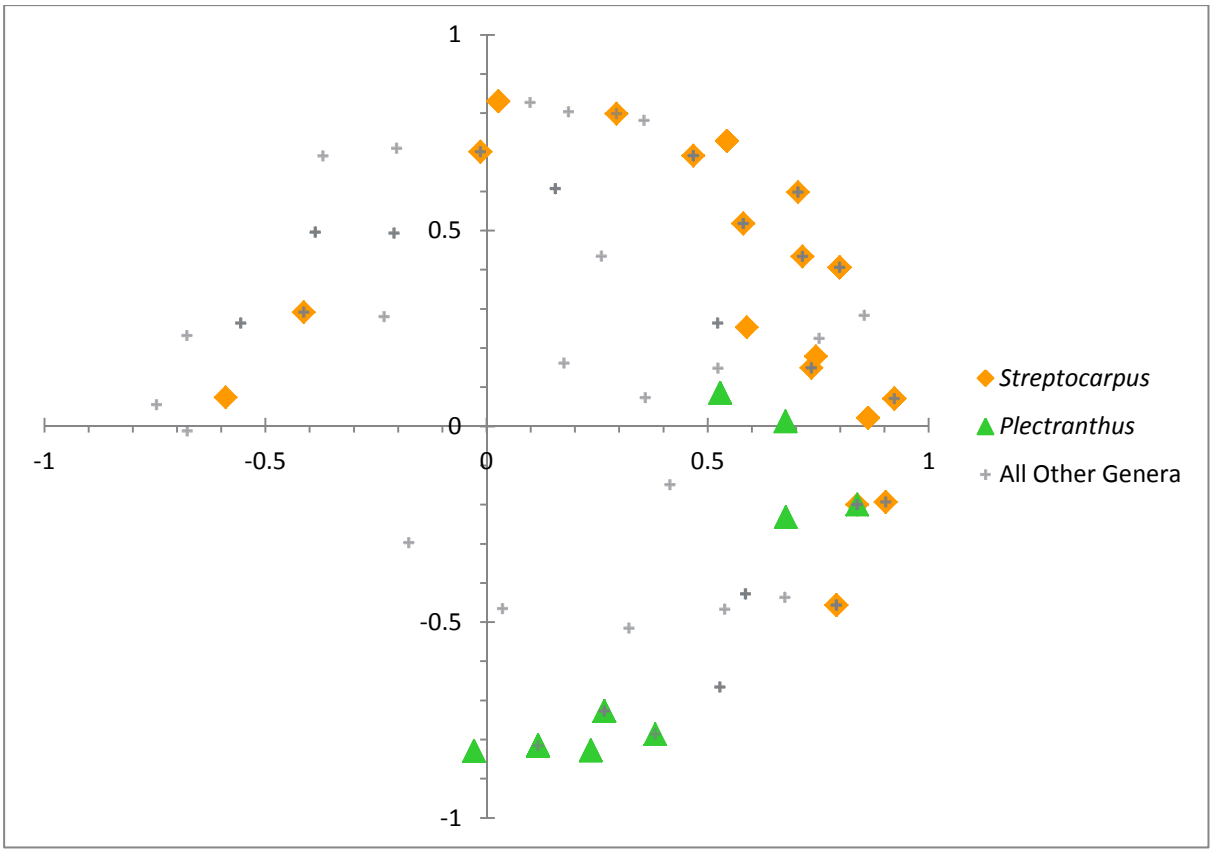

Figure 4.1b. Scatterplot of the factor analysis on the flowering of dicotyledonous herb genera (Broad Growth Form 2)

The last of the scatterplots (Figure 4.1c.) shows the variation in flowering of the dicotyledonous woody genera. *Searsia* has the most species, with *Cussonia*, *Gymnosporia* and *Pavetta* having significantly fewer. Irrespective, both *Gymnosporia* and *Cussonia* do not have any evident flowering pattern, which may be linked to species having varied distribution ranges in different environments. There is great flowering variability amongst the *Cussonia* species, whereas flowering patterns of the *Gymnosporia* species seem to be similar to those of a few *Searsia* species, illustrating common inter-generic flowering patterns. Furthermore, *Searsia* species do not have distinct clustered flowering patterns, but are more loosely grouped. This indicates similar flowering amongst some species, as a result of varying extrinsic and intrinsic factors. The only evident flowering pattern identified is in *Pavetta*, illustrating that flow ering amongst species is quite similar in this genus. This flowering pattern observed in *Pavetta* corresponds to that seen in *Streptocarpus* on the previous graph (Figure 4.1b.). This may be due to species having the same flowering times and duration, but also suggesting that the inter-generic variation in flowering patterns may extend beyond the growth form of these genera. Furthermore, the comparable flowering patterns of *Pavetta* and

Streptocarpus could be due to these species occurring in similar regions, therefore are influenced by the same factors that determine flowering season.

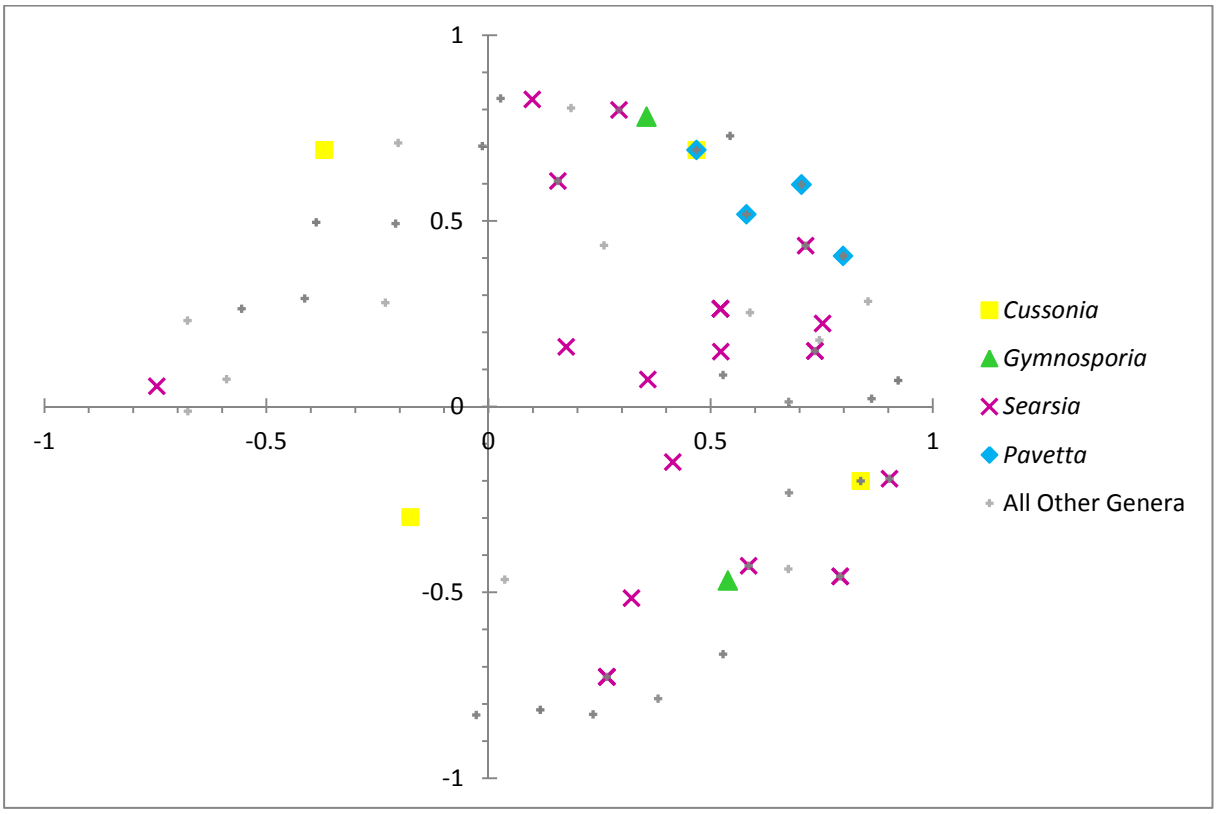

Figure 4.1c. Scatterplot of the factor analysis on the flowering of dicotyledonous woody genera (Broad Growth Form 3)

4.2. Patterns in range size (Box-and-Whisker Plots)

The patterns of range size are depicted in three box-and-whisker plots (Figure 4.2a., 4.2b. and 4.2c.). Figure 4.2a. depicts the three different broad growth forms of the various genera used in the study. The data distributions are skewed to the left in the three broad growth forms, thus indicating numerous narrow endemics with relatively small range sizes. The dicotyledonous herb growth form has the most outlying data points, suggesting large dissimilarity of distributional range size amongst species within the growth form and therefore indicating both broad and narrow distributions. This further suggests that there are possibly fewer narrow endemic species within this growth form. In comparison, the other growth forms have similar patterns with regard to range size; therefore species in these growth forms are likely to be widespread endemics as a result of successful distribution and

suitable environmental conditions. The larger variability seen between the range sizes of dicotyledonous woody and herb growth forms could indicate that various other morphological characteristics can give rise to variations in range size. However, the range size pattern of the monocotyledonous herbs is similar to that of dicotyledonous woody plants, suggesting that species in this growth form may not rely on morphological characteristics to determine the range size patterns, but rather on successful pollination and dispersal events. The adaptations amongst the various broad growth forms could also explain the variation in the range size patterns seen.

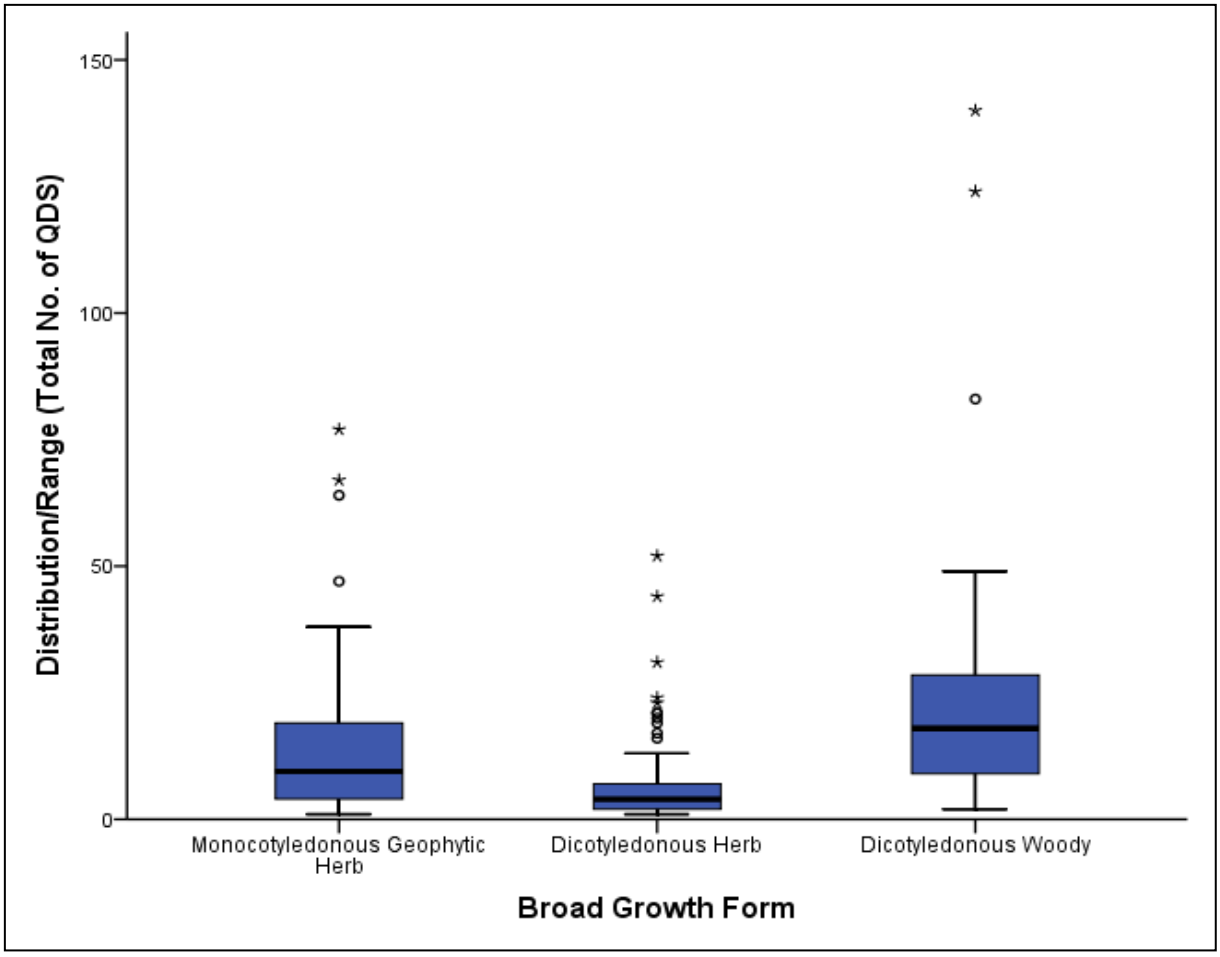

Figure 4.2a. Box-and-whisker plot of broad growth forms and the distribution range of all genera

The distributional range patterns seen in the narrow growth forms (Figure 4.2b.) are somewhat similar to the broad growth forms, because narrow growth forms are nested within the broad growth forms. Most of the data has a skewed distribution, with the exception of trees, which have a relatively normal distribution. The data ranges of each of the narrow growth forms differ significantly. *Streptocarpus*, has the smallest range in data and a number

of outliers, indicating extreme variation in distributional range of species which is observed in the broad growth form, dicotyledonous herb. Therefore these are likely to be more narrowly distributed endemic species. The range sizes of shrubs and trees shows that the distribution of species is similar, which is essentially linked to the woody characteristic that both growth forms share. Trees, however, seem to have more widespread endemics in contrast to shrubs. *Streptocarpus* comprises a number of very narrow endemic species, with a few exceptions that have slightly larger range sizes. Dicotyledonous and monocotyledonous geophytic herbs share some similarity in range size patterns. However, monocotyledonous geophytic herbs have more variability in range size. Similarities are also seen between *Zantedeschia* and *Kniphofia* and shrubs, suggesting that patterns of distributional ranges of species in these narrow growth forms are also similar, possibly due to species occurring in the same regions or areas.

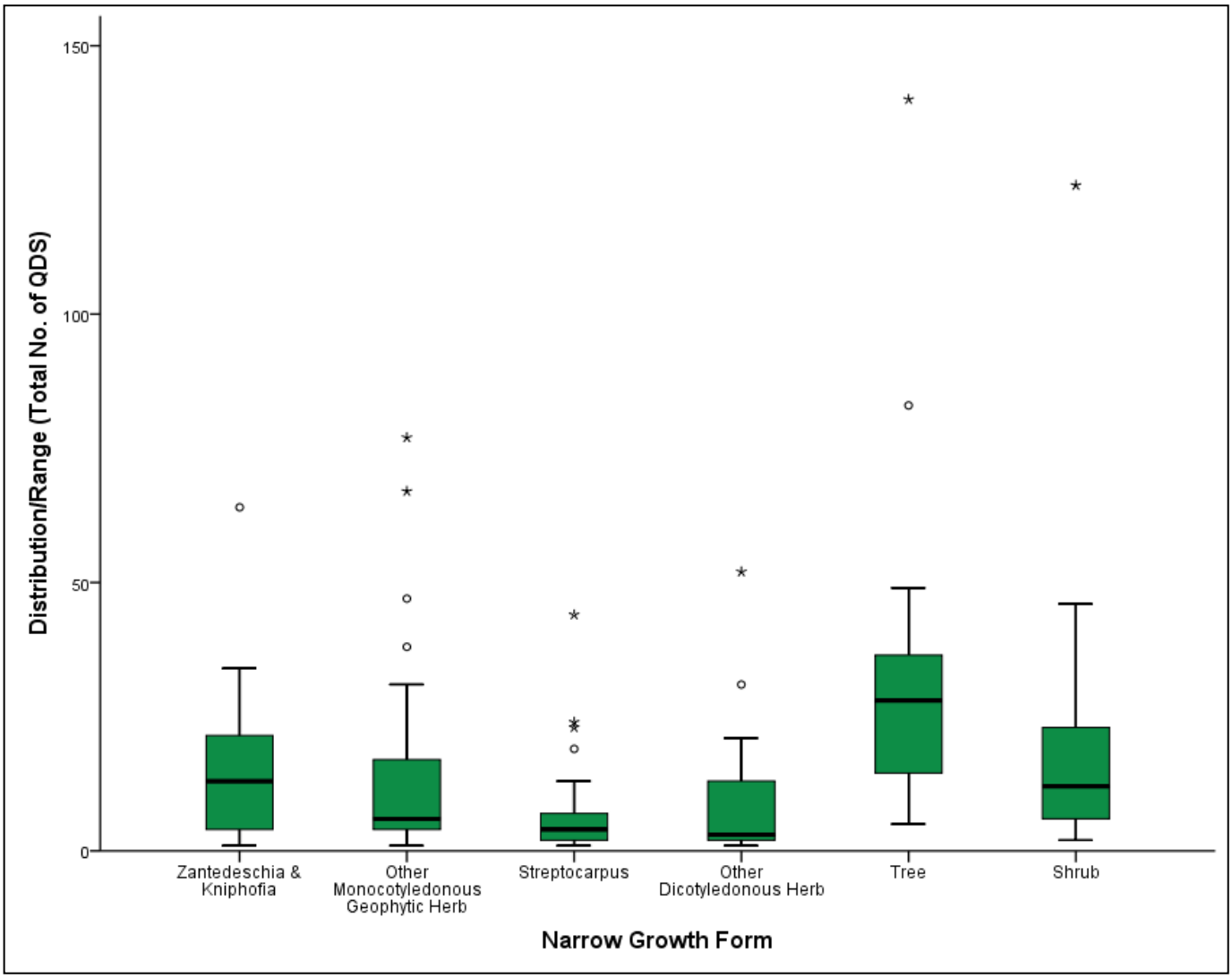

Figure 4.2b. Box-and-whisker plot of narrow growth forms and distribution range of all genera.

The last of the box-and-whisker plots illustrates the distribution of the distributional ranges within various genera (Figure 4.2c.).

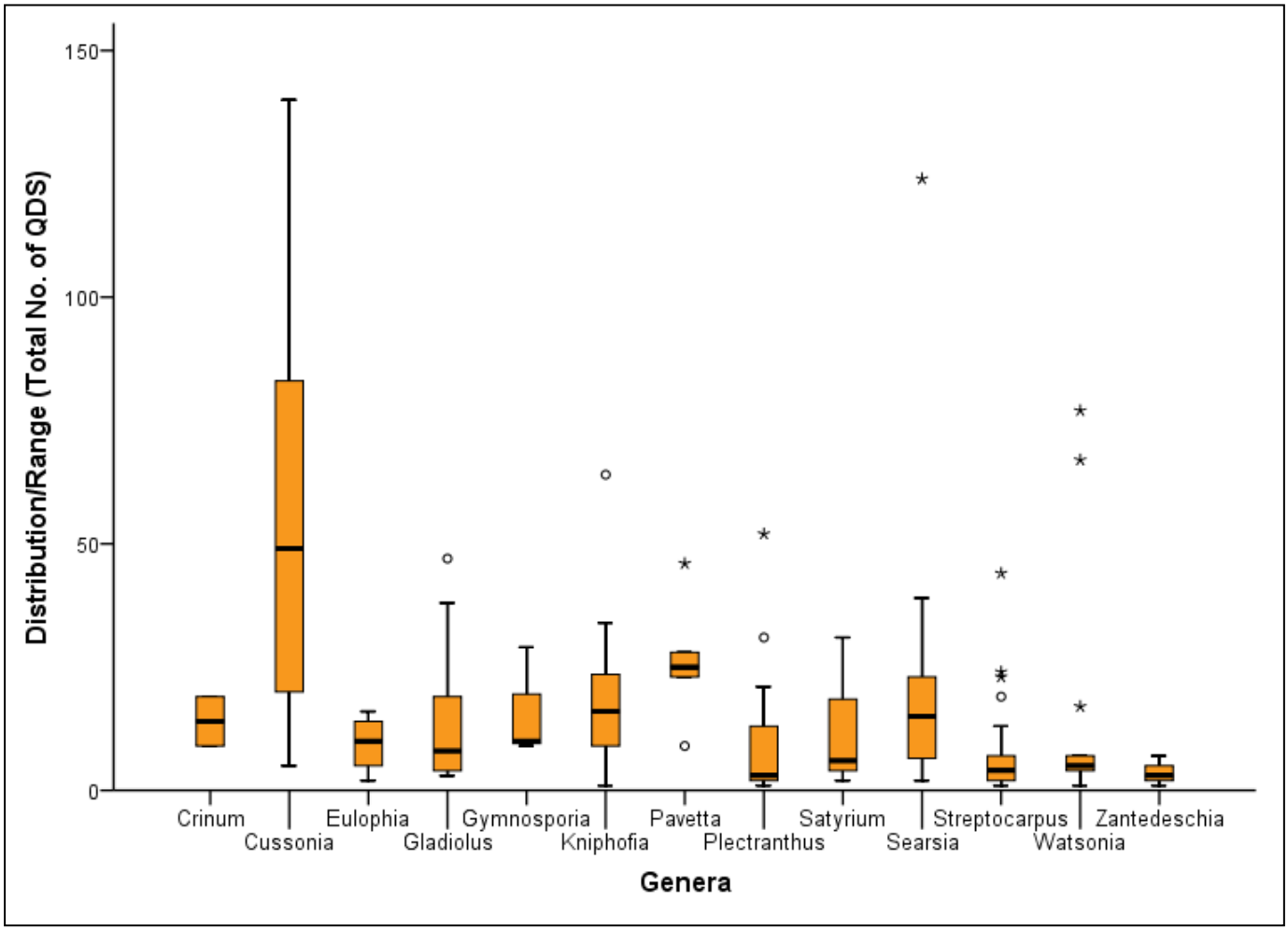

Figure 4.2c. Box-and-whisker plot of all the genera and the distribution range

Zantedeschia evidently has very few endemics species with relatively narrow range sizes, because it does not have any outliers. In comparison, *Cussonia*, *Kniphofia* and *Searsia* have lots of endemics species which are widespread. Genera with lower medians, such as *Plectranthus*, *Satyrium* and *Streptocarpus*, have narrow endemics which are not widespread. The majority of *Watsonia* species also have narrow range size patterns, with a few exceptions which seem to be widespread. This is also observed in *Streptocarpus*. However, in *Streptocarpus*, there are a few more widespread species. *Pavetta* endemics are widespread in comparison to other genera, with larger range sizes. In *Gymnosporia*, *Crinum* and *Eulophia* range sizes seem limited, with none of these genera having any outlying species with larger or smaller range sizes. This may indicate that these species are found in similar environments or

do not readily spread as much as other genera (which could be due to having specific pollinating and dispersal agents). There is some variation seen amongst the range sizes of the *Gladiolus* species. Furthermore, *Searsia* and *Gladiolus* have similar range size patterns. It may therefore suggest that the distribution of species extends beyond different growth forms, as *Gladiolus* is a monocotyledonous geophytic herb and *Searsia* is a dicotyledonous woody shrub/tree. In general, there is distinct variability amongst the different genera and the associated range size patterns. These patterns are likely to be influence by numerous factors, of which the duration of the flowering season may be one.

The results above indicate that the likelihood of variables such as broad and narrow growth forms and genus have an effect on the flowering duration. Patterns seem plausible and it is therefore essential to determine if any relationships exist between the flowering and distributional ranges patterns that have been observed.

4.3. Linking flowering to range size (Correlations and ANCOVAs)

The correlation analyses looked for possible relationships that may exist between the duration of flowering (also referred to as number of flowering months) and the different measures of distribution, within genera that had data for five or more species. The results (Table 4.3a.) indicate that the majority of the genera did not show any significance between flowering duration and the measures of distribution. However, in *Eulophia* species flowering duration is influenced by the number of rainfall zones (Pearson's Correlation Coefficient = 0.9303; *p*-value = 0.022). This may be due to *Eulophia* having a broad distributional range in most, if not all, of the rainfall zones. Alternately, it may have a narrow distribution in an area that is influenced by many climatic patterns, such as the Pondoland region of South Africa. Furthermore, as a result of the link between flowering duration and rainfall zones, it also suggests that the climatic seasonality together with flowering duration may be a key determinant of the distributional range of *Eulophia* species. Similarly, *Kniphofia* and *Streptocarpus* had a direct relationship to the distribution range (QDS), with significant *p*-values of 0.031 and <0.001, respectively. This suggests that longer flowering periods would result in greater successful pollination events, which ultimately leads to a larger range size. It is also worth noting that both genera consist of numerous endemic species, therefore suggesting the range sizes of the various species are similar. This was also seen in previous statistical analyses. In addition, *Streptocarpus* reflected a significant relationship between

flowering duration and the number of Perera Units that species are found in. This significant relationship effectively suggests that there is a link between flowering duration and distribution range in the genus, which is not evident in *Kniphofia*. The fact that there is this direct relationship in *Streptocarpus* may also indicate that climate is not as influential on the range sizes as in the case of *Eulophia*.

Table 4.3a. Correlation coefficients for the relationship between flowering duration and the three measures of distribution for each genus included in the study.

Genus	**Pearson's Correlation Coefficient**		
	QDS	*Perera Units*	*Rainfall Zones*
Cussonia	0.0982	0.2390	0.3101
Eulophia	0.8623	0.5812	***0.9303****
Gladiolus	***0.8592****	***0.8544****	***0.5437****
Kniphofia	***0.4400****	0.3074	0.2589
Pavetta	0.5591	0.4145	0.6103
Plectranthus	0.0410	0.0308	0.0060
Searsia	0.3048	0.2211	0.4111
Streptocarpus	***0.5191****	***0.5340****	0.1873
Watsonia	0.0218	0.2336	0.0060
All Genera	0.0737	0.1255	0.0728

* = ***significant correlation*** (*p-value* ≤ 0.05)

On the contrary, *Gladiolus* is the only genus that showed significant relationships with all three measures of distribution. Relationships exist between flowering duration and QDS, Perera Units and rainfall zones (Pearson's Correlation Coefficients are 0.8592, 0.8544 and 0.5437, respectively). *Gladiolus*, like *Streptocarpus*, is likely to be widely distributed across a variety of Perera Units and areas of different climates. As a result of Perera Units having significance, also implies that *Gladiolus* is less likely to be narrowly distributed in an area that is influenced by the various climatic factors, which may be the case with *Eulophia*. This indicates that flowering duration is a successful trait that influences the adaptation and spread of the genus. However, the influence of climate has also been a critical factor that has allowed the *Gladiolus* species to spread across a large distributional range.

The overall correlation included all genera, even those that had data for fewer than five endemic species. QDS, Perera Units nor rainfall zones were significantly linked to the duration of flowering in this case. Therefore, from a general perspective, it is unlikely that flowering duration is correlated to distribution range, and may rather be limited to specific genera. Various traits or adaptations, that genera possess, may suggest that flowering effects distribution patterns in some genera, but not in others. Furthermore, the other correlations that did not show any significance between flowering duration and the measures of distribution may be a result of other floral or morphological traits being more successful than the duration of flowering. Alternately, in some cases certain genera may have to rely on more than one trait to determine successful reproduction and distribution, which then results in wider distribution range sizes. In most cases, for species to be successful, the adaptations that it requires may not allow for extended flowering durations. It is also essential to consider the various factors that may contribute to the patterns that are observed, such as climate and other reproductive traits.

Results from the Analysis of Covariance (ANCOVA) tests in Table 4.3b. (corresponding to Table 3.2.3b.), represents the influence of certain factors and flowering duration on the different measures of distribution. The factors used included both broad and narrow growth forms, as well as genus (all as categorical variables). The adaptations of factors within an environment or various traits amongst different growth forms or genera often determine the success of many species. Therefore, these successful adaptations together with flowering duration may affect the distribution range sizes. The *F*-statistics in Table 4.3b. indicates if there is any significance from the ANCOVA tests or not.

The results show that the fixed factors all have a significant effect on the distributional range size. All fixed factors showed great significance (*p*-values were all 0.001 or less) as determinants of distributional range, together with flowering. Test 1 (QDS, Broad Growth Form, Flowering months) had the highest fixed factor *F*-statistic at 14.248, whereas the *F*-statistic for Test 6 (Perera Units, Genus, Flowering months) had a value of 3.896. It is, however, important to note that the *F*-statistic values of the fixed factors vary according to the fixed factor that was used in the test. Therefore, tests where the broad growth form variable was used have higher *F*-statistic values than those where the genus variable was used. This is likely due to the nature of the values that the groups within each categorical variable were assigned, as well as the number of groups within each categorical variable. The significance

of these statistics suggests that even though flowering may not directly have an effect of distributional range, together with factors such as growth form or genus it does have an indirect effect.

Table 4.3b. The *F*-statistics results of the ANCOVA (Analysis of Covariance)

Set	Test	Source 1 (Fixed Factor)	Source 2 (Covariate)
		F	*F*
A	1	14.248 ***	4.712 *
	2	6.931 ***	4.081 *
	3	5.142 ***	9.222 **
B	4	10.164 ***	8.093 **
	5	4.290 ***	7.495 **
	6	3.896 ***	12.057 ***
C	7	12.850 ***	3.468
	8	5.146 ***	3.256
	9	4.318 ***	4.735 *

(Where No* = $p > 0.05$; *= $p < 0.05$; **= $p < 0.01$ and ***= $p < 0.001$)

Furthermore, from these observations it is possible to additionally deduce that the effect of genus is far greater than the influence of growth from (both broad and narrow) on the distribution range size of different species. Therefore, flowering duration and possibly other floral traits are likely to be nested within genera. Despite the presence of different traits amongst various growth forms, these may have minimal influence on the flowering patterns and traits of species. The flowering patterns amongst species in genera may be a result of adaptability and not only a successful reproductive trait. Consequently, flowering patterns together with other factors indirectly influences the distribution range size of species.

The suggestion of flowering duration being determined within genera becomes more apparent when the majority of the covariate (flowering months) *F*-statistics also show significance. All tests where genus was used as a fixed factor (Test 3; 6 and 9) also had significant covariate values (*F*-statistics and *p*-values) and were the highest within each set. The significance of the

covariates were far greater than the significance of broad and narrow growth forms. This is evident in set C; where the covariates that incorporated broad and narrow growth forms did not have any significant outcomes. This outcome again suggests that genus together with flowering duration have a greater influence on measures of distribution, in comparison to the influence that growth form (broad or narrow) has together with flowering. This could be a result of different flowering adaptations within genera, which may have been a consequence of species radiation or adaptation.

The variation of the significant covariates also illustrates that growth form, even though it does influence distribution to an extent, is not as influential as the genus factor. Additionally, the narrow growth form factor may not have yielded any significant results because, in this case, narrow growth form is nested in broad growth form. Therefore, if broad growth form does influence the relationship between flowering duration and distribution range, so should the respective narrow growth forms. Likewise, growth forms extend beyond genera, therefore the number of species that it includes can be vast and the distributions, as well as flowering durations may be largely varied. Hence there is no apparent effect on the relationship between flowering duration and distribution range size. Various genera may also rely on a number of extrinsic factors that determine the timing of flowering and may also affect the duration of flowering, such a fire, dormancy or pollinators. Flowering is therefore very time sensitive in many species and despite there being some apparent links between flowering duration and distribution range size, other intrinsic and extrinsic factors also need to be taken into consideration.

However, from these results it can be further deduced that flowering duration together with genus characteristics has the most significance on the total distribution of species (QDS) and their distribution in biogeographical units (Perera Units). The significance of flowering and growth form is also evident in the results, but is not as obvious as the influence of genera. However, in the case of rainfall zones, growth forms have no significance on the distribution range size of species. Therefore flowering duration is less likely to effect the distribution of species according to rainfall zones, only in the case where genus characteristics are involved. Hereafter the relationship that these results yield will have to be considered further in discussion with regard to what factors may be manipulating the patterns that have been observed.

Chapter Five
Discussion

5.1. Introduction

Flowering phenology has been extensively studied, incorporating both cross-species coincidence in seasonal patterns, and geographic patterns. Research looking at the duration of flowering has focused primarily on the seasonality of flowering, the changes observed over a few seasons and questions what factors give rise to these changes (e.g. Bawa *et al.*, 2003; Amasino, 2010; Tooke and Battey, 2010). However, these studies rarely focus on patterns directly or indirectly linked to variation in species range size across genera. The flowering patterns seen across the various genera considered in this study is undeniably also due to a number of intrinsic and extrinsic factors that drive these flowering patterns. The first few statistical analyses performed were exploratory ways of identifying any possible patterns among the various genera and the endemic species. However, the Analysis of Covariance (ANCOVA) tested the hypothesis that the duration of flowering seasons has an influence on the range size patterns. The statistical analyses supported this hypothesis, particularly when considering other factors that can influence the length of flowering seasons. However, it is essential to further consider the outcomes of the flowering and distribution patterns observed and the links that exist between them. Furthermore, it is important to understand the possible drivers of these patterns and how these patterns may vary at different geographic scales.

5.2. Flowering patterns

Clear flowering patterns were seen in some genera. These flowering patterns are a good indication of interactions with environmental factors. Some of the distinct flowerings patterns were seen in genera such as *Plectranthus*, *Streptocarpus* and *Pavetta*. The patterns in *Pavetta*, for example, suggest that the species in this genus have similar flowering seasons on an intra-generic level. Tachiki *et al.* (2010), state that flowering synchrony can be observed amongst similar species and between different species too. The intra-generic flowering patterns seen in *Plectranthus* and *Streptocarpus* vary substantially within each of these genera. The flowering patterns of *Plectranthus* show that there are two separate flowering events amongst endemic

species. Factors such as range, climate and pollinator availability could be significant determinants of these patterns. *Streptocarpus* species seem to have a variety of flowering patterns, that may indicate a prolonged flowering season, where some species seem to flower simultaneously, but for various durations; therefore having comparable flowering times. This may occur as a result of widely distributed species, occurring in similar or close environments that are influenced by similar flowering determinants, but at different times over a given period. Johnson (1992) found similar patterns in flowering seasonality in the Cape Floristic Region, where rainfall seasonality was a determinant of flowering of species in both spring and early summer. Species that occurred in winter rainfall areas, had a strong flowering peak in spring, whereas those found in areas that received non-seasonal rainfall were inclined to flower during early summer (Johnson, 1992). This could be used to explain the two distinct flowering patterns seen amongst the endemic *Plectranthus* species. The rainfall seasonality for *Plectranthus* species in eastern South Africa is somewhat different to that in the Cape Floristic Region, but may display flowering patterns according to the rainfall patterns of eastern South Africa. Tachiki *et al*. (2010) also found that across different environments, there is a diversity of flowering season determinants. For example, in tropical regions, flowering seasons of plants are determined not only by environmental cues but some are dependent on availability of pollinators. Similarly, this could be attributed to the flowering pattern of the endemic *Streptocarpus* and *Pavetta* species.

Moreover, *Streptocarpus* and *Pavetta* share similar flowering seasonality patterns. Although from different genera and different growth forms, the flowering durations of some of the species are in fact identical. *Eulophia*, *Watsonia* and *Zantedeschia* species also show inter-generic similarities which could possibly be a result of endemic species occurring in the same area and competing for the same resources and hence flower at the same time. Species such as *E. cooperi* and *E. meleagris* occur in close proximity to *W. occulata*; *W. confusa*; *W.wilmsii* and *Z. elliottiana* and *Z. pentlandii*, particularly in the northern areas of the Great Escarpment and the Pondoland region; therefore suggesting that these species may be constrained by similar environmental factors. Stevenson *et al.* (2008) recognised that flowering synchrony, was one of the most common flowering patterns observed among tropical species, in comparison to continuous flowering which was found to be quite rare. In addition to this, Tachiki *et al.* (2010) examined synchronised flowering of phylogenetically distant species in a tropical region. Their findings showed that the synchronisation allowed for optimal pollinator attraction. As flowering peaked, the number of pollinators increased, therefore

decreasing the effect of interspecific competition between species (Tachiki *et al.*, 2010). Additionally, the pollinator activity of the *Eulophia, Watsonia* and *Zantedeschia* species may coincide with the flowering time of these species. Alternately, species may also choose to flower at different times to avoid competition for resources, pollinators or dispersers, suggesting why the rest of the genera used in the study do not display major intra-generic or inter-generic flowering pattern similarities.

In assessing these intra-generic and inter-generic flowering pattern similarities, such as those in genera like *Streptocarpus*, *Pavetta* and *Plectranthus*, the possible effect of phylogenetics was not taken in to account. The flowering patterns of individual or numerous species therefore; could also be a result of inherited shared pattern from a common ancestor or of the convergence of distantly related lineages or species (Saldana-Acosta *et al.*, 2008). The effect of genetic variation within species cannot be discarded either, in assessing the patterns observed in this study. Gitzendanner and Soltis (2000) compare the genetic variation between rare and widespread species, suggesting that the genetic variation is limited amongst rare species, in comparison to widespread congener species. This suggestion that rare species have limited genetic variability could advocate why the endemic species of genera such as *Streptocarpus* and *Pavetta* have similar or coinciding flowering patterns. Nevertheless, Wright and Calderon (1995) identified that phylogenetics only had a significant influence on the timing and onset of flowering patterns, and not necessarily on the duration. Therefore phylogenetics may only explain a limited proportion of the overlapping flowering patterns seen.

Other factors, such as growth form, which are also linked to phylogenetics, could also be assumed to be a driver of flowering patterns that have been identified, particularly in the case of *Streptocarpus* and *Plectranthus*. The similarities of flowering patterns amongst a few species, suggest that these species occur in a similar environment where dicotyledonous herbs may flourish. *Streptocarpus* and *Plectranthus* species are well-represented in certain vegetation types in eastern South Africa, such as forest, which may allow these species to have similar flowering times (Hilliard and Burtt, 1972; Van Jaarsveld, 2006). This may also be equally applicable to *Eulophia*, *Watsonia* and *Zantedeschia*, the monocotyledonous geophytic herbs, which have similar flowering patterns. This may suggest that herbaceous plants have greater similarities with regard to flowering patterns than woody plants do. However, the similarities between the flowering patterns in *Streptocarpus* and *Pavetta* cannot

be ignored, *Pavetta* being a woody genus, while *Streptocarpus* is herbaceous. In this case other drivers of flowering would have to be considered as causes of the observed patterns.

The duration of flowering is in fact clearly affected by the seasonal onset of flowering. Kang and Jang (2004) illustrated that flowering duration in temperate Korean angiosperms were dependant on season. Species had extended flowering during summer and autumn months, rather than spring. Furthermore, duration of flowering was not correlated to temperature or rainfall, but rather to the variations in season and phylogenetics. Longer flowering durations are also found to result in greater successional rates of species (Kang and Bawa, 2003). When closely examining the data, most *Streptocarpus* species begin flowering during the summer months, and do not have unusually long flowering as suggested by Kang and Bawa (2003). However, species that flower from late spring or early summer, such as *S. haygarthii* and *S. polyanthus* (all three subspecies) have relatively extended flowering periods of up to eight months. Therefore, some *Streptocarpus* species do not necessarily flower longer during summer months, but rather when the onset of flowering is before the summer and then extends into early or mid-autumn. It must be noted that Kang and Bawa (2003) observed these patterns in tropical tree species, whereas *Streptocarpus* is a temperate herb. However, it may be possible that these patterns are not limited to growth form, but rather to climatic variations.

It is also possible, from a different perspective, to consider the variability that exists across the geographic ranges of species that may act as drivers of flowering patterns. Flowering patterns across different ranges and environments are determined by a number of other extrinsic and intrinsic factors. For example, when considering the intra-generic relationships that occur in *Plectranthus*, with two distinct flowering season clusters, then the influence of within-range environmental variability has to also be taken account when analysing these patterns. Newstrom *et al.* (1994) found that phenological patterns, which include flowering seasonality, vary between temperate and tropical species. Greater phenological variability in tropical species is identified, than in temperature species (Newstrom *et al.*, 1994). Furthermore, the main differences found in tropical and temperate regions are in temperature and photoperiod. These two extrinsic factors have been widely examined in explaining flowering phenology and the onset and timing of flowering. Although there is no evidence that there is a link between photoperiod or temperature and flowering duration in this study, these factors do vary significantly across diverse ranges, and may affect flowering seasonality indirectly. *Plectranthus* species may be likely to experience these differences in eastern South

Africa, as temperatures can vary in the region at any given time. Therefore flowering durations may be similar, but the timing slightly altered as a result of differing temperatures, particularly from low-lying coastal areas to the inland plateau. *Plectranthus* species which have longer flowering durations from late spring until end of summer, such as *P. saccatus* (subsp. *saccatus*) and *P. purpuratus* (subsp. *purpuratus*), which occur in the coastal areas of eastern South Africa, in comparison to species such as *P. ramosior* and *P. xerophilus*, which occur in the Highveld areas and flower over late summer into autumn for significantly shorter periods. Therefore, the variation of temperature across geographic ranges amongst various species from coastal to Highveld areas, may act as an influence. Though these patterns may not be blatantly obvious it does suggest that variability in geographic range is one of many key drivers of timing, duration and variability in flowering seasons.

In order to support some of these points, however, it is important to do extensive field research on the various flowering phenologies of these genera, and investigate the possible community-level interactions that may exist. The results of this study, based on secondary data, of selected genera has limited application. The patterns identified may obscure a great amount of variation, especially intra-specific. Field work is needed to validate these observed patterns. Identifying particular flowering patterns at given localities would also allow for the identification of inter-specific similarities, such as synchronized or prolonged flowering seasons or even increases in pollinator availability.

5.3. Range size patterns

Range size patterns can vary widely across different plant species and may depend significantly on environmental factors or ecosystem dynamics, which ultimately determine the range of a species (Brown *et al.*, 1996). The plant species considered here show a great amount of variation in the range sizes of the different broad and narrow growth forms, as well as at genus level. Among the growth forms, dicotyledonous herbs have the most limited array of geographic range sizes. The majority of these species are narrow endemics, thereby their distribution being limited, irrespective of the measures used. The extensive representation of rare endemics and small distributional range patterns has been identified in many macroecological studies in the past, particularly with regard to conservation efforts (Gaston, 1991; Gaston, 1994; Myers, 2000). This pattern is a likely determinant of the range size patterns seen in the dicotyledonous herbs. However, not all dicotyledonous herbs have a

narrow range, with a few species having larger distributional ranges, depicted by outliers on the box-and-whisker plot (Figure 4.2b.).

The range size patterns of the monocotyledonous geophytic herbs and dicotyledonous woody species indicate that these lineages or taxa have a wider distribution in comparison to dicotyledonous herbs, though among geophytes larger ranges are mostly noted in *Zantedeschia* and *Kniphofia*. These patterns may be determined by factors such as dispersal mechanisms, as geophytes seldom have specialised long-distance dispersal (but *Zantedeschia* fruit is fleshy and is presumably bird-dispersed). Dicotyledonous woody species may rely more often on generalist pollinators, rather than specific pollinators and this may allow them to achieve wider distributional ranges. Dicotyledonous herbaceous species may also have smaller range sizes because of reliance on specific pollinators. Kelly and Woodward (1996) found that wind-pollinated species in British flora had greater range sizes in comparison to non-wind pollinated species.

Subdividing broad growth forms into narrow growth forms showed that, in woody plants, both trees and shrubs have the greatest distributional ranges, with trees having slightly larger range sizes. Kelly and Woodward (1996) also identified this in the British flora, where trees had larger range sizes than woody shrubs. Besides, woody species in general are less likely to be susceptible to factors such as predation and fires once established. In the box-and-whisker plot *Streptocarpus* is the dicotyledonous herb that consists of numerous narrowly distributed species (Figure 4.2c.). However, in contrast, the range size patterns of other dicotyledonous herbs are similar to those of the monocotyledonous geophytic herbs.

Similarly, when considering variation in the range size patterns at genus level, it is essential to consider specific factors that might determine range sizes in particular genera. It is clear that *Cussonia* species have the largest range sizes amongst the included genera (Figure 4.2c.). It may be argued that patterns such as these can be related to niche breadth. According to Williams *et al.* (2006), species with broad ecological niches are likely to have wide distributional ranges, as these species are likely to be well adapted to a variety of environments. Species such as those in the genus *Cussonia* could be adapted to establish and survive in a broad range of environmental conditions, resulting in larger range sizes. Niche breadth could perhaps also describe why genera such as *Zantedeschia*, *Streptocarpus*, *Eulophia* and *Watsonia* have such narrowly distributed species. These species may require

specific environmental conditions, which may only occur in a highly localised (small) area, to establish and survive. The specific niche dimensions involved may vary from one genus to another, or even within genera. The resources species require to expand their respective range sizes could span a number of different factors, from pollinators to nutrients or even water availability.

The seed size of species is another aspect that could partly explain the range size patterns seen at genus level. The smaller the seed size, the greater the potential dispersal range, which allows species to expand the geographic ranges in which they occur (Westoby *et al.*, 1996). The broad range sizes of some *Searsia*, *Satyrium*, *Kniphofia* and *Gladiolus* species could be a result of this. Additionally, the link between seed size and range size it is dependent on how many seeds a plant produces that are distributed and establish successfully. This factor, however, may have to be disregarded in the case of *Cussonia*. If this assumption were valid for all genera, then *Cussonia* species may produce high numbers of small-sized seeds, which are easily dispersed and established successfully. However, the association between seed size and geographic range may not necessarily be the only determinant and would have to be considered with other biotic and abiotic factors.

Many of these possible geographic range size determinants have not been accounted for in the data set or even in this discussion section, but may represent explanations of the patterns that are being observed in the genera considered here. Many of the determinants described so far are extrinsic factors, part of the environment in which the species exist. However, from an intrinsic perspective, two of the most important determinants of range size patterns are phylogenetic relatedness and phenotypic plasticity across genera and species. The latter could be linked to the concept of niche breadth. Species with greater phenotypic plasticity have greater chances of evolving adaptations in new environments, therefore allowing the geographic range of the species to expand (Pohlman *et al.*, 2005). Kelly and Woodward (1996) believe that phylogenetic relatedness is an important aspect of ecological explanations of range size patterns or other traits that may be identified.

Despite the fact that phylogenetics was not taken into account in this study, the relationship that possibly exists between the flowering patterns and range size patterns can still be explained and understood from various other perspectives. Thus it is still essential to

understand all the possible contributing factors that have been discussed thus far, and how these factors influence the main findings of this study.

5.4. Linking flowering and range size patterns

It was necessary to find a way to uncover the possible relationship that exists between the flowering and range size patterns, both of which have been discussed so far. Correlations were first used, to explore links between flowering durations and the different measures of distribution, at a genus level. Thereafter, ANCOVAs were used to include other variables to determine if there are any indirect links between flowering durations across the various measures of distribution. What was the most important factor in using the correlation and ANCOVA analyses was to test the hypothesis that the relationship between flowering and range sizes exists. The results from both the correlation and ANCOVA analyses support the hypothesis in different ways, therefore supporting the assertion that there are both direct and indirect links that influence this relationship.

The correlation results showed that the direct association between flowering duration and range size, at genus level, is not a general pattern seen across all individual plant genera or generally across all plant genera taken together. Only four genera showed significant links to some or all the measures of distribution. Flowering duration in *Eulophia* species is closely linked to the rainfall zones that the species occur in. According to data these endemic species which are found in various parts of eastern South Africa, may require the seasonality of rainfall to flower. This is exhibited in these patterns, which are similar to those identified by Johnson (1992) in Cape species and Bawa *et al.* (2003) in tropical tree species and is hence correlated to the distribution of species across these rainfall seasonality zones.

Streptocarpus, which has been noted for its flowering and range size patterns, also exhibited a correlation between the general (Quarter Degree Square-QDS) distribution of species, as well as the distribution of species across Perera Units. The association between the general (QDS) distribution of *Streptocarpus* species and flowering suggests that the extended flowering season is significant in determining the distribution of endemic species. When considering narrow distribution patterns, however, the link between flowering and distribution appears less apparent. In cases where a few species flower for a shorter duration in comparison to other species, such as *S. modestus* and *S. pogonites*, distribution sizes are relatively small.

Furthermore, there may be various drivers across the Perera Units in which *Streptocarpus* species occur, that allow the initiation of flowering to occur at different, yet closely-related times. In addition, these drivers may further limit the extent of how far these narrow endemics can spread.

There were no obvious flowering and distribution patterns exhibited by *Kniphofia*, prior to the correlation identifying the link between the flowering duration and general (QDS) distribution. Often when scrutinising flowering patterns, episodic flowering is also considered a flowering pattern (Stevenson *et al.*, 2008). The flowering duration of *Kniphofia* species still effectively links to the distributional range sizes. Furthermore, the correlation between general (QDS) range size and flowering duration seen in *Streptocarpus* and *Kniphofia* also suggests that longer flowering periods allows for more successful pollination events, ultimately expanding the range of these endemic species. Alternately, shorter flowering period may result in fewer pollination events and a smaller range, as species may rely on specific pollinators.

Unlike other genera, *Gladiolus* was the only genus to show a significant correlation between flowering season duration and all three measures of distribution (QDS, Perera Units and rainfall zones). In *Gladiolus* most species have overlapping flowering periods, but the length of these periods differs slightly. Some species that have narrow distributions have significantly shorter flowering durations than species that flower over longer periods. For example, species which flower for two months or less such as *G. microcarpus* and *G. macneilii* have significantly smaller range sizes in comparison to species which flower for five months or more, such as *G. oppositiflorus* and *G. sericeoviliosus* (subsp. *sericeoviliosus*) which have wider distributions. Furthermore, species flowering for three or four months have varied range sizes, however, it can strongly be suggested that endemics species that have longer flowering periods have wider distributions. This may be similar when considering the range size patterns, which are varied, but not to a large extent. This correlation across all the measures of distribution suggests that *Gladiolus* has a wide niche breadth, as it is able to adapt to a number of different environmental conditions.

The ANCOVA results showed the overall effect of flowering duration, together with other factors, on the distribution ranges of endemic eastern South African species. Results suggested that growth form (whether broad or narrow) and genus, together with flowering

time, has a significant effect on the general distribution range (QDS) of species and Perera Units. Although the correlation results did not show any overall relationship between flowering and range size, the ANCOVA results do. This suggests that flowering duration patterns influence the distribution of plant species across various ranges, when considering other intrinsic factors. The hypothesis that flowering length has an effect on the geographic range size of endemic plant species is hence supported.

Moreover, when considering the rainfall zones, only flowering duration with the incorporation of genus, showed significance. Growth forms (broad and narrow) did not have any effect on the range size across various rainfall zones, when considered with the flowering times. Thus this failed to confirm the fact that there is a strong association between growth form and flowering (e.g. Stevenson *et al.*, 2008). This assumption is clearly not supported when taking rainfall seasonality into account. When general distribution sizes and distribution across Perera units are considered, growth form is closely associated to flowering variations and hence associated with the different measures of distribution. Furthermore, these results suggested that flowering duration is characteristic to genera rather than to growth forms, because flowering duration in interaction with genus identity influenced all the measures of distribution significantly.

Flowering durations and variations are closely associated with genus identity, thus phylogenetics may still be assumed to have an underlying influence on both the flowering duration of species, or, alternatively, on the distribution range sizes. Phylogenetics, as mentioned previously, was not taken into account in this study. Bawa *et al.* (2003) state that flowering can be constrained by phylogenies, through evolutionary traits, but this is not necessarily the case when taking into account flowering duration as it is more likely to influence the initiation of flowering. Conversely, Stevenson *et al.* (2008) found that taxonomically related (and therefore phylogenetically related) species that had varied distributions did not flower simultaneously, therefore suggesting that flowering, even the initiation of flowering, is not completely phylogenetically constrained.

If flowering is not entirely phylogenetically constrained, then validation of flowering times through field work becomes more important. As mentioned previously, no field work was conducted for this study, due to the vast area that was covered and the time constraints of the project. The number of genera and documentation of flowering would require a substantial

time in the field over several years. However, field work would enable the validation of data that was gathered from all the primary sources. Additionally, it would also allow for the identification of any changes with regard to the measured variables. Particularly with regard to flowering times which may shift as a result of changes from various environmental dynamics, such as biological invasions and climate change.

5.5. Relevance for biological invasions and climate change

The growing concern of biological invasions has resulted in extensive research on this issue across various geographic scales, and has increasingly been of interest in the southern African region. Some of the main concerns with biological invasion events are the changes associated with ecosystem functioning, biodiversity and evolutionary processes (Küster *et al.*, 2008). In a macroecological perspective, invasions can simply be viewed as a mechanism for certain species to expand their geographic range sizes. However, biological invasion, both plant and animal, are both creating several ecological issues on a global scale and are of particular threat to sensitive and biodiverse environments. The outcome of repeated successful invasive events would be the mixing of global biota on various scales, which will ultimately lead to homogeneous ecosystems with similar functions. Some species are likely to also evolve certain adaptations in order to survive in the new ranges and might even, as a consequence, continue to expand their geographic ranges. Ecologists have therefore primarily looked at trait specifics which have enabled alien species to become invasive across various ranges (Lake *et al.*, 2004; Pyšek and Richardson, 2007; Küster *et al.*, 2008; Pyšek *et al.*, 2009).

Flowering phenology is one of the traits that has been considered to assist species in becoming successfully invasive in different environments. In contrast to other studies, such as Pyšek and Richardson (2007), Lake *et al.* (2004) found that the growth form, like flowering patterns, has little influence on invasiveness. However, flowering duration was found to play a significant role in the expansion of geographic range sizes of alien species. Goodwin *et al.* (1999) found that invasive European species flowered for a longer duration than native species in Canada. Similarly, Lloret *et al.* (2005) reported that invasive species on Mediterranean islands flowered for long durations and are hence more prolific than some native species. It may therefore be possible to identify species that have potentially invasive flowering traits using the methodological approaches advocated in this study. Godoy *et al.* (2009) also established that flowering is a conservative trait, as species have the ability to

retain specific flowering traits that are determined through the species' genetic makeup and therefore will not alter the flowering times of alien species when introduced into a new environment. However, species originating from certain climatic environments, such as temperate or tropical areas, may alter their flowering dynamics according to the new environment over time. Therefore flowering duration together with climatic conditions can be used to determine the invasibility of species. Flowering traits will play an increasingly important role in invasibility given the predicted rate of climate change (Hulme, 2010).

Flowering phenology, in particular the initiation of flowering, of many species is dependent on seasonal changes. Recent evidence has shown that the changes in climate are now causing major shifts in plant regimes, particularly in flowering phenology (Fitter and Fitter, 2002; Primack and Miller-Rushing, 2011; Cleland *et al.*, 2012). Hovenden *et al.* (2008) suggested that flowering durations are likely to change according to variations in rainfall and temperature, which will results in range shifts for many plant species. In addition to the range shifts, Ward and Masters (2007) believe that climate change will also increase the availability of niches, further worsening the problems associated with invasiveness. However, it is likely that plant species that flower for a longer duration, such as species described by Lloret *et al.* (2005), are bound to adapt quicker and be more successful. If changes such as these occur amongst the species considered in this study, the patterns that are currently being observed are likely to change in the future or become non-existent. Furthermore, Davis *et al.* (2010) found that taxonomically related species, irrespective of geographic relation, had similar phenological responses to climate change. Therefore only a limited number of species may be able to survive rapid changes in climate. In addition, the changing patterns in flowering phenology will also affect pollinator availability, which has already been identified by Burkle and Alarcón (2011) and Miller-Rushing and Primack (2008). By examining and understanding the effects of flowering seasonality and duration, these drastic changes may be better understood. Future studies need extensive and regular field work so that these shifts in flowering phenology are well documented and understood across various plant species.

The scale of the study area and allocated time, should be taken in to account if field work is being conducted, as flowering patterns undoubtedly varying across different scales. The flowering patterns and respective relationships that are identified at local or regional scales are different to those seen at a global scale. Most studies conducted on aspects of flowering phenology, including the present study, are based on regional data (e.g. Kang and Bawa,

2003; Godoy *et al.*, 2009; Ranjitkar *et al.*, 2012). In these studies there are regional variations in flowering phenology, which are influenced by various environmental factors. However, each study aims to explain flowering phenologies that may be experienced in regions with similar species and environmental conditions. Regional studies also allow for smaller areas to be investigated in more depth, so details accounting for flowering patterns can be described. Global ecological perspectives describe patterns and relationship of various organisms at a global level. The coarse geographic scale used in many studies results in patterns being wide-ranging and deficient in the more complex details that may be identified at finer scales. This is seen in Kier *et al.* (2005); Kreft and Jetz (2007) and Baselga *et al.* (2012), where reference is made to one or a few different environments from a global perspective and the drivers that affect the plant diversity patterns that are observed across these environments.

Like global range size shapes, flowering patterns are likely to exist. Therefore; if flowering patterns can be identified at a global scale, similar to the range size patterns and shapes established by Baselga *et al.* (2012), it may then also be possible to determine the most common and main determinants or drivers of flowering patterns on a global level, in particular regard to the duration of flowering.

Despite the brief, but similar assumptions made by Kang and Jang (2004) and Godoy *et al.* (2009), from these outcomes it can safely be assumed that there is no single determinant of the link between flowering and range size patterns. There are many drivers of flowering seasonality, both on an interspecific and intraspecific level. Range size patterns are also determined by a number of factors, resulting in a large variation of flowering durations amongst genera. However, results suggested that for genera such as *Kniphofia*, *Gladiolus*, *Streptocarpus* and *Eulophia* there is both a direct and indirect relationship between the length of flowering seasons and range size, largely supporting the main hypothesis of this study. It is also further probable that this link between flowering duration and distribution operates both ways, where wider distributions of a species allows for longer flowering seasons and longer flowering seasons allows for the expansion of range. Future research in the field would, however, have to take into account the global changes that are occurring across various environments and how this affects the flowering duration as well as the distribution of species.

Chapter Six
Conclusions

This study compared the flowering season length and distribution ranges of thirteen plant genera, which consist of numerous species endemic to eastern South Africa. The assessment allowed for the identification of any possible relationships that may exist between the flowering duration and range sizes of these species. The overall results supported the hypothesis that the length of flowering seasons of endemic species significantly influences the distributional range that these species occupy. The influence of flowering durations had both a direct and indirect association with the range size of these species. The significance of the relationship between flowering and distribution in four genera suggested that both the flowering and distribution patterns were either a result of successful pollination events due to extended flowering (or *vice versa*) or these genera have a large range across diverse climatic zones, allowing flowering season to differ. The relationship between the two variables were genus dependent, more than growth form dependent. Moreover, it could be safely assumed that flowering is not entirely constrained by phylogenies; therefore there is no single variable or driver that is able to determine flowering patterns, particularly across wide distributions (Stevenson *et al*., 2008). The relationship is hence assumed to be significant in both ways (i.e. flowering affects distribution and distribution affects flowering).

In identifying the relationship between the length of flowering seasons and geographic range sizes, this area of study could become of growing importance. Especially as flowering seasons vary and geographic distributions shift as a result of current changes in climate, biological invasion and various other environmental fluctuations. Many mechanisms of the complexities of flowering phenology and geographic range determinants are well understood. These mechanisms can therefore be applied adequately to create greater depth of understanding of the relationship between flowering durations and geographic range sizes. Additionally, by understanding the individual drivers that work synergistically to forge these patterns between flowering and distribution, particularly in climate change scenarios and increased biological invasions, effective strategies can be developed in managing these current issues by conservationists.

Recommendations for future research in this field would be to consider evolutionary closely related endemic species for both flowering and distribution patterns, despite the broad statement of Stevenson *et al*. (2008) that flowering is not entirely controlled by phylogeny. Furthermore, dependent on the extent of the study area, adequate field data should be collected and compared to primary data sources, similar to those used in this study.

In conclusion, the general patterns linking flowering and geographic distribution sizes of endemic species are apparent at a regional scale. These patterns could vary accordingly at smaller (local) scales or at a global scale. It would be of great interest, however, if similar patterns are seen across several regions that are ecologically similar, and how these patterns may vary across diverse regions and amidst climatic and biological changes in the environment.

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APPENDICES

Appendix A. Three letter codes for the Perera (geographic) Units as used by Perera *et al.* (2011)

Code	Name
ACB	*Albany Coastal Belt*
AKR	*Intrusion of Lower Karoo into Albany*
AWB	*Amatola-Winterberg*
CBV	*Central Bushveld*
DBP	*Drakensberg Plateau*
DEE	*Drakensberg-Eastern-Cape Escarpment*
DKE	*Drakensberg-KwaZulu-Natal Escarpment*
HUK	*Highveld-Upper Karoo*
INH	*Inhambane*
KBV	*Kalahari Bushveld*
KNY	*Knysna*
MLV	*Mozambique Lowveld*
NBV	*Northern Bushveld*
NCB	*Natal Coastal Belt*
NDH	*Northern Dry Highveld*
NGO	*Ngoye*
NMD	*Natal Midlands*
NME	*Northern Mpumalanga Escarpment*
NMH	*Northern Mesic Highveld*
NMO	*Northern Mopane*
NMP	*Northern Maputaland*
NMV	*Northern Middleveld*
NNT	*Northern Natal*
PND	*Pondoland*
SDH	*Southern Dry Highveld*
SME	*Southern Mpumalanga Escarpment*
SMH	*Southern Mesic Highveld*
SMO	*Southern Mopane*
SMP	*Southern Maputaland*
SMV	*Southern Middleveld*
SNB	*Sneeuberg*
SPB	*Soutpansberg*
STR	*Southern Transkei Coastal Belt*
TMD	*Transkei Midlands*
UKR	*Upper Karoo*
WLB	*Wolkberg*
WTB	*Waterberg*

Appendix B 1a. Distribution, flowering and growth form data collected for *Cussonia*, *Eulophia*, *Gymnosporia*, *Pavetta* and *Satyrium* species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Cussonia	*gamtoosensis* Strey	3	5	5	2	2	1
(1)	*nicholsonii* Strey	3	5	20	7	3	5
	paniculata Eckl. & Zeyh. subsp. *paniculata*	3	5	140	17	5	3
	thyrsiflora Thunb.	3	5	49	6	4	3
	transvaalensis Reyneke	3	5	83	19	3	3
Eulophia	*calanthoides* Schltr.	1	2	16	9	2	3
(8)	*coddii* A.V.Hall	1	2	2	2	1	1
	cooperi Rchb.f.	1	2	10	5	2	2
	macowanii Rolfe	1	2	14	5	3	4
	meleagris Rchb.f.	1	2	5	5	2	2
Gymnosporia	*bachmannii* Loes.	3	5	9	3	3	8
(2)	*rubra* (Harv.) Loes.	3	5	29	7	2	12
	uniflora Davison	3	6	10	4	2	6
Pavetta	*bowkeri* Bremek.	3	6	23	4	4	2
(5)	*capensis* (Houtt.) Bremek. subsp. *capensis*	3	6	46	9	4	4
	capensis (Houtt.) Bremek.subsp. *komghensis* (Bremek.) Kok	3	5	28	8	4	4
	kotzei Bremek.	3	6	25	13	3	3
	natalensis Sond.	3	5	9	3	2	3
Satyrium	*hallackii* subsp *hallackii* Bolus	1	2	6	3	2	3
(11)	*membranaceum* Sw.	1	2	31	7	4	3
	rhodanthum Schltr.	1	2	2	2	2	1

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 1b. Distribution, flowering and growth form data collected for *Searsia* species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Searsia	*acocksii* (Moffett) Moffett	3	6	9	2	2	2
(3)	*albomarginata* (Sond.) Moffett	3	6	3	2	1	1
	batophylla (Codd) Moffett	3	6	6	3	2	1
	carnosula (Schönland) Moffett	3	6	16	4	4	3
	crenata (Thunb.) Moffett	3	5	39	4	3	4
	dracomontana (Moffett) Moffett	3	6	3	2	1	4
	engleri (Britten) Moffett	3	5	15	5	2	2
	fastigata (Eckl. & Zeyh.) Moffett	3	6	24	7	3	2
	gracillima (Engl.) Moffett	3	6	22	4	3	4
	keetii (Schönland) Moffett	3	6	21	6	3	6
	kwazuluana (Moffett) Moffett	3	6	4	1	2	2
	longispina (Eckl. & Zeyh.) Moffett	3	5	34	3	3	5
	magalismontana. (Sond.) Moffett subsp. *coddii* (R.& A.Fern.) Moffett	3	6	9	2	2	6
	maricoana (Baker f.) Moffett	3	6	2	1	1	2
	pondoensis (Schönland) Moffett	3	6	15	4	3	5
	pterota (C.Presl) Moffett	3	5	14	2	1	1
	refracta (Eckl. & Zeyh.) Moffett	3	5	20	6	3	1
	rigida (Mill.)	3	6	124	21	5	5
	rudatisii (Engl.) Moffett	3	6	2	1	2	5
	sekhukhuniensis (Moffett) Moffett	3	6	7	1	2	2
	tridactyla (Burch.) Moffett	3	5	28	3	2	2

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 1c. Distribution, flowering and growth form data collected for *Searsia* (cont.), *Gladiolus* and *Zantedeschia* species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Searsia	*wilmsii* (Diels) Moffett	3	6	12	4	3	2
(3)	*zeyheri* (Sond.) Moffett	3	6	34	8	2	2
Gladiolus	*calcaratus* G.J.Lewis	1	2	6	1	2	3
(9)	*cruentus* T.Moore	1	2	3	1	2	2
	exiguous G.J.Lewis	1	2	6	2	2	3
	gueinzii Kunze	1	2	21	5	2	3
	macneilii Oberm.	1	2	4	2	2	1
	microcarpus G.J.Lewis	1	2	3	1	1	2
	oppositiflorus Herb.	1	2	38	11	3	5
	pole-evansii I.Verd.	1	2	4	2	2	2
	pretoriensis Kuntze	1	2	11	1	1	2
	robertsoniae F.Bolus	1	2	8	3	2	3
	rufomarginatus G.J.Lewis	1	2	4	1	2	3
	sericeovillosus Hook.f. subsp. *sericeovillosus*	1	2	47	14	3	7
	vernus Oberm.	1	2	11	7	2	3
	vinosomaculatus Kies	1	2	17	5	2	3
	wilsonii (Baker) Goldblatt & J.C.Manning	1	2	29	8	4	3
Zantedeschia	*elliottiana* (W.Watson) Engl.	1	1	3	2	2	3
(13)	*jucunda* Letty	1	1	3	1	2	3
	pentlandii (R.Whyte ex W.Watson) Wittm.	1	1	7	3	2	2
	valida (Letty) Y.Singh	1	1	1	1	1	6

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 1d. Distribution, flowering and growth form data collected for *Kniphofia* species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Kniphofia	*albescens* Codd	1	1	20	6	2	3
(10)	*baurii* Baker	1	1	28	10	2	3
	breviflora Baker	1	1	11	3	1	3
	buchananii Baker	1	1	14	4	2	2
	citrina Baker	1	1	11	4	2	3
	coralligemma E.A.Bruce	1	1	12	3	2	3
	drepanophylla Baker	1	1	3	1	2	3
	ensifolia Baker subsp. *autumnalis* Codd	1	1	20	4	3	2
	evansii Baker	1	1	3	1	1	2
	fibrosa Baker	1	1	10	5	3	2
	flammula Codd	1	1	1	1	1	3
	fluviatilis Codd	1	1	17	6	2	2
	gracilis Baker	1	1	29	6	2	5
	ichopensis Schinz	1	1	24	5	2	4
	latifolia Codd	1	1	4	2	1	2
	laxiflora Kunth	1	1	64	8	3	4
	littoralis Codd	1	1	18	4	2	3
	parviflora Kunth	1	1	34	8	2	3
	pauciflora Baker	1	1	4	3	2	3
	rigidifolia E.A.Bruce	1	1	8	2	2	2
	rooperi (T.Moore) Lem.	1	1	18	6	3	4

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 1e. Distribution, flowering and growth form data collected for *Kniphofia* (cont.) and *Streptocarpus* species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Kniphofia **(10)**	*triangularis* Kunth subsp. *obtusiloba* (A.Berger) Codd	1	1	15	6	3	4
	typhoides Codd	1	1	23	8	2	2
	tysonii Baker subsp. *tysonii*	1	1	33	6	2	3
Streptocarpus **(4)**	*baudertii* L.L.Britten	2	3	2	2	2	3
	caeruleus Hilliard & B.L.Burtt	2	3	2	1	2	6
	candidus Hilliard	2	3	2	2	1	4
	cooksonii B.L.Burtt	2	3	4	3	1	5
	cooperi C.B.Clarke	2	3	4	3	1	4
	cyaneus S.Moore subsp. *longi-tommii* Weigend & T.J.Edwards	2	3	4	1	2	5
	cyaneus S.Moore subsp. *nigridens* Weigend & T.J.Edwards	2	3	13	5	2	5
	cyaneus S.Moore subsp. *polackii* (B.L.Burtt) Weigend & T.J.Edwards	2	3	11	3	2	5
	decipiens Hilliard & B.L.Burtt	2	3	2	1	1	2
	denticulatus Turrill	2	3	2	1	2	3
	fanniniae Harv. ex C.B.Clarke	2	3	4	3	1	6
	gardenii Hook.	2	3	23	8	1	6
	grandis N.E.Br. subsp. *grandis*	2	3	9	5	2	6
	haygarthii N.E.Br. ex C.B.Clarke	2	3	24	5	2	8
	johannis L.L.Britten	2	3	3	2	2	3
	kentaniensis L.L.Britten & Story	2	3	2	1	1	3
	latens Hilliard & B.L.Burtt	2	3	2	1	1	4
	meyeri B.L.Burtt	2	3	19	7	5	4

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 1f. Distribution, flowering and growth form data collected for *Streptocarpus* (cont.) species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Streptocarpus	*modestus* L.L.Britten	2	3	2	2	2	2
(4)	*molweniensis* Hilliard subsp.. *eshowicus* Hilliard & B.L.Burtt	2	3	1	1	1	3
	molweniensis Hilliard subsp. *molweniensis*	2	3	2	1	2	3
	montigena L.L.Britten	2	3	1	1	1	3
	parviflorus Hook.f. subsp. *parviflorus*	2	3	4	2	2	4
	parviflorus Hook.f. subsp. *soutpansbergensis* Weigend & T.J.Edwards	2	3	2	1	1	4
	pogonites Hilliard & B.L.Burtt	2	3	1	1	1	2
	pole-evansii I.Verd.	2	3	4	2	2	3
	polyanthus Hook. subsp. *dracomontanus* Hilliard	2	3	7	2	1	8
	polyanthus Hook. subsp. *polyanthus*	2	3	6	4	2	8
	polyanthus Hook. subsp. *verecundus* Hilliard	2	3	5	3	2	8
	porphyrostachys Hilliard	2	3	4	2	2	3
	primulifolius Gand.	2	3	12	4	4	5
	prolixus C.B.Clarke	2	3	4	1	2	3
	rexii (Bowie ex Hook.) Lindl.	2	3	44	10	4	7
	rimicola Story	2	3	1	1	1	4
	saundersii Hook.	2	3	1	1	1	2
	silvaticus Hilliard	2	3	7	4	2	4
	trabeculatus Hilliard	2	3	3	2	2	5
	vandeleurii Baker f. & S.Moore	2	3	7	3	2	4
	wendlandii Spreng.	2	3	3	2	2	4

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 1g. Distribution, flowering and growth form data collected for *Plectranthus* species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Plectranthus	*aliciae* (Codd) Van Jaarsv. & T.J.Edwards	2	4	10	2	2	3
(6)	*dolichopodus* Briq.	2	4	21	10	3	8
	dolomiticus Codd	2	4	1	1	1	2
	ecklonii Benth.	2	4	52	13	5	3
	elegantulus Briq.	2	4	7	3	2	3
	ernstii Codd	2	4	5	1	2	8
	hilliardiae Codd subsp. *hilliardiae*	2	4	5	2	1	5
	lucidus Van Jaarsv. & T.J.Edwards	2	4	1	1	1	3
	malvinus Van Jaarsv. & T.J.Edwards	2	4	1	1	1	3
	mutabilis Codd	2	4	17	5	2	5
	mzimvubensis Van Jaarsv.	2	4	1	1	1	4
	oertendahlii T.C.E.Fr.	2	4	4	2	2	5
	oribiensis Codd	2	4	2	1	2	3
	pentheri (Gürke) Van Jaarsv. & T.J.Edwards	2	4	2	2	2	3
	petiolaris E.Mey. ex Benth.	2	4	20	7	3	2
	porcatus Van Jaarsv. & P.J.D.Winter	2	4	1	1	1	2
	praetermissus Codd	2	4	2	2	2	4
	psammophilus Codd	2	4	3	1	2	3
	purpuratus Harv. subsp. *montanus* Van Jaarsv. & T.J.Edwards	2	4	2	2	1	9
	purpuratus Harv. subsp. *purpuratus*	2	4	6	3	2	9
	purpuratus Harv. subsp. *tongaensis* Van Jaarsv. & T.J.Edwards	2	4	2	1	1	9
	ramosior (Benth.) Van Jaarsv.	2	4	21	9	1	4

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 1h. Distribution, flowering and growth form data collected for *Plectranthus* (cont.), *Crinum* and *Watsonia* species

Genus (code)*	Taxa	Broad Growth Form	Narrow Growth Form	QDS	Perera Units	Rainfall Zones	No. Flowering months
Plectranthus	*reflexus* Van Jaarsv. & T.J.Edwards	2	4	2	3	2	3
(6)	*rehmannii* Gürke	2	4	3	1	1	3
	saccatus Benth. subsp. *pondoensis* Van Jaarsv. & Milstein	2	4	1	1	1	8
	saccatus Benth. subsp. *saccatus*	2	4	31	5	3	8
	venteri Van Jaarsv. & Hankey	2	4	3	2	1	3
	xerophilus Codd	2	4	16	4	2	4
Crinum	*campanulatum* Herb.	1	2	9	3	3	7
(7)	*moorei* Hook.f.	1	2	19	9	4	4
Watsonia	*amatolae* Goldblatt	1	2	5	1	1	3
(12)	*bachmannii* L.Bolus	1	2	4	1	1	4
	canaliculata Goldblatt	1	2	2	1	1	2
	confusa Goldblatt	1	2	17	7	2	6
	densiflora Baker	1	2	67	13	2	4
	inclinata Goldblatt	1	2	5	2	1	2
	mtamvunae Goldblatt	1	2	3	1	1	3
	occulta L.Bolus	1	2	7	2	2	2
	pillansii L.Bolus	1	2	77	11	4	2
	pondoensis Goldblatt	1	2	1	1	1	2
	strubeniae L.Bolus	1	2	4	2	1	3
	transvaalensis Baker	1	2	5	1	2	4
	wilmsii L.Bolus	1	2	4	2	1	4

*** NOTE:** numbers/codes given after each genus name are employed in the analysis section of the methodology (refer to section 3.2.3 Data Analysis)

Appendix B 2a. Flowering months and factor analysis values for *Cussonia*, *Gymnosporia*, *Pavetta*, *Eulophia* and *Satyrium* species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Cussonia	*gamtoosensis*	0	0	0	0	1	0	0	0	0	0	0	0	-0.176	-0.297
	nicholsonii	0	0	0	0	0	0	0	1	1	1	1	1	-0.370	0.691
	paniculata subsp. *paniculata*	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	thyrsiflora	1	0	0	0	0	0	0	0	0	0	1	1	0.468	0.691
	transvaalensis	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
Gymnosporia	*bachmannii*	1	1	1	1	1	1	1	0	0	0	0	1	0.539	-0.468
	rubra	1	1	1	1	1	1	1	1	1	1	1	1	-	-
	uniflora	1	1	0	0	0	0	0	0	1	1	1	1	0.356	0.781
Pavetta	*bowkeri*	1	0	0	0	0	0	0	0	0	0	0	1	0.581	0.517
	capensis subsp. *capensis*	1	1	0	0	0	0	0	0	0	0	1	1	0.705	0.598
	capensis subsp. *komghensis*	1	1	0	0	0	0	0	0	0	0	1	1	0.705	0.598
	kotzei	1	0	0	0	0	0	0	0	0	0	1	1	0.468	0.691
	natalensis	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
Eulophia	*calanthoides*	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
	coddii	0	0	0	0	0	0	0	0	0	0	0	1	0.260	0.434
	cooperi	0	0	0	0	0	0	0	0	0	1	1	0	-0.208	0.493
	macowanii	1	1	0	0	0	0	0	0	0	0	1	1	0.705	0.598
Satyrium	*hallackii* subsp. *hallackii*	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
	membranaceum	0	0	0	0	0	0	0	0	1	1	1	0	-0.387	0.496
	rhodanthum	0	0	0	0	0	0	0	0	0	1	0	0	-0.232	0.280

Appendix B 2b. Flowering months and factor analysis values for *Searsia* species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Searsia	*acocksii*	0	0	0	0	0	0	0	0	0	0	1	1	0.156	0.607
	albomarginata	1	0	0	0	0	0	0	0	0	0	0	0	0.523	0.264
	batophylla	0	0	1	0	0	0	0	0	0	0	0	0	0.322	-0.516
	carnosula	1	0	0	1	0	0	0	0	0	0	0	1	0.523	0.148
	crenata	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457
	dracomontana	1	0	0	0	0	0	0	0	0	1	1	1	0.294	0.798
	engleri	0	0	1	1	0	0	0	0	0	0	0	0	0.267	-0.728
	fastigata	1	1	0	0	0	0	0	0	0	0	0	0	0.735	0.149
	gracillima	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457
	keetii	1	0	1	0	1	1	0	0	0	0	1	1	0.359	0.073
	kwazuluana	1	1	0	0	0	0	0	0	0	0	0	0	0.735	0.149
	longispina	0	0	0	0	1	0	1	1	1	1	0	0	-0.746	0.055
	magalismontana subsp. *coddii*	1	1	1	0	0	0	0	0	0	1	1	1	0.715	0.433
	maricoana	0	0	1	1	0	0	0	0	0	0	0	0	0.267	-0.728
	pondoensis	1	1	1	1	0	0	0	0	0	0	0	1	0.903	-0.194
	pterota	1	0	0	0	0	0	0	0	0	0	0	0	0.523	0.264
	refracta	1	0	0	0	0	0	0	0	0	0	0	0	0.523	0.264
	rigida	1	1	1	0	0	0	0	0	0	1	0	1	0.752	0.224
	rudatisii	1	0	0	0	0	0	0	0	1	1	1	1	0.099	0.827
	sekhukhuniensis	0	0	1	1	0	0	0	0	0	0	0	0	0.267	-0.728
	tridactyla	0	1	1	0	0	0	0	0	0	0	0	0	0.586	-0.429

Appendix B 2c. Flowering months and factor analysis values for *Searsia* (cont.), *Gladiolus* and *Zantedeschia* species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Searsia	*wilmsii*	1	0	0	1	0	0	0	0	0	0	0	0	0.415	-0.150
	zeyheri	0	1	0	0	0	0	0	0	0	1	0	0	0.175	0.161
Gladiolus	*calcaratus*	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	cruentus	1	0	0	0	0	0	0	0	0	0	0	1	0.581	0.517
	exiguus	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	gueinzii	0	0	0	0	0	0	0	0	0	1	1	1	-0.013	0.701
	macneilii	0	0	0	1	0	0	0	0	0	0	0	0	0.037	-0.466
	microcarpus	1	1	0	0	0	0	0	0	0	0	0	0	0.735	0.149
	oppositiflorus	1	1	1	0	0	0	0	0	0	0	1	1	0.855	0.283
	pole-evansii	0	1	1	0	0	0	0	0	0	0	0	0	0.586	-0.429
	pretoriensis	0	1	1	0	0	0	0	0	0	0	0	0	0.586	-0.429
	robertsoniae	0	0	0	0	0	0	0	0	0	1	1	1	-0.013	0.701
	rufomarginatus	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	sericeovillosus subsp. *sericeovillosus*	1	1	1	1	1	1	0	0	0	0	0	1	0.675	-0.437
	vernus	0	0	0	0	0	0	0	0	1	1	1	0	-0.387	0.496
	vinosomaculatus	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	wilsonii	0	0	0	0	0	0	0	0	1	1	1	0	-0.387	0.496
Zantedeschia	*elliottiana*	1	0	0	0	0	0	0	0	0	0	1	1	0.468	0.691
	jucunda	1	0	0	0	0	0	0	0	0	0	1	1	0.468	0.691
	pentlandii	0	0	0	0	0	0	0	0	0	0	1	1	0.156	0.607
	valida	1	1	1	0	0	0	0	0	0	1	1	1	0.715	0.433

Appendix B 2d. Flowering months and factor analysis values for *Kniphofia* species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Kniphofia	*albescens*	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	baurii	0	0	0	0	0	0	0	0	1	1	1	0	-0.387	0.496
	breviflora	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	buchananii	0	1	1	0	0	0	0	0	0	0	0	0	0.586	-0.429
	citrina	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	coralligemma	0	1	1	1	0	0	0	0	0	0	0	0	0.528	-0.666
	drepanophylla	0	0	0	0	0	0	0	1	1	1	0	0	-0.555	0.264
	ensifolia subsp. *autumnalis*	0	1	1	0	0	0	0	0	0	0	0	0	0.586	-0.429
	evansii	1	1	0	0	0	0	0	0	0	0	0	0	0.735	0.149
	fibrosa	0	1	1	0	0	0	0	0	0	0	0	0	0.586	-0.429
	flammula	1	0	0	0	0	0	0	0	0	0	1	1	0.468	0.691
	fluviatilis	0	0	0	0	0	0	0	0	0	0	1	1	0.156	0.607
	gracilis	1	1	1	1	0	0	0	0	0	0	0	1	0.903	-0.194
	ichopensis	1	1	1	0	0	0	0	0	0	0	0	1	0.923	0.070
	latifolia	0	0	0	0	0	0	0	0	0	1	1	0	-0.208	0.493
	laxiflora	0	1	1	1	1	0	0	0	0	0	0	0	0.382	-0.786
	littoralis	0	0	0	0	0	0	0	1	1	1	0	0	-0.555	0.264
	parviflora	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	pauciflora	0	0	0	0	0	0	0	0	1	1	1	0	-0.387	0.496
	rigidifolia	0	0	0	0	0	0	0	0	0	1	1	0	-0.208	0.493
	rooperi	0	0	0	0	0	1	1	1	1	0	0	0	-0.676	-0.012

Appendix B 2e. Flowering months and factor analysis values for *Kniphofia* (cont.) and *Streptocarpus* species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Kniphofia	*triangularis* subsp. *obtusiloba*	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457
	typhoides	0	1	1	0	0	0	0	0	0	0	0	0	0.586	-0.429
	tysonii subsp. *tysonii*	0	1	1	1	0	0	0	0	0	0	0	0	0.528	-0.666
Streptocarpus	*baudertii*	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
	caeruleus	1	1	1	1	0	0	0	0	0	0	1	1	0.863	0.021
	candidus	1	1	0	0	0	0	0	0	0	0	1	1	0.705	0.598
	cooksonii	1	1	1	1	0	0	0	0	0	0	0	1	0.903	-0.194
	cooperi	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457
	cyaneus subsp. *longi-tommii*	1	1	0	0	0	0	0	0	0	1	1	1	0.544	0.729
	cyaneus subsp. *nigridens*	1	1	0	0	0	0	0	0	0	1	1	1	0.544	0.729
	cyaneus subsp. *polackii*	1	1	0	0	0	0	0	0	0	1	1	1	0.544	0.729
	decipiens	1	1	0	0	0	0	0	0	0	0	0	0	0.735	0.149
	denticulatus	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
	fanniniae	1	1	1	1	0	0	0	0	0	0	1	1	0.863	0.021
	gardenii	1	1	1	1	0	0	0	0	0	0	1	1	0.863	0.021
	grandis subsp. *grandis*	1	1	1	0	0	0	0	0	0	1	1	1	0.715	0.433
	haygarthii	1	1	1	1	0	0	0	0	1	1	1	1	0.589	0.253
	johannis	0	0	0	0	0	0	0	0	0	1	1	1	-0.013	0.701
	kentaniensis	0	0	0	0	0	0	1	1	1	0	0	0	-0.589	0.074
	latens	1	1	1	0	0	0	0	0	0	0	0	1	0.923	0.070
	meyeri	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457

Appendix B 2f. Flowering months and factor analysis values for *Streptocarpus* (cont.) species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Streptocarpus	*modestus*	0	0	0	0	0	0	0	0	1	1	0	0	-0.413	0.291
	molweniensis subsp. *eshowicus*	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
	molweniensis subsp. *molweniensis*	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
	montigena	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	parviflorus subsp. *parviflorus*	1	1	1	0	0	0	0	0	0	0	0	1	0.923	0.070
	parviflorus subsp. *soutpansbergensis*	1	1	1	0	0	0	0	0	0	0	0	1	0.923	0.070
	pogonites	1	0	0	0	0	0	0	0	0	0	0	1	0.581	0.517
	pole-evansii	1	1	0	0	0	0	0	0	0	0	0	1	0.799	0.405
	polyanthus subsp. *dracomontanus*	1	1	0	0	0	0	1	1	1	1	1	1	0.028	0.830
	polyanthus subsp. . *polyanthus*	1	1	0	0	0	0	1	1	1	1	1	1	0.028	0.830
	polyanthus subsp. *verecundus*	1	1	0	0	0	0	1	1	1	1	1	1	0.028	0.830
	porphyrostachys	1	0	0	0	0	0	0	0	0	0	1	1	0.468	0.691
	primulifolius	1	1	1	1	0	0	0	0	0	0	0	1	0.903	-0.194
	prolixus	0	0	0	0	0	0	0	0	0	1	1	1	-0.013	0.701
	rexii	1	1	1	1	0	0	0	0	0	1	1	1	0.745	0.179
	rimicola	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457
	saundersii	1	0	0	0	0	0	0	0	0	0	0	1	0.581	0.517
	silvaticus	1	0	0	0	0	0	0	0	0	1	1	1	0.294	0.798
	trabeculatus	1	1	0	0	0	0	0	0	0	1	1	1	0.544	0.729
	vandeleurii	1	1	1	0	0	0	0	0	0	0	0	1	0.923	0.070
	wendlandii	1	1	1	0	0	0	0	0	0	0	0	1	0.923	0.070

Appendix B 2g. Flowering months and factor analysis values for *Plectranthus* species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Plectranthus	*aliciae*	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	dolichopodus	1	1	1	1	1	0	0	0	0	1	1	1	0.676	0.012
	dolomiticus	0	0	1	1	0	0	0	0	0	0	0	0	0.267	-0.728
	ecklonii	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	elegantulus	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	ernstii	1	1	1	1	1	0	0	0	0	1	1	1	0.676	0.012
	hilliardiae subsp. *hilliardiae*	0	1	1	1	1	1	0	0	0	0	0	0	0.236	-0.828
	lucidus	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	malvinus	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	mutabilis	0	1	1	1	1	1	0	0	0	0	0	0	0.236	-0.828
	mzimvubensis	0	0	1	1	1	1	0	0	0	0	0	0	-0.028	-0.830
	oertendahlii	0	1	1	1	1	1	0	0	0	0	0	0	0.236	-0.828
	oribiensis	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	pentheri	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	petiolaris	0	0	1	1	0	0	0	0	0	0	0	0	0.267	-0.728
	porcatus	0	0	1	1	0	0	0	0	0	0	0	0	0.267	-0.728
	praetermissus	0	1	1	1	1	0	0	0	0	0	0	0	0.382	-0.786
	psammophilus	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	purpuratus subsp. *montanus*	1	1	1	1	1	0	0	0	1	1	1	1	0.529	0.085
	purpuratus subsp. *purpuratus*	1	1	1	1	1	0	0	0	1	1	1	1	0.529	0.085
	purpuratus subsp.. *tongaensis*	1	1	1	1	1	0	0	0	1	1	1	1	0.529	0.085
	ramosior	0	0	1	1	1	1	0	0	0	0	0	0	-0.028	-0.830

Appendix B 2h. Flowering months and factor analysis values for *Plectranthus* (cont.), *Crinum* and *Watsonia* species

Genus	Taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Flowering Season 1	Flowering Season 2
Plectranthus	*reflexus*	1	1	1	0	0	0	0	0	0	0	0	0	0.838	-0.201
	rehmannii	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	saccatus subsp. *pondoensis*	1	1	1	1	1	1	0	0	0	0	1	1	0.677	-0.232
	saccatus subsp. *saccatus*	1	1	1	1	1	1	0	0	0	0	1	1	0.677	-0.232
	venteri	0	0	1	1	1	0	0	0	0	0	0	0	0.117	-0.816
	xerophilus	0	0	1	1	1	1	0	0	0	0	0	0	-0.028	-0.830
Crinum	*campanulatum*	1	1	0	0	0	0	0	1	1	1	1	1	0.186	0.803
	moorei	0	0	0	0	0	0	0	0	1	1	1	1	-0.203	0.710
Watsonia	*amatolae*	1	0	0	0	0	0	0	0	0	0	1	1	0.468	0.691
	bachmannii	0	0	0	0	0	0	1	1	1	1	0	0	-0.677	0.232
	canaliculata	0	0	0	0	0	0	0	0	0	0	1	1	0.156	0.607
	confusa	1	1	1	0	0	0	0	0	0	1	1	1	0.715	0.433
	densiflora	1	1	1	0	0	0	0	0	0	0	0	1	0.923	0.070
	inclinata	0	0	0	0	0	0	0	0	1	1	0	0	-0.413	0.291
	mtamvunae	0	0	0	0	0	0	0	1	1	1	0	0	-0.555	0.264
	occulta	1	0	0	0	0	0	0	0	0	0	0	1	0.581	0.517
	pillansii	1	0	0	0	0	0	0	0	0	0	0	1	0.581	0.517
	pondoensis	0	0	0	0	0	0	0	0	1	1	0	0	-0.413	0.291
	strubeniae	0	1	1	1	0	0	0	0	0	0	0	0	0.528	-0.666
	transvaalensis	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457
	wilmsii	1	1	1	1	0	0	0	0	0	0	0	0	0.792	-0.457

Appendix C1.1. Test 1: Homogeneity-of-Regression results

*(Dependent variable: *QDS*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	10243.502[a]	5	2048.700	6.183	.000
Intercept	2503.254	1	2503.254	7.555	.007
Broad Growth Form	2481.849	2	1240.924	3.745	.026
No. Flowering Months	1972.299	1	1972.299	5.952	.016
Broad Growth Form * No. Flowering Months	483.020	2	241.510	.729	.484
Error	54011.054	163	331.356		
Total	98309.000	169			
Corrected Total	64254.556	168			

a. R Squared = .159 (Adjusted R Squared = .134)

Appendix C1.2. Test 2: Homogeneity-of Regression results

*(Dependent variable: *QDS*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	13286.416[a]	11	1207.856	3.721	.000
Intercept	2320.964	1	2320.964	7.149	.008
No. Flowering Months	1821.459	1	1821.459	5.611	.019
Narrow Growth Form	5410.614	5	1082.123	3.333	.007
Narrow Growth Form * No. Flowering Months	1675.703	5	335.141	1.032	.401
Error	50968.140	157	324.638		
Total	98309.000	169			
Corrected Total	64254.556	168			

a. R Squared = .207 (Adjusted R Squared = .151)

Appendix C1.3 Test 3: Homogeneity-of-Regression results

*(Dependent variable: *QDS*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	21562.709[a]	25	862.508	2.889	.000
Intercept	225.527	1	225.527	.755	.386
No. Flowering Months	1395.780	1	1395.780	4.675	.032
Genus	3048.520	12	254.043	.851	.598
Genus * No. Flowering Months	3017.940	12	251.495	.842	.607
Error	42691.847	143	298.544		
Total	98309.000	169			
Corrected Total	64254.556	168			

a. R Squared = .336 (Adjusted R Squared = .219)

Appendix C1.4. Test 4: Homogeneity-of-Regression results

*(Dependent variable: *Perera Units*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	299.057[a]	5	59.811	5.323	.000
Intercept	187.592	1	187.592	16.696	.000
No. Flowering Months	119.252	1	119.252	10.613	.001
Broad Growth Form	67.910	2	33.955	3.022	.051
Broad Growth Form * No. Flowering Months	35.501	2	17.750	1.580	.209
Error	1831.464	163	11.236		
Total	4763.000	169			
Corrected Total	2130.521	168			

a. R Squared = .140 (Adjusted R Squared = .114)

Appendix C1.5. Test 5: Homogeneity-of –Regression results

*(Dependent Variable: *Perera Units*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	373.302[a]	11	33.937	3.032	.001
Intercept	190.714	1	190.714	17.039	.000
No. Flowering Months	82.272	1	82.272	7.351	.007
Narrow Growth Form	139.428	5	27.886	2.491	.033
Narrow Growth Form * No. Flowering Months	94.554	5	18.911	1.690	.140
Error	1757.219	157	11.192		
Total	4763.000	169			
Corrected Total	2130.521	168			

a. R Squared = .175 (Adjusted R Squared = .117)

Appendix C1.6. Test 6: Homogeneity-of-Regression results

*(Dependent variable: *Perera Units*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	718.316[a]	25	28.733	2.909	.000
Intercept	50.831	1	50.831	5.147	.025
Genus	142.452	12	11.871	1.202	.287
No. Flowering Months	56.753	1	56.753	5.747	.018
Genus * No. Flowering Months	198.840	12	16.570	1.678	.078
Error	1412.205	143	9.876		
Total	4763.000	169			
Corrected Total	2130.521	168			

a. R Squared = .337 (Adjusted R Squared = .221)

Appendix C1.7. Test 7: Homogeneity-of-Regression results

*(Dependent variable: *Rainfall Zones*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	22.003[a]	5	4.401	5.592	.000
Intercept	106.442	1	106.442	135.249	.000
Broad Growth Form	5.091	2	2.545	3.234	.042
No. Flowering Months	3.677	1	3.677	4.672	.032
Broad Growth Form * No. Flowering Months	1.060	2	.530	.673	.512
Error	128.281	163	.787		
Total	871.000	169			
Corrected Total	150.284	168			

a. R Squared = .146 (Adjusted R Squared = .120)

Appendix C1.8. Test 8: Homogeneity-of-Regression results

*(Dependent variable: *Rainfall Zones*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	24.555[a]	11	2.232	2.787	.002
Intercept	96.873	1	96.873	120.966	.000
Narrow Growth Form	7.083	5	1.417	1.769	.122
No. Flowering Months	2.491	1	2.491	3.110	.080
Narrow Growth Form * No. Flowering Months	3.268	5	.654	.816	.540
Error	125.729	157	.801		
Total	871.000	169			
Corrected Total	150.284	168			

a. R Squared = .163 (Adjusted R Squared = .105)

Appendix C1.9. Test 9: Homogeneity-of-Regression results

*(Dependent variable: *Rainfall Zones*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	46.652[a]	25	1.866	2.575	.000
Intercept	30.812	1	30.812	42.517	.000
Genus	5.641	12	.470	.649	.797
No. Flowering Months	1.794	1	1.794	2.475	.118
Genus * No. Flowering Months	8.403	12	.700	.966	.484
Error	103.632	143	.725		
Total	871.000	169			
Corrected Total	150.284	168			

a. R Squared = .310 (Adjusted R Squared = .190)

Appendix C2.1. Test 1: ANCOVA Results

*(Dependent variable: *QDS*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	9760.482[a]	3	3253.494	9.851	.000
Intercept	3141.967	1	3141.967	9.513	.002
No. Flowering Months	1556.116	1	1556.116	4.712	.031
Broad Growth Form	9411.266	2	4705.633	14.248	.000
Error	54494.074	165	330.267		
Total	98309.000	169			
Corrected Total	64254.556	168			

a. R Squared = .152 (Adjusted R Squared = .136)

Appendix C2.2. Test 2: ANCOVA Results

*(Dependent variable: *QDS*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	11610.713[a]	6	1935.119	5.955	.000
Intercept	3706.353	1	3706.353	11.405	.001
No. Flowering Months	1326.071	1	1326.071	4.081	.045
Narrow Growth Form	11261.497	5	2252.299	6.931	.000
Error	52643.843	162	324.962		
Total	98309.000	169			
Corrected Total	64254.556	168			

a. R Squared = .181 (Adjusted R Squared = .150)

Appendix C2.3. Test 3: ANCOVA results

*(Dependent variable: *QDS*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	18544.768[a]	13	1426.521	4.837	.000
Intercept	1302.028	1	1302.028	4.415	.037
No. Flowering Months	2719.491	1	2719.491	9.222	.003
Genus	18195.552	12	1516.296	5.142	.000
Error	45709.788	155	294.902		
Total	98309.000	169			
Corrected Total	64254.556	168			

a. R Squared = .289 (Adjusted R Squared = .229)

Appendix C2.4. Test 4: ANCOVA results

*(Dependent variable: *Perera Units*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	263.556[a]	3	87.852	7.764	.000
Intercept	233.990	1	233.990	20.680	.000
No. Flowering Months	91.573	1	91.573	8.093	.005
Broad Growth Form	230.019	2	115.010	10.164	.000
Error	1866.965	165	11.315		
Total	4763.000	169			
Corrected Total	2130.521	168			

a. R Squared = .124 (Adjusted R Squared = .108)

Appendix C2.5. Test 5: ANCOVA results

*(Dependent variable: *Perera Units*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	278.748[a]	6	46.458	4.064	.001
Intercept	245.493	1	245.493	21.477	.000
No. Flowering Months	85.676	1	85.676	7.495	.007
Narrow Growth Form	245.211	5	49.042	4.290	.001
Error	1851.773	162	11.431		
Total	4763.000	169			
Corrected Total	2130.521	168			

a. R Squared = .131 (Adjusted R Squared = .099)

Appendix C2.6. Test 6: ANCOVA results

*(Dependent variable: *Perera Units*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	519.475[a]	13	39.960	3.845	.000
Intercept	157.523	1	157.523	15.155	.000
No. Flowering Months	125.318	1	125.318	12.057	.001
Genus	485.939	12	40.495	3.896	.000
Error	1611.045	155	10.394		
Total	4763.000	169			
Corrected Total	2130.521	168			

a. R Squared = .244 (Adjusted R Squared = .180)

Appendix C2.7. Test 7: ANCOVA results

*(Dependent variable: *Rainfall Zones*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	20.943[a]	3	6.981	8.906	.000
Intercept	116.687	1	116.687	148.858	.000
No. Flowering Months	2.719	1	2.719	3.468	.064
Broad Growth Form	20.146	2	10.073	12.850	.000
Error	129.341	165	.784		
Total	871.000	169			
Corrected Total	150.284	168			

a. R Squared = .139 (Adjusted R Squared = .124)

Appendix C2.8. Test 8: ANCOVA results

*(Dependent variable: *Rainfall Zones*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	21.287[a]	6	3.548	4.455	.000
Intercept	115.712	1	115.712	145.316	.000
No. Flowering Months	2.592	1	2.592	3.256	.073
Narrow Growth Form	20.489	5	4.098	5.146	.000
Error	128.998	162	.796		
Total	871.000	169			
Corrected Total	150.284	168			

a. R Squared = .142 (Adjusted R Squared = .110)

Appendix C2.9. Test 9: ANCOVA results

*(Dependent variable: *Rainfall Zones*)

	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	38.249[a]	13	2.942	4.071	.000
Intercept	88.534	1	88.534	122.487	.000
No. Flowering Months	3.422	1	3.422	4.735	.031
Genus	37.452	12	3.121	4.318	.000
Error	112.035	155	.723		
Total	871.000	169			
Corrected Total	150.284	168			

a. R Squared = .255 (Adjusted R Squared = .192)