Life history, population dynamics and conservation status of *Oldenburgia grandis* (Asteraceae), an endemic of the Eastern Cape of South Africa

THESIS

Submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE
of
RHODES UNIVERSITY

by

CARIN SWART

Department of Botany
Rhodes University

March 2008

Oldenburgia grandis is a rare, long-lived woody paleoendemic of the Fynbos Biome of South Africa. Confined to quartzite outcrops, it has a small geographic range and narrow habitat specificity. *O. grandis* responds to its fire-prone environment by resprouting. Elasticity analysis of *O. grandis* reveals that growth and fecundity were traded off for persistence of adult, mature and sapling stages. Morphological adaptations such as a corky fire-resistant bark and the ability to resprout after fire are traits that *O. grandis* have evolved to persist in a frequently disturbed environment. Population growth rate for sites undisturbed by fire for a number of years ($\lambda = 1.01$) and sites at various stages of recovery after fire ($\lambda = 1.00$) were very similar. The highest variation in transition probabilities for all sites was seen in the persistence of the seedling stage and growth from seedling to sapling. Observed population structure and stable stage distribution determined by the matrix model show that sites recently undisturbed by fire had high abundances of the adult and sapling stages. A peak in sapling stages was seen for the stable stage distribution where similar peak in sapling numbers were seen for population structures of sites at various stages of recovery after fire. Favourable environmental conditions for the persistence of *O. grandis* populations include no fire with transition probabilities between the observed minimum and maximum and fire frequency at a 10 year interval where seedling protection from the fire is high and adult and mature mortalities during the fire are low. Stochastic environmental events that could put populations (particularly small populations) at an increased risk of extinction include high to moderate fire intensities where seedling protection from the fire is low and adult and mature mortalities are high as a result of the fire.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

ACKNOWLEDGEMENTS

My supervisor, Dr. Susi Vetter is thanked for her excellent support and advice throughout the various stages of this thesis. She is especially thanked for her support, encouragement and motivation at times when it was most needed. I could not have asked for a better supervisor. My co-supervisor, Prof. Nigel Barker is thanked for all his help regarding the administrative aspects of this project and for providing invaluable input during the final stages of the thesis.

Thank you to Greg Hood for answering my questions, no matter how basic. Thank-you to the Addo Elephant National Park and farm owners within my study area for allowing me access to their properties.

Funding for this project came from three sources for which I am extremely grateful. The National Research Foundation funded tuition fees. The Threatened Species Programme (division of the South African Biodiversity Institute) made the mapping and additional sampling possible. The Joint Research Council funded most aspects of my fieldwork and transportation.

Additional thanks is extended to Quintus Hahndiek, an understanding boss who gave me time when needed especially during the final write-up stages of this thesis. Thanks to Ben Cobbing for help with the mapping and to Gareth Coombs for assisting me with setting up plots and for experiencing hair-raising adventures with me while mapping in the Suurberg Mountains.

Special acknowledgement goes to my father Ron Swart who instilled in me a love of nature from an early age and to Steven Boy for putting up with my moods and complaints and for helping me through stressful times.

CHAPTER 1 INTRODUCTION

Oldenburgia grandis is a rare endemic of South Africa. It is an unusual member of the Asteraceae family with a small woody tree growth form and is a long-lived sprouter. *Oldenburgia grandis* populations are confined to outcrops of Witteberg Quartzite and found within the eastern limits of the Fynbos Biome. The aim of this project was to understand the rarity and population dynamics of this interesting species.

Rare plants and risks of extinction

The concept of rarity in plants has been explored by various authors to understand what makes a species rare (Harper 1981; Kruckeberg and Rabinowitz 1985; Murray et al. 2002), different categories of rarity (Rabinowitz, 1981) and the importance of rare plant conservation (Schemske et al. 1994; Bevill and Louda 1999). In an attempt to categorise the nature of rarity, Rabinowitz (1981) proposed 7 forms of rarity defined by geographic range, habitat specificity and local abundance of the species (Table 1.1). Geographic range and habitat specificity can be either narrow or wide while local abundance can be either high or low.

Table 1.1 Seven **forms of rarity defined by Rabinowitz (1981) where O. grandis conforms to a species with a small geographic range and narrow habitat specificity (shaded block)**

GEOGRAPHIC RANGE	**LARGE**		**SMALL**	
HABITAT SPECIFITY	**WIDE**	**NARROW**	**WIDE**	**NARROW**
local population size: large, dominant somewhere	locally abundant over large range in several habitats	locally abundant over a large range in a specific habitat	locally abundant in several habitats but restricted geographically	locally abundant in a specific habitat but restricted geographically
local population size: small, non-dominant	constantly sparse over a large range and in several habitats	constantly sparse in a specific habitat but over a large range	constantly sparse and geographically restricted in several habitats	constantly sparse and geographically restricted in a specific habitat

What are the consequences of rarity for species persistence and why is it important for conservation? Rare species are taxa with small world populations and are at risk as some unexpected threat could cause a critical decline (Spellerberg 1992). Small populations are more at risk of going extinct than larger populations (Kruckeberg and Rabinowitz 1985; Schemske et al. 1994; Matthies et al. 2004). A single stochastic event can cause extinction of a locally endemic species because of its highly limited range. The conservation of rare plants is therefore an important consideration in the conservation of biodiversity (Bevill and Louda 1999).

The main contributors to biological diversity include the process of evolution (if resulting in high levels of speciation) as well as promoting persistence of existing species (Ricklefs and Schluter 1993). Depending on how recently a species has attained the rare status, natural selection may favour traits that assist a species in adapting to small local population sizes thereby reducing risks to extinction (Rabinowitz 1981). Narrow endemism is a form of rarity described by Kruckeberg and Rabinowitz (1985) as taxa occurring in one or a few small populations. Two processes can describe how endemics arise: factors that influence evolution and thus the evolution of new endemics (neoendemism) and survival of ancient relics that were once widespread (paleoendemism) (Kruckeberg and Rabinowitz 1985). Possible indicators of paleoendemism include species with more than one isolated population and those that are either high polyploids or diploids (Kruckeberg and Rabinowitz 1985). Brigham (2003) suggests that paleoendemics may have advantages over neoendemics in that they have a history of rarity and may have evolved certain adaptations to the rare state that enables them to persist.

Events that ultimately lead to the extinction of a species are either deterministic or stochastic in nature (Given 1994). Deterministic factors are those that alter the population growth rate from long-term average growth to population decline as a result of certain threats (Lacy et al. 2003). Stochastic events result from unpredictable fluctuations in the environment or environmental disturbances (Given 1994). Once populations become small and fragmented, random or stochastic forces may ultimately determine the fate of the population, particularly for rare populations. Four separate stochastic forces that independently contribute to population extinction (especially small populations) have been suggested (Gilpin and Soulĕ 1986):

a. Demographic stochasticity resulting from random events in the survival and reproduction of individuals;
b. Environmental stochasticity, where random changes are experienced by all individuals in the population;
c. Genetic stochasticity such as genetic drift and loss of fitness;
d. Natural catastrophes such as large scale fires or floods

A stochastic environment does not cause demographic stochasticity. The primary cause of demographic stochasticity is population size (McPeek and Kalisz 1993) as deterministic stochasticity involves a chance variation in the structure of a local population affecting the demography of small populations (Silvertown and Charlesworth 2001). McPeek and Kalisz (1993) suggest this is because variation associated with transition probabilities increases with decreasing population size. According to Gilpin and Soulĕ (1986), if a population is subject to habitat loss, for example by invasions of its habitat by non-native invasive trees, a reduction in population size and distribution occurs. This either results directly in extinction or a population becoming increasingly vulnerable to stochastic extinction (either demographic or environmental). In addition to this, species with restricted habitats may become vulnerable to habitat alterations either directly or indirectly induced by human activities (Primack 1993).

Three main types of threats to rare plant persistence have been described (Oostermeijer 2003): 1) changes in the environment in which the organism exists, either natural or human induced, 2) threats resulting from disturbances of interactions with other species and 3) genetic threats. The second and third threats are particularly associated with small population sizes. Conservation strategies to protect rare and threatened species will clearly be to identify and focus on removing or reducing threats to existing populations. Conservation policies designed to maintain and conserve biodiversity are not necessarily appropriate for species-specific conservation efforts as there is no reason to suppose that rare species are inexorably linked to areas of high diversity (Harper 1981; van Wyk and Smith 2001).

What category of rarity and what type of endemic is *Oldenburgia grandis*? The rocky outcrops to which *Oldenburgia grandis* is restricted are patchy and scattered. Habitat size is small and patchy but the number of habitats is relatively large spanning over a distance of 100 km. In terms of the categories described by Rabinowitz (1981), *O. grandis* can be considered as having a small geographic range and narrow habitat specificity and can be categorised as constantly sparse and geographically restricted in a specific habitat.

Evidence suggests that O. *grandis* is a paleoendemic (Goldblatt 1987). Chromosome cytology reveals that *O. grandis* has a diploid chromosome number of 2n = 36 (Goldblatt 1987). Sprouting is also an ancestral trait in many angiosperm clades (Vesk and Westoby 2004). Pollen records suggest that that much of the angiosperm radiation occurred when the continents of Gondwanaland were close together, allowing the exchange of floristic elements (Jones and Luchsinger 1987). As a member of the Asteraceae family and classified as part of tribe Mutisieae, *O. grandis* has been placed in the subfamily Carduoideae (Panero and Funk 2002; Funk at al. 2005). Pollen from the tribe Mutisieae dates back to between the Eocene and middle Oligocene epochs in the Cenozoic era (Graham 1996; Funk et al. 2005). Bond (1987) suggests that taxonomically, the genus *Oldenburgia* has a stronger link to the South American genus *Cnicothamnus* than any other known genera of Muticeae on the African continent. The Mutisieae are poorly represented in South Africa but widespread in South America (Goldblatt 1987). This suggests an ancient biogeographic link between the two genera.

<u>Monitoring and modeling the population dynamics of rare species</u>

The monitoring, involving the repeated census, of rare species answers two important questions (Primack 2003):

1. Is the population of a rare species stable, declining or increasing in numbers over time?
2. Is the species likely to remain established at its current site given present conditions?

It is possible to answer these questions and to determine extinction risks of a species by the use of matrix models. Matrix models can be used to simulate deterministic and stochastic factors as well as to tease out important life history information of a species. Estimation of population growth rate (λ) will provide answers to question 1. Determining the structure of the model will depend on the availability of data and types of management questions posed (Akçakaya et al. 1999) and assist in providing answers for question 2 above. Population Viability Analysis (PVA) is a tool commonly used to test the persistence or extinction risk of a population. PVA is fundamentally based on matrix models and is used to project the future size of a population under study. Caswell (2001) listed four important stages in a demographic study incorporating matrix modelling and PVA: assessment, diagnosis, prescription and prognosis. An assessment of the population growth rate is the first step to determine the status of a population. If it is found that the population growth rate is declining, the diagnosis will attempt to find the cause of decline. Tools used for this assessment include elasticity analysis where populations in different environments can be compared and important life history stages for population persistence are determined. Once the possible cause of the decline is found, the prescription would then include management scenarios targeted at important life-cycle stages. Once all management interventions are in place, the prognosis should determine what the likely fate of the population is (or the probability of extinction over a specified time period).

This study makes use of stage-structured projection matrices (Lefkovitch, 1965) where stages rather than age classes are used to build the model. Long-lived woody trees with low levels of fecundity show plastic rates of growth and development (Silvertown and Charlesworth 2001) that makes the use of stage rather than age more biologically meaningful when analysing the demographics of the species. This means that two individuals can be the same age but because they experience different local environmental conditions they may be at different stages in the life cycle. The inclusion of biological details that can be incorporated into the matrix model make them especially useful (Brigham 2003).

Scepticism in the application of PVA in certain plant studies (Ludwig 1999; Ellner et al. 2002) has raised some of the important complications and sources of error in this type of analysis. The strength of PVA projections is highly dependent on the quality of the data available and the assumptions made in the modelling process. It has therefore been recommended that results should always be accompanied by an assessment of confidence levels (Reed et al. 2002). Reed et al. (2002) go further to suggest that PVA should not be used to determine minimum population size or probability of extinction but rather for testing the effects of various management options on population growth and or persistence. Simulation of management or environmental effects, where it is not possible to sample for the combination of a large number of factors such as fire regime, different levels of recruitment, is possible using matrix models. A study to determine whether matrix models provide accurate predictions where there is high individual variation found that matrix models are robust except where there is strong difference in size-dependent growth between individuals in a population (Pfister and Stevens 2003). Schemske et al. (1994) suggest that the best approach to assessing the biological status of a species is by censusing populations and construction of a matrix model.

Matrix models have been widely applied to plant demographic studies (Caswell 1989; Caswell 2001). They have been used in the comparison of life histories between rare and common species in the same genus (Fiedler 1987), to assess the impact of bio-control agents in pest management studies (Shea and Kelly 1998), to evaluate different land management methods (Lennartsson and Oostermeijer 2001; Hunt 2001). They have also been used for studies on the population dynamics on long-lived tree species (Manders 1987; Kaneko et al. 1999; Raimondo and Donaldson 2003) and to assess the demographic variability between different populations (Menges et al. 1998).

Red Data Listing for rare and threatened species

The World Conservation Union (IUCN) launched a program to create awareness regarding globally threatened species through their Red Data Lists (RDLs) which are used as a guide to conservation bodies to prioritise species in need of conservation (Golding 2002). The IUCN Red List of Threatened Species requires that a quantitative risk assessment be carried out for any species to be considered Critically Endangered, Endangered or Vulnerable (IUCN 2006). PVAs are widely used to assess population persistence or risk of extinction of a species for possible inclusion on the

Red List Database (IUCN 2006). South Africa boasts a total of 23 420 known plant taxa, 4% of which are listed Red Data species (Victor 2002). Of the 948 RDL taxa, 35% are categorised as “Lower Risk near threatened” (LR-nt) to which *O. grandis* belongs. *O. grandis* was classified as a rare endemic in the original assessment by Hilton-Taylor (1996). Subsequent to this, the re-assessment of (based on IUCN ver 2.3 criteria) included *O. grandis* in its current non-threatened category (Victor 2002). At the time of this study, the re-assessment of *O.grandis* under the latest IUCN version 3.1 was not available, although the IUCN 3.1 criteria have been available for use since January 2001.

<u>Rarity and endemism in South Africa</u>

South Africa is renowned for its floral diversity and high levels of endemism. More specifically the Eastern Cape Province is unique in that all four of the biomes converge giving it its rich mosaic of vegetative diversity. The distributional range of *O. grandis* falls within the Albany Centre of Endemism, a WWF-IUCN global centre of plant diversity and region with high levels of floristic endemism encompassing a large area of the Eastern Cape Province (van Wyk and Smith 2001). Figure 1.1 shows the locality of the Eastern Cape Province in South Africa and the Albany Centre of Endemism.

The Albany Centre includes a total of approximately 4000 plant species, of which over 15% are considered endemic or near endemic (van Wyk and Smith 2001). Outliers of the Fynbos Biome on quartzitic sandstone including vegetation of the Suurberg Mountains and areas around Grahamstown are included in the Albany Centre. Fynbos can be described as shrubland with a mixture of plant types displaying different forms of growth (Cowling and Richardson 1995) with proteoids, ericoids, restioids and geophytes as identifiable taxa of this biome (Lubke and van Wijk 1998). Three types of Fynbos occur with the Eastern Cape Province: Mountain Fynbos, Grassy Fynbos and Dune Fynbos. Mountain Fynbos occurs in small patches west of Grahamstown and to a greater extent in the Suurberg Mountains further west towards Port Elizabeth. Grassy Fynbos has a wider distribution extending from the Great Fish River in the east to the Sundays River in the west (Lubke and van Wijk 1998). It has been suggested (Cowling and Richardson 1995) that Grassy Fynbos occurs in areas where grasses outcompete the restioids in areas with higher summer rainfall.

Figure 1.1 The Fynbos Biome and Albany Centre of Endemism (after van Wyk and Smith 2001) in relation to the Eastern Cape Province, South Africa

Fynbos and fire

Fire is a natural process in the Fynbos biome and many species have adaptive traits to deal with fire disturbances. The four components of fire regime include frequency, season, intensity and scale. The average fire regime for fynbos vegetation is moderately intense fires occurring mostly in the summer months at a 12 to 15 year interval (Cowling and Richardson 1995). However, differences between fire regime between the eastern and western extremes of the Fynbos Biome are marked and are discussed in more detail in Chapter 2. The way in which fynbos plants respond to fire is either to seed or sprout. Seeders are killed by a fire and depend on post-fire seed germination for regeneration. Sprouters are likely to survive fires by resprouting from protective buds (Cowling 1992; Cowling and Richardson 1995). The life histories of sprouters and seeders are different in response to their different strategies of post-fire survival. Differences, particularly in reproductive traits, are observed (Vesk and Westoby 2004) where sprouters generally produce fewer seeds and allocate resources to growth of woody tubers and a thick bark. The establishment of seedlings therefore plays a small part in the overall persistence of predominantly resprouting species (Cowling and Richardson 1995).

<u>Fynbos and exotic vegetation</u>

Next to habitat alteration, invasions of exotic vegetation have been listed as the most important threat to the fynbos biome (Cowling 1992). Woody, tall growing alien species are particularly successful invaders in many non-woody habitats as they often have the competitive advantage over other species (Given 1994; Richardson et al. 1992). Seven of the most prevalent invaders of the fynbos biome include *Acacia cyclops*, *A. saligna*, *A. mearnsii*, *Pinus radiata*, *P. pinaster*, *Hakea gibbosa* and *H. sericea*. Advantages of these species over fynbos species include enhanced nutrient acquisition mechanisms, high levels of seed production, high rates of seedling survival, fast growth rates (Given 1994) and in some instances high levels of resilience to fire. Mountain and Grassy Fynbos vegetation types are very susceptible to exotic plant invasions, particularly *Pinus pinaster*, *Hakea gibbosa, H. sericea* and *Acacia longifolia* (Lubke and van Wijk 1998).

<u>Rationale for the study and selection of *Oldenburgia grandis*</u>

Studies on rare species may help to understand life histories that contribute to rare plant persistence in order to predict which species are at a risk of decline in the near future (Brigham 2003). It is not always possible to obtain life history information on all rare species and it may be necessary to generalise by comparing plants with similar life histories when planning preliminary conservation strategies where limited data is available (Bevill and Louda 1999; Oostermeijer 2003). It may be possible to extrapolate information on the life history and ecology of *O. grandis* to other long-lived woody sprouters in the Fynbos Biome. There has also, to date, been no detailed study on the life history and conservation status of *O. grandis*, neither has a quantitative PVA been carried out. These are vital components when determining conservation strategies and plans for this rare, near threatened species. Species considered for inclusion on South Africa's RDL include species of special botanical interest such as endemics or species with a restricted range (Golding 2002). Criteria for prioritising species for detailed research have also been suggested by Given (1994), including charismatic or unusually attractive species such as *O. grandis*. Trees are a rare growth form in Fynbos vegetation (Cowling, 1992) and represent a small division of the Asteraceae Family making *O. grandis* an extremely interesting study species.

Objectives and thesis overview

The main objectives of this study listed below and are explored in detail in chapters 2 to 5:

- To determine the life-history strategy of *O. grandis* including an assessment of population structure, fecundity, growth and persistence;
- To determine which life history strategies contribute the most to the population growth rate;
- To extend the results from objective 1 and 2 to a wider study on population structure across the range of *O. grandis*;
- To assess the status of *O. grandis* according to IUCN categories and criteria and to determine whether *O. grandis* should be upgraded to the next category;
- To perform a population viability analysis for the species by modelling the effects of environmental stochasticity including climatic variation and fire regime;
- To recommend conservation strategies for persistence of the species including suggestions of where conservation efforts should be focussed.

Chapter 2 reviews the life history and present demography of *O. grandis* revealing insight into its life history and population dynamics. An assessment of demographic parameters including fecundity, growth and survival as well as adaptations to environmental disturbances such as fire was explored.

To extend the results from Chapter 2 on the life-history of *O. grandis*, Chapter 3 includes a larger sample of population structure. To get baseline data for red data listing and future monitoring on the distribution of the species, population numbers and sizes were mapped across the range of *O. grandis* distribution.

Chapter 4 presents the results of a PVA including an analysis of the viability of various populations under various stochastic environmental influences by using a stochastic population model. Environmental stochasticity excluding the effects of fire was modelled, including different levels of fecundity. In addition to this, stochastic environmental effects including different fire regimes, high and low levels of seedling survival during fires and high and moderate levels of adult and mature mortalities as a result of fire was modelled under various scenarios.

Chapter 5 includes a summary of the chapters dealt with in this thesis, conservation recommendations for the persistence of the species as well as further research suggestions.

CHAPTER 2 LIFE HISTORY OF *OLDENBURGIA GRANDIS*

Introduction

Plant life histories

The life history of an organism can be described as its lifetime pattern of growth, longevity and reproduction (Barbour et al. 1987). The allocation of resources to these life history patterns is dependent on the stochastic influences affecting the organism (Franco and Silvertown 2002). Competing demands for a limited supply of resources results in a negative trade-off between life history traits (Franco and Silvertown 2002) although negative correlations do not always imply a trade-off (Vandermeer et al. 2003). The life-history characteristics of a species determine whether it will survive in the long-term at a site with a particular severity and frequency of disturbance (Silvertown and Charlesworth 2001). Barbour et al (1987) describes the trade-off between life history traits in economic terms. The limited supply of resources comes from the autotrophic production of carbohydrates, fats and proteins by plants. These resources will be allocated to three life history processes: growth, reproduction or persistence. The products and profits of this allocation depend on the amount of resources allocated which is dependent on the environment in which the organism lives.

Silvertown and Franco (2002) identified three main components in the life cycle of plants: survival with positive growth (including progression and clonal growth), survival without positive growth (persistence and retrogression) and fecundity (seed production and seedling recruitment). For the sake of simplicity in this study survival with positive growth is termed growth (G); persistence includes survival without growth (P), movement into smaller stages is termed retrogression (R) and fecundity (F) includes seed production and seedling establishment. Long-lived species that depend on persistence for population persistence, rather than growth or fecundity, have S-selected life history strategies (Grime 1977) enabling them to persist in high stress environments in habitats with low nutrients and low disturbances.

Understanding the life history of an organism is essential when planning conservation strategies and recommending management options for its continued survival. It has been suggested (Silvertown et al. 1993) that slow growing long-lived plant species (a life history strategy displayed by *O. grandis*) often trade seed recruitment and growth for persistence. Protein rich seeds have a high production cost compared to woody serotinous structures made from carbohydrates in nutrient poor environments. If an organism grows, it also contributes to persistence by not dying. Growth can therefore also be also viewed as persistence and are not necessarily traded off against one another (Franco and Silvertown 2002).

<u>Fynbos and fire</u>

Fire is a natural, necessary process within the fynbos biome essential for the persistence of many fynbos species (Cowling and Richardson 1995). The destruction and disturbance of a fire also returns valuable minerals back into the soil and increases the availability of N, P and cations (le Maitre and Midgley 1992).

Fire regime can be broken down into four components: frequency, season, intensity and size. Fire frequency is largely dependent on the rate of biomass accumulation, fuel properties (i.e. how flammable the type of vegetation is) and the likelihood of ignition. Grassy Fynbos in the eastern extremes of the Fynbos Biome accumulates biomass much more quickly than in the west. This is because the more fertile soils with a higher summer rainfall stimulate the growth of sub-tropical grasses which results in fire frequencies averaging between 4 and 6 years (Cowling and Richardson 1995).

An important consideration of the impact of fire on fynbos plants is the season in which the fire occurs. In the eastern sections of the fynbos biome, the higher summer rainfall and drier winter weather (with hot, dry bergwinds interspersed with the cold weather) results in most fires occurring in the cooler months between May and August (Cowling and Richardson 1995).

Fire intensity is the most unpredictable component of fire regime as it depends on fuel moisture, air temperature, wind speed and age of vegetation (le Maitre and Midgley 1992). Conditions for an intense fire include: hot temperatures and old vegetation where the accumulation of biomass is high with a dense layer of fine litter (Cowling and Richardson 1995).

Life-history strategies of fynbos species will determine how plants deal with and survive fire. There are two ways in which a fynbos plant can survive a fire: either by seed or by resprouting (Cowling and Richardson 1995). Seeders are killed by fire, but establishment from seed depends on fire for suitable conditions. Sprouters have adapted to surviving a fire by sprouting from protected buds. Sprouters produce fewer seeds that their seeder counterparts due to the fact that they allocate most of their energy to the growth of lignotubers and a thick bark (Bond and Midgley 2001; Hoffman 1999). Fire has an impact on all stages of a plants life cycle including sexual and vegetative reproduction, seedling establishment, individual size, growth and mortality, which in turn affect the population growth rate.

Factors that affect the dynamics of fire in fynbos include grazing practices and exotic vegetation (le Maitre et al. 1992). Threats to *O. grandis* populations may include invasions by exotic vegetation that either increases the intensity of fire or by competition (overtopping). van Wilgen et al. (1985) found that fire intensities in invaded fynbos areas were only higher than pristine fynbos under extreme weather conditions. Richardson (1997) suggests that fire frequency promotes that spread of invasive trees as well-established stands of alien vegetation will grow faster and taller than other fynbos vegetation after one or two fire cycles eventually resulting in close stands.

Examples of life history patterns in plants

Comparison of life-history strategies between rare and common or threatened and non-threatened species may reveal clues with regards to life-history traits that are an advantage to persistence of a species in certain environments. Raimondo and Donaldson (2003) found that life history strategies of long-lived cycad species

Encepharlartos cycadifolius and *E. villosus* render them sensitive to loss of adults from the population compared to loss of seeds which did not threaten the survival of either species, more so in the case of the long-lived resprouter, *E. cycadifolius*. A study on the long-lived Australian shrub (*Atriplex vesicaria*) found that adult survival was the greatest contributor to population growth rate for sampled populations (Hunt 2001).

Long-lived species found associated with fynbos such *Widdringtonia cedarbergensis* and *Widdringtonia nodiflora* show different life-history strategies in their response to fire. *Widdringtonia cedarbergensis* is critically endangered whereas *Widdringtonia nodiflora* has been classified as non-threatened; both species are found on rocky outcrops in the Western Cape Province of South Africa (Manders 1987). The adults of both species are easily burnt by fire, but the important difference is that *W. nodiflora* sprouts from the base after fire damage whereas *W. cedarbergensis* adults are easily killed and do not re-sprout. *W. cedarbergensis* survives by releasing seed after a fire which germinate relatively quickly. The consequences are that *W. cedarbergensis* is likely to go extinct under a regime where fires are frequent whereas *W. nodiflora* are likely to persist under the same fire regime.

In a comparison between sprouters and seeders of *Erica* species in fynbos, Ojeda et al. (2005) found that climate plays a role is the success of either seeders of sprouters in fynbos vegetation. The authors conclude that the seeder life history will invade and replace a sprouter population in mild Mediterranean climate conditions with short, moderate summer droughts and seasonal water stress. The seeder life history has an advantage over the sprouter if the seeder recruits after a fire outnumber post fire recruits of sprouters plus the post-fire survivors. This does not usually occur in non-Mediterranean areas with all-year round rainfall regime (such as the climate in the eastern extreme of the Fynbos Biome where *O. grandis* is found) where seeder cohorts are prone to local extinction if consecutive fire years are too close (i.e. less than a 15 year fire return interval).

The Mountain Golden Heather (*Hudsonia montana*), a rare shrub found in North Carolina, is restricted to quartzite ledges associated to areas of open heath vegetation dominated by Ericaceae (Kruckeberg and Rabinowitz 1985). It has been suggested that its restricted habitat is due to inter-specific competition by overtopping and shading by other species (Kruckeberg and Rabinowitz 1985). In another comparison of life-histories between rare and common species of Mariposa lilies, Fiedler (1987) found that the rare species had low levels of seedling survival and seedling establishment with low adult mortality and slow growth compared to the common species.

Oldenburgia grandis is a species that sprouts after experiencing fire damage. Sprouting is a life history strategy whereby plants regain biomass lost during a fire (Bellingham and Sparrow 2000). Sprouting enables plants to persist after a disturbance. The ability to sprout is correlated to persistence, which can be seen as a trade-off against growth and reproduction (Bond and Midgley 2001; Vesk and Westoby 2004). Rather than investing in future generations, investment is placed in the current generation (Bellingham and Sparrow 2000). Characteristics of sprouters include production of fewer seeds, slower growth, slower maturation rate from seed, fewer seedlings and poorer seedling survival (Bond and Midgley 2001). This ability of individuals to re-sprout after fire reduces the dependence on seeds for recruitment (Enright 1998). Sprouting plants also have the advantage of growing faster than seedlings after a disturbance (as growth will depend on stored resources) thus reoccupying their previous positions in the population (le Maitre and Midgley 1992). Sprouters also tend to dominate frequently disturbed, less productive sites (Bond and Midgley 2001). The suggestion is that the trade-off between sprouting and seeding is determined by the frequency of disturbance in an area (Bellingham and Sparrow 2000). In areas that experience frequent fire, sprouter adults tend to exclude seedlings, whereas in areas that experience long intervals between fires sprouter mortality tends to be high (le Maitre and Midgley 1992).

O. grandis is a strong basal sprouter and the rocky habitat on which *Oldenburgia* grows provides some refuge against fire, protecting individuals from the flames fuelled by the surrounding biomass. This was observed in the field where *Oldenburgia* trees remained completely un-burnt after a fire that had burnt all the vegetation on the perimeter surrounding the population. Basal sprouters in particular (compared to other sprouters) are common in sites experiencing severe and/or frequent disturbance (Bellingham and Sparrow 2000; Bond and Midgley 2001).

Sprouters are generally unlikely to experience recruitment failure and are therefore less vulnerable to inbreeding effects while being able to survive more disturbances (Bond and Midgley 2001). Morphological characteristics such as a corky bark may serve as an insulator against cooler flames in *Oldenburgia*.

Aims

This chapter is aimed at exploring aspects of the life history of *Oldenburgia grandis* including an assessment of population structure, fecundity, growth, survival and adaptations to environmental disturbances in particular the effects of fire.

The first aim of this chapter was to explore demographic variability between populations at five sites. Insight into the effects of fire on stage structure and mortality reveals which traits *O. grandis* has adapted to fire disturbances. Information on reproduction will determine levels of reproductive success between sites and for the species in general. Differences in transition probabilities and population growth rates between sites, especially at various stages of recovery after fire, give insight into the effects of fire on population persistence. This chapter attempts to answer the following questions:

1. Does the stage structure between sites differ and do they correspond to differences in time since last fire? It is expected that populations between sites will differ in their structure as different life stages will be in different phases of recovery after fire;
2. What is the change in stage structure after a fire and how is mortality of the various stages affected by fire? The prediction is that immature, adult and mature mortalities will be the lowest after a fire as these are the stages that resprout. There is expected to be high variation in seedling and sapling mortalities after a fire depending how well protected they are by rock refuges;
3. Is there a relationship between rock protection from fire and stage of an individual? A relationship between the rock substrate on which an individual grows and the life stage of an individual may be an indication of stages that

have survived previous fires because they are more protected by rock and therefore have more chance of progressing into the next life stage;

4. How successful is *O. grandis* at sexual reproduction and is there evidence of spatial variation in fecundity? Success in sexual reproduction will determine how capable *O. grandis* populations are at regeneration and should the population numbers crash, how successful will it be at re-establishing its numbers through recruitment.
5. How do transition probabilities and population growth rate differ between sites? A difference in population growth rate between sites will indicate the spatial variability of transition probabilities and if there is a correlation between population growth rate and last time since a population was disturbed by fire.

A further aim was to explore the general life history of the species. Data from five sites was pooled (Schwartz 2003; Raimondo and Donaldson 2003) to account for spatial variability (Kaneko et al. 1999). A single matrix was constructed to answer the following questions:

1. Are populations (represented by the pooled data from sampled populations) currently stable, declining or increasing?
2. What are the life history stages that contribute most to the population growth rate for the species under condition represented by the pooled data?
3. Are there differences between the observed stage distribution and stable stage distribution for the species, and if so, what accounts for these differences?

Methods

Study species

Oldenburgia grandis is a rare endemic species restricted to the Eastern Cape region of South Africa (Hilton-Taylor 1996). It is a small tree reaching up to 3.6m high with both upright and prostrate forms. The brittle leaves are a dark glossy green on the upper surface with a fine layer of white hairs on the under surface. Young leaves are covered with long “whip” hairs (Hanel 1990), hence the common name “Rabbits ears”. This hairiness is lost from the upper surface as leaves mature. The thick bark is corky and gnarled, which suggests that it is a good insulator against fire. Inflorescences begin as hairy rosettes on the tips of branches. These eventually become large flowerheads (or capitula) on the end of a long stalk with cylindrical rows of deep purple involucral bracts surrounding a ring of pink ray florets and a central cluster of yellow disc florets. Flowering occurs between September and January months (Bond 1987; Gledhill 1981). The root systems of *O. grandis* follow the fissures and cracks in the rocks, firmly anchoring the plant to the substrate. *O. grandis* is one of four species in the genus the others being *O. paradoxa, O. intermedia and O. papionum.*. The remaining three species are restricted to fynbos areas within the Western Cape Province and their distribution does not extend into the Eastern Cape (Bond 1987).

Study area

Climate

The study area extends from the Suurberg National Park in the west to Grahamstown in the east, which covers the full E-W extent of the range of *O. grandis*. The study sites and the surrounding areas are situated between the coastal climatic zone and the inland semi-arid zones. The hottest periods of the year are from February to March. Average maximum temperature is 23.1 ºC and average minimum temperature 13.7 ºC (Schultz 2001). Mean annual precipitation ranges from 716mm at the Suurberg Park to approximately 600mm in the Grahamstown region (Schultz 2001). The Suurberg section of the Addo Elephant National Park and surrounding area experiences winter as the driest month, with the highest rainfall in spring and autumn. Thunderstorms are common in summer where lightning fires are most likely to happen (Van Wyk et al. 1988). In the park, the slopes that tend to burn more frequently are the warmer, drier northern slopes compared to the moister southern slopes (Van Wyk et al. 1988). Grahamstown and surrounding areas experience rainfall ranges from all year round to very late summer. All study sites fall within the Southern Folded Mountain Eco-region (Kleynhans et al. 1999). Eco-regions are relatively homogenous ecological systems derived from terrain, vegetation information as well as consideration of altitude, rainfall, runoff variability, air temperature, geology and soil characteristics of the area indicating that the sampled sites experience fairly similar climatic environments. All study sites are within Suurberg the Quartzite Fynbos vegetation type (Mucina et al. 2006) dominated by either Mountain or Grassy Fynbos.

Geology and soils

Extending from the west, a peripheral outlier of the Fynbos Biome occurs on the quartizitic outcrops of the Suurberg Mountains east of Port Elizabeth and around the town of Grahamstown in the Eastern Cape province. These quartzitic outcrops of the Witteberg Group are part of the Cape Supergroup forming part of the Cape Fold Mountains (McCarthy et al. 2005). The Cape Supergroup consists of three major layers: Witteberg group (top layer), Bokkeveld Group (middle layer) and Table Mountain Group (bottom layer), originating in the Ordorvician to Devonian ages and approximately 8700m thick (McCarthy et al. 2005). The Cape Fynbos region is strongly associated with the weakly developed soils and rocky terrain of the Cape Supergroup.

Oldenburgia grandis is typically found on outcrops derived from Witteberg Quartzite where the layers of un-weathered quartzite are exposed (Olivieri 1977). Trees are easy to see from a distance as they follow the line of the outcrops. These quartzites extend from the Suurberg Range in the west and continue into the Highlands Range and Grahamstown Hills. Soils of this range are nutrient poor, sandy and acidic. Olivieri (1977) suggested that *Oldenburgia* is limited to Witteberg quartzite soils due to the fact that these soils have optimal pH, phosphorus and aluminium content for the establishment of the tree. The effects of fire and competition with other species as a possible cause for restriction to these outcrops however were not considered in that study.

Vegetation and fire

Oldenburgia grandis populations are associated with both Grassy and Mountain Fynbos vegetation, encompassed in the Suurberg Quartzite Fynbos broader vegetation type (Mucina et al. 2006). The largest area of Fynbos is contained within the Cape Floral Region Centre of Endemism; whereas the eastern extremity of this biome occurs within the Albany Centre of Endemism (van Wyk and Smith 2001). Cowling and Richardson (1995) describe fynbos as a shrub land with a mixture of plants of different growth forms including proteoids, ericoids, restoids and geophytes.

Grassy Fynbos is distinguished from Mountain Fynbos by a high cover of grass, non-proteoid nanophylls and forbs (Cowling 1992). *O. grandis* is fairly unique in that trees are a rare growth form within Fynbos vegetation, particularly in Grassy Fynbos (Cowling 1992). Grassy Fynbos consists of a number of key grass species such as *Themeda triandra*, *Heteropogon contortus*, *Trachypogon spicatus*, *Eragrostis* species and *Brachiaria serrata* which replace the Restionaceae dominant in the Mountain Fynbos (Lubke and van Wijke 1998).

Mountain Fynbos is more common in areas closer to the western distributional limit of *Oldenburgia grandis* common on wet southern slopes (Van Wyk et al., 1988). Acocks (1988) listed "false fynbos" or Mountain Fynbos present in the Suurberg region to include the following identifying genera: *Elytropappus, Phylica, Erica, Cliffortia*, *Passerina*, *Leucospermum*, *Metalasia*, *Coleonema*, *Euryops*, *Ficinia*, *Bobartia*, *Themeda, Pentaschistis* and *Restio*. Grass cover is low in Mountain Fynbos vegetation forming the under storey to the woody canopy; grasses that do occur in these areas are C3 grasses such as *Festuca*, *Pentaschistis* and *Merxmuellera*. *Protea lorifolia* and *P. repens* are common canopy species in this vegetation type (Van Wyk et al. 1988).

Fire is a major disturbance factor for both vegetation types, the frequency of the disturbance depending on fire regime. Grassy Fynbos experiences more frequent fires than Mountain Fynbos with a large proportion of species common to the vegetation type having the ability to re-sprout (Van Wyk et al. 1988). Longer fire intervals in some areas will result in the increase of Mountain Fynbos (Cowling 1984).

<u>Study sites</u>

Five sites, including a total of seven populations were chosen for collecting census data over three years (summers of 2004, 2005 and 2006). The term "population" is used loosely to describe separate demes and not necessarily genetically distinct entities. Study sites were chosen according to differences in land use, conservation status and previous fire history (Figure 2.1). Detail of each study site including geographical co-ordinates is included in Appendix 2.1.

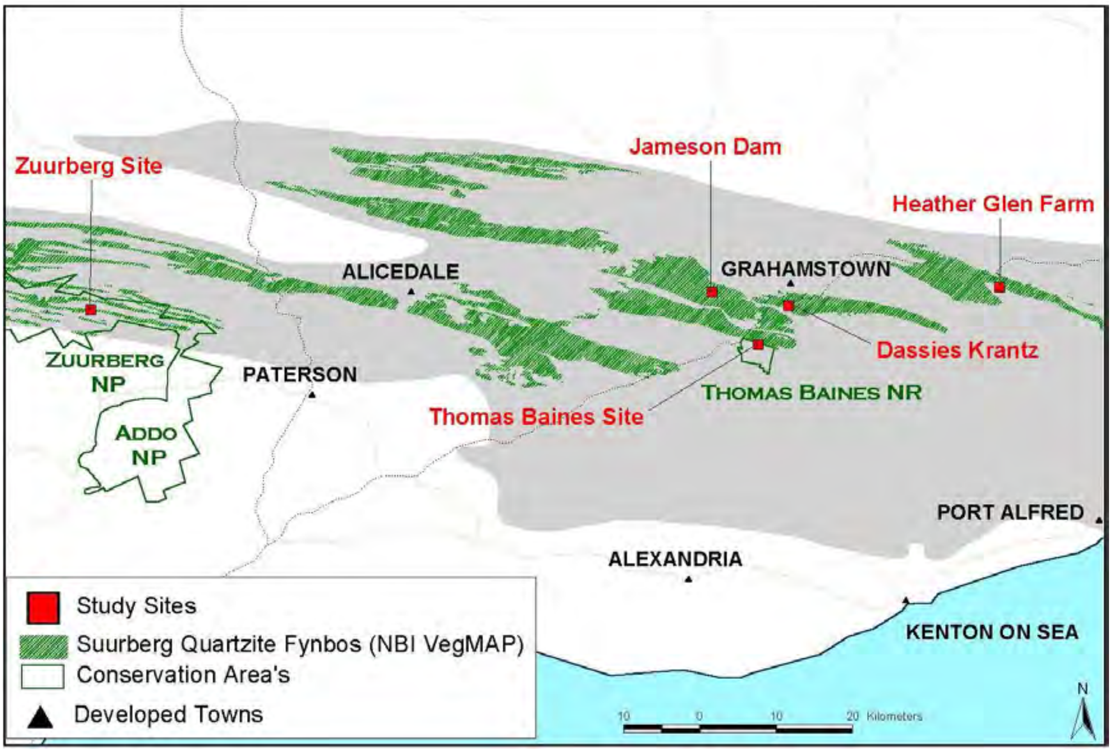


Figure 2.1 Map showing location of 5 study sites where 7 populations were sampled over 3 years. Grey shading indicates the Witteberg geological group

Certain sites have experienced fire more frequently and recently at the time of sampling than others. As no accurate fire histories could be found, estimates of fire disturbances in the study were based on evidence such as blackened stems, wilted brown leaves, with charcoal present in the soil as well as lack of surrounding woody vegetation. The presence of bracken ferns also indicated that a site had been burnt recently. Differences in current or past invasions by exotic vegetation at the study site were also considered. Sites were chosen to cover a range of environmental conditions encountered by *O. grandis* populations.

Heather Glen (HG)

The Heather Glen population is located on a cattle farm and is part of a much larger population extending across the Kap River Mountains, forming the eastern limit of *Oldenburgia* distribution. It was evident that cattle trample through the population forming well-trodden pathways through the trees. Grassy Fynbos vegetation dominate the hillside on which the scattered *Oldenburgia* trees grow. Scattered populations are defined here as covering between 5 and 25% of the surveyed area. The *Oldenburgia* population faces southwest at 620 masl. Time since the last fire burnt through this population was estimated to exceed 10 years. No trees sampled had black or discoloured stems as is usually seen on stems that had been recently burnt (Figure 2.2).

Figure 2.2 Example of an *Oldenburgia* site recently burnt by fire. Blackened soil is visible, surrounding vegetation has been charred and *O. grandis* individuals have blackened stems and leaves.

Jameson Dam (JD)

The population to the north of Jameson Dam is a few kilometres outside Grahamstown and constitutes the largest, densest population encountered during the period of this study. The site on which this dense stand of *Oldenburgias* occurs is used for cattle grazing. The high density of the population leaves little room for other vegetation to co-exist as an under storey. Most of the ground cover in the area consists of decomposing *Oldenburgia* leaves. No cattle were seen to venture into the population and there was no evidence of cowpats among the *Oldenburgia* plants. Minimal grazing does occur on the outskirts of the population. The area is covered by Grassy Fynbos vegetation (Figure 2.3 shows an example of grassy fynbos vegetation) with scattered alien pine trees. No trees had blackened or discoloured stems indicating that the population had not been burnt for some time.

A small isolated sub-population (JD_F) in the same area separated from the main population by 500 m of Grassy Fynbos vegetation was also sampled. This sub-population was estimated to have burnt a few months before the site was sampled as the *Oldenburgia* stems were blackened, there was very little vegetation cover around the population and the soil has evidence of charcoal. Other than the time since the last fire, the site experienced the same environmental influences as the larger population.

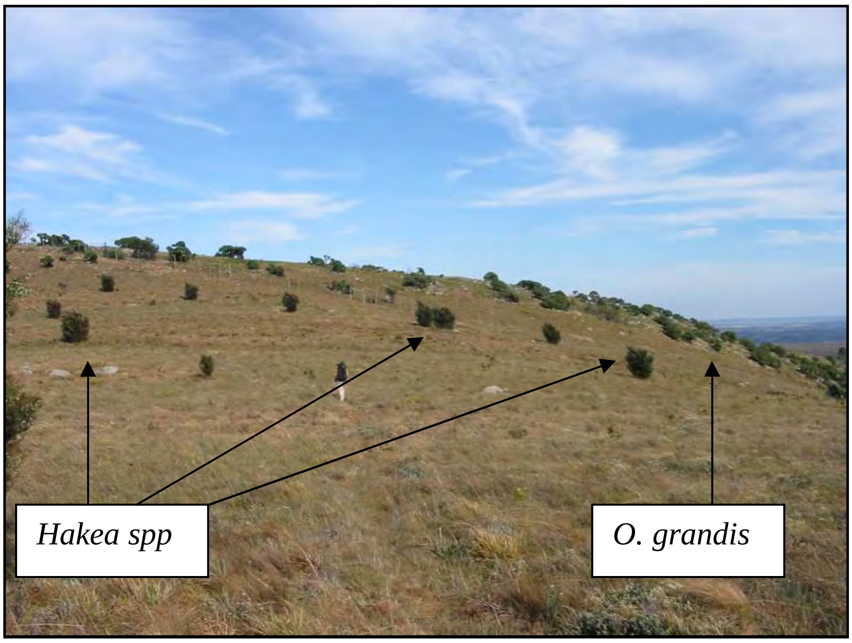


Figure 2.3 Photo showing *Oldenburgia grandis* scattered in the background on the quartzite outcrops with *Hakea sp* in the foreground growing amongst Grassy Fynbos vegetation along the last section of the *Oldenburgia* hiking trail

Suurberg (ZB)

The Suurberg site is found within the Suurberg section of the Addo Elephant National Park (AENP). This forms the western most distribution of *Oldenburgia grandis* (Croeser 1982). This section of the AENP constitutes one of the largest conservation areas for Grassy Fynbos (Van Wyk et al. 1988). Exotic plants are not present in this section of the park, but are gradually spreading from the northern sections of the park, particularly on the road verges of the Suurberg Pass. Time since the last fire is estimated to be greater than 10 years given the lack of burnt stems and evidence of resprouting. A section of this population was very dense (much like that at Jameson Dam). This was also the only site with a NNW aspect and not a southern aspect as with the other sites sampled. Vegetation in the area was mixed Mountain Fynbos and

Grassy Fynbos in some areas. Grassy Fynbos was predominantly found in and around the population sampled.

Approximately 1 km south of the ZB population, on a north-facing slope, a small isolated sub-population (ZB_F) surrounded by shoulder high Mountain Fynbos vegetation (Figure 2.4 shows an example of Mountain Fynbos found in the Suurberg Park) was sampled. The sub-population had burnt just before the site was sampled.

Figure 2.4 Photo showing *Oldenburgia grandis* surrounded by tall woody Mountain Fynbos vegetation along the Suurberg Pass

Thomas Baines (TB)

The Thomas Baines site is situated on a cattle farm just outside the Thomas Baines Nature Reserve (approximately 12 km south west of Grahamstown). The area forms part of the *Oldenburgia* hiking trail between Grahamstown and the reserve and is part of the proposed *Oldenburgia* conservancy. Exotic trees are found in small patches on the hilltop above where the *Oldenburgia*s are growing on the south-to-south western slopes. The population, although fairly scattered, is relatively large and is estimated to consist of over 500 trees.

Dassie Krantz (DK)

Dassie Krantz (formerly the Grahamstown Nature Reserve) is situated approximately 10 km from Grahamstown. The population growing on the SSW slopes is scattered, between 100 to 300 trees. Although the area now only has the occasional exotic tree, the site has a history of being heavily invaded by *Pinus* species. The earliest records of exotics planted in the area date back to 1867. The early 1900’s saw a well-established pine plantation growing close to and spreading toward the reserve. By the 1930s the western and southern slopes of the reserve were invaded (Haigh and Ilgner 2001). In 1934 and 1935, an effort to remove the encroaching pines from the reserve was successful except along the northern perimeter (according to the minutes of the Grahamstown Nature Reserve Society 1937). From 1997, the Working for Water project has been actively clearing the pine trees in the reserve and today Dassie Krantz is largely free of exotics (Figures 2.5 and 2.6).

Figure 2.5 Dassie Krantz invaded by Pine trees (Liebenberg 1930s, exact year unknown)

Figure 2.6 Photo taken in 2005 showing an area almost completely free of pine trees

Burnt stems and recently sprouted individuals indicated that the site had burnt between 3 and 5 years ago. Sprouting individuals had developed basal stems whereas more recently burnt sites such as JD_F and ZB_F the leaves sprout directly out the burnt stems as the basal stem are not yet developed (Figure 2.7).

Figure 2.7 A recently sprouted plant at JD_F where the new basal stems have not developed

Most fire records for the Dassie Krantz area exist for Featherstone Kloof (which Dassie Krantz is part of) as a general area. From personal observations in the field, fires are very patchy and can burn an area around the population without affecting the individuals in the population due to the rocky terrain forming a barrier around the population.

<u>Sampling design</u>

Demographic data were collected from three permanent 10 x 10 m quadrats at each study site over a three-year period. Each individual within the quadrat was marked with a metal tag so that the same individuals over the 3-year sampling period could be monitored (Figure 2.8). Seedlings that were too small were marked with a wire and the position under a tagged tree was noted.

Figure 2.8 Tagged plant growing on rock surface

Survival and recruitment were recorded annually during the summer months, as this is usually the season where there is a peak in growing conditions. The new seedlings counted each year were tagged. Size measurements (maximum height, maximum canopy diameter and circumference of basal stems), number of basal stems and number of flowering stalks (including number and size of capitula per stalk) were recorded in the first year. In subsequent years, height, canopy diameter and the number of developed flowering stalks including the number of captitula per stalk were recorded for each tagged individual. One site burnt during the second sampling year and deaths due to fire were recorded in this case.

The substrate type on which each individual occurred was divided into three categories: rock, leaf litter/other vegetation and soil. As individuals may be growing on all three types, the proportion of each type was estimated in the first sampling year. This was done to determine the potential protection each individual tree had from fire if it had to occur. It was then possible to assess whether individuals growing on predominantly rock were more protected from a fire than individuals growing among vegetation, debris or surrounded by bare soil.

For all statistical analysis in this chapter excluding the matrix modelling, STATISTICA 7.0 (StatSoft 2004) software was used.

Stage classes

For studies on woody tree species it is better to use size than age to describe population structure and to project its future (Harper 1977). Life history traits such as persistence and reproduction are more likely to be linked to size rather than age in woody plant species (Harper 1977; Caswell 2001). As noted previously, two types of error are possible when choosing stage classes. If the classes are too many, the assumption that individuals in the same class have the same transition probabilities is violated (Moloney 1986) and the importance of persistence relative to growth is overemphasised (Raimondo and Donaldson 2003). If there are too many classes (i.e. each class is too small) they may have too few individuals increasing the potential for sampling error. Algorithms and mathematical models have been formulated to determine stage classes (Moloney 1986) but Caswell (2001) argues that these methods should be used with caution and that stage structure should be biologically meaningful. This approach was used in this study where stages were guided by the knowledge of the morphology, reproductive and sprouting behaviour of *O. grandis*.

The life-history stages of *O. grandis* were determined using size, fecundity and estimates on recent fire damage (see Table 2.2). Six stage classes were determined: seedling, sapling, suffrutice, immature, adult and mature. The difference between a seedling and sapling was determined by the height of the plant. Saplings are non-reproductive individuals that develop into immature then adult plants. Immature and adult plants are not differentiated according to height, but rather by the ability to reproduce sexually. Once a plant is capable of sexual reproduction, the levels of reproduction differentiate adult and mature plants. Suffrutice individuals were seen in populations that had recently been affected by fire. These are multi-stemmed individuals that have sprouted as a response to damage by fire.

Class 1: Seedlings

Seedlings can be identified as single-stemmed individuals with 2 – 4 leaves with a height limit of 10 cm, above which the basal stem count was found to increase above 1. Field observations showed that seedlings displayed hardly any growth over the duration of the study period; this stage classification is therefore not restricted to individuals under a year old.

Class 2: Saplings

Individuals classified in the sapling stage were between 10 and 54 cm in height. It was found that individuals at 55 cm and taller had the potential to flower and therefore become potentially reproducing individuals.

Class 3: Suffrutice

Individuals sprouting after fire damage could not be classed as a seedling or sapling. A suffrutice plant could have either regressed from being an immature, adult or mature plant. Carbon stores in the stems of the larger stages are likely to differ from these stores in seedlings or saplings. A distinction therefore was made between an individual that had grown from a seedling and an individual that had lost all canopy cover from the fire (previously immature, adult or mature) and had now sprouted. Sprouting individuals were therefore categorised separately in the suffrutice class.

Classes 4 and 5: Immature and adult

Individuals above 54 cm high were categorised as either immature or adult, depending on their reproductive status. In most cases it was possible to determine if an individual had flowered in its lifetime due to the presence of a flowering stalk scar. In this instance, the individual would be classified as adult. Individuals with no evidence of a previous flowering scar or that were not flowering at the time of the census were classified as immature.

Class 6: Mature

Trees above 190 cm in height or with a maximum canopy diameter of over 290 cm were distinguished from adult individuals. It was at this height or canopy diameter where individuals tended to have higher number of fully developed capitula per flowering stalk.

A summary of stage classes is given in Table 2.2.

Table 2.2 Stage classes determined according to height, flowering status and canopy diameter

Stage	Definition	Class
seedling	single-stemmed; between 1-4 leaves; ≤ 10 cm in height	1
sapling	single/multi-stemmed; > 10 ≤ 54 cm in height	2
suffrutice	multi-stemmed; re growth after a fire; > 10 ≤ 54 cm in height	3
immature	≥ 55 cm; no previous flowering stalk scars	4
adult	≥ 55 cm; flowering stalks present or scars visible	5
mature	flowering stalks present or scars visible; ≥ 55 cm ≥ 190 cm in height or ≥ 55 cm ≥ 290 cm canopy diameter	6

Matrix construction

Stage-structured 6 x 6 projection matrices based on the Lefkovitch (1965) matrix model were constructed for the population at each site. A spreadsheet was used to construct a transition matrix based on the mean observed transition values for each site. The transition matrix was then used to project change in the population (and each stage) over a fixed time period. *PopTools ver. 2.6.6* (Hood, 2005) was used to analyse the matrix and to calculate the population growth rate (λ) and the elasticity values.

A general equation to determine population growth rate is given by the following formula:

$$\mathbf{AN_t = \lambda N_t}$$

Where A is a square matrix containing transition probabilities, N is the population vector, N_t describes the stage distribution of the population at the present time. By multiplying the present stage class distribution with the matrix transition probabilities, the stage class distribution for the next time period can be calculated. A population can therefore be projected for any number of time periods, t, into the future. As time increases a stable stage distribution (SSD) is attained (in a model where the assumption is that there is no environmental variation). The SSD can be described as the proportion of individuals in each category remaining the same as the matrix continues to be applied (Caswell, 2001).

A generalised stage projection matrix shown below (after Vandermeer et al. 2003) where p_n describes the probability of an individual surviving and remaining in the same stage (persistence). Growth (g_n) describes the probability that an individual will survive and progress to the next stage. Fecundity (f_n) describes the rate of reproduction for an individual.

$$\begin{pmatrix} p_1 & f_2 & f_3 & f_4 & f_n \\ g_1 & p_2 & 0 & 0 & 0 \\ 0 & g_2 & p_3 & 0 & 0 \\ 0 & 0 & g_3 & p_4 & 0 \\ 0 & 0 & 0 & g_{n-1} & p_n \end{pmatrix}$$

This is the usual pattern attained if the stages of a species are ordered for example from small to large trees. Transitions on the diagonal relate to an individual remaining in the same stage over a defined time period usually 1 year. Transitions just below the diagonal indicate an individual progressing to the next stage by growth. Elements on the top row indicate reproduction rate by the individual in that stage.

The value of interest from the matrix modelling exercise in this study is the population growth rate (λ) as the dominant eigenvalue of the matrix and SSD values as the eigenvector. A stable population will have a $\lambda = 1$; an increasing population will have a $\lambda > 1$ and $\lambda < 1$ indicates a decreasing population (Caswell, 2001).

Transition matrix elasticity analysis makes it possible to determine whether persistence (P), growth (G) or fecundity (F) play the most important role in determining the growth rate of a population. Elasticity analysis is an additional tool that can be used to assess the contribution of each stage to P, F and G and therefore determining the critical life history stages for species survival. Transitions that have the smallest elasticity values are often the observed transitions that vary the most and have the least effect on λ (Silvertown and Charlesworth 2001). These life-history stages that are vulnerable to stochastic variation have theoretically been selected to have a minimal effect on the overall fitness of the species or population (Silvertown and Charlesworth 2001).

Elasticities for each matrix element (e_{ij}) are defined by:

$$\mathbf{e_{ij} = \frac{\delta\,\lambda\,a_{ij}}{\delta\,a_{ij}\,\lambda}}$$

Where a_{ij} are the transition matrix elements and λ is the population growth rate (Caswell 1989).

The number of life cycle stages chosen to describe a species may affect the relative importance of G, P or F (Enright et al. 1995, Silvertown et al. 1993). A source of possible inaccuracy comes into the elasticity analysis in the number of stages chosen to represent each life cycle stage. Using few life cycle stages may result in higher elasticity values for persistence whereas the elasticity for progressing to the next stage (i.e. growth) would be greater if using many life cycle stages. In a study of 18 herbaceous and 19 woody species, Ramula and Lehtilä (2005) found that decreasing matrix dimensions (i.e. using fewer stage classes or combining certain stages) does not adversely affect the value of λ in woody species, but does significantly in herbaceous species (i.e. woody species are not sensitive to reduction in the dimensions of a matrix according to their study).

The projection matrix was based on the transitions observed from census data (Table 2.3). Results from three consecutive years of sampling yielded two sets of transition probabilities. This has been considered an unrealistic depiction of population dynamics as density-dependence or stochastic effects are not well represented (Fieberg and Ellner 2001). To render the model more representatve, data for sites that had not recently experienced fire were pooled to construct a single matrix. It has been suggested (Kaneko et al. 1999) that studies where data for long-lived species are collected for a single stand over many years may include a range of temporal variations the species may encounter, but this only characterises a species over a small portion of its habitat. Including various sites includes spatial variation encountered by populations and may reduce the problem of data collected over too few years especially for long-lived species (Schwartz 2003).

Some authors have cautioned against averaging transition data of a few sample years (Brigham and Thompson 2003; Menges and Quintana–Ascencio 2003) but the primary reason given is that the short sampling time period may have missed episodic events in the plants life-cycle (Menges and Quintana–Ascencio 2003; Schwartz 2003). Averaging transition probabilities will therefore be problematic when demographic variability is as a result of environmental gradients. Averaging transition probabilities made it possible to produce a single matrix that was representative of sites that had not experienced fire for at least 10 years. Life history stages that contribute most to population growth could be estimated for sites in this condition.

Fieberg et al. (2001) suggested that one is able to increase the effective sample size by artificially manipulating environmental conditions in the model such as fire regime. In this way it is possible to overcome time constraints concerning collection of data. It was also necessary to produce a single matrix model with transitions between observed limits to simulate various fire regimes, fecundity and mortality levels (see Chapter 4) and to assess the conservation status of the species from a realistic model based on spatial rather than temporal variation. In this study, data from four sites were averaged over a three-year study period yielding two transitions (year 1 to 2 and year 2 to 3). Sites that had recently experienced fire where not averaged, as the DK site was vastly different to the JF_F and ZB_F sites due to having been burnt during the time of the study.

Table 2.3 Transition matrix showing possible transitions for *O. grandis* individuals. The diagonal (shaded) denotes individuals staying in the same stage, values below the diagonal are individuals progressing to the next stage class while values above the diagonal indicate retrogression into a smaller stage class except for f_{ad} and f_{ma} which are fecundity parameters

	seedling	sapling	suffrutice	immature	adult	mature
seedling	$a_{se,se}$				f_{ad}	f_{ma}
sapling	$a_{se,sa}$	$a_{sa,sa}$				
suffrutice			$a_{su,su}$	$a_{im,su}$	$a_{ad,su}$	$a_{ma,su}$
immature		$a_{sa,im}$	$a_{su,im}$	$a_{im,im}$		
adult			$a_{su,ad}$	$a_{im,ad}$	$a_{ad,ad}$	
mature					$a_{ad,ma}$	$a_{ma,ma}$

Determination of fecundity transition probabilities

Fecundity transitions were calculated as a direct transition from adult to seedling. Soil samples from each study site placed in a greenhouse yielded no seedlings. Seeds collected from plants germinated within two weeks or were found to be unviable. From this evidence it was concluded that the seed class should not be included as a separate category as seeds germinate within a year.

The number of new seedlings was divided by the number of flower heads from the previous sampling year for adult and mature stages. The values derived from this were based on new seedling establishment between the years and the probability of these seedlings being either a product of adult or mature trees. The formula used to calculate fecundity transition values for the adult stage was as follows:

$$\mathbf{F_{a,y} = se_y / ((N_{a,y})+(N_{m,y}R_{m,y}))}$$

where, $F_{a,y}$ is the fecundity parameter for the adult stage in year y. The number of new seedlings found in the same year is denoted by se_y. $N_{a,y}$ is the number of adults in the same year and $N_{m,y}$ the number of mature individuals in the same year. $R_{m,y}$ is the ratio of the number of flower heads between the adult and mature stage for year y (i.e. the average number of flower heads per mature plant divided by average number of flower heads per adult plant).

The formula used to calculate fecundity transition values for the mature stage was:

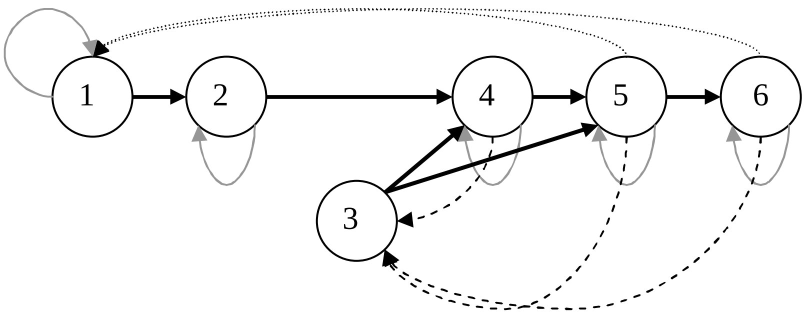
$$\mathbf{F_{m,y} = (se_y – (N_{a,y}F_{a,y})) / N_{m,y}}$$

where, $F_{m,y}$ is the fecundity parameter for the mature stage in year y.

Results

Life stages of *O. grandis*

A life cycle graph constructed for *O. grandis* is shown in Figure 2.9. Each node represents a stage class. The lines between the nodes indicate the transitions within and between stages.



Stages:
1: seedling
2: sapling
3: suffrutice
4: immature
5: adult
6: mature

Figure 2.9 Life cycle graph of *O. grandis* derived from transition matrices
Key:
growth ——; persistence ——; retrogression – – –; reproduction ········

Stage structure in sampled sites

All sites had between 10 and 20% of the sample made up of mature trees, except for the burnt site ZB_F. This was the only recently burnt site associated with Mountain Fynbos vegetation while all other sites were found in Grassy Fynbos (Figure 2.10). The number of adult trees varied between sites where HG, ZB and JD samples had the highest proportion of adults. Sites that had not been affected by fire for many years (HG, TB, ZB and JD) had similar proportions of immature individuals to the site burnt more recently (DK) whereas sites burnt less than a year before the time of sampling had considerably lower proportions of immature individuals. The proportion of saplings was highest for sites not affected by fire for a number of years except for the ZB site that had similar proportions to DK. No saplings featured in either of the two most recently burnt sites. A similar pattern was seen for the proportion of seedlings found at the most recently burnt sites where no seedlings were encountered.

Of the four sites unaffected by fire for a number of years at the time of sampling, the HG site had the lowest proportion of seedlings in the sample.

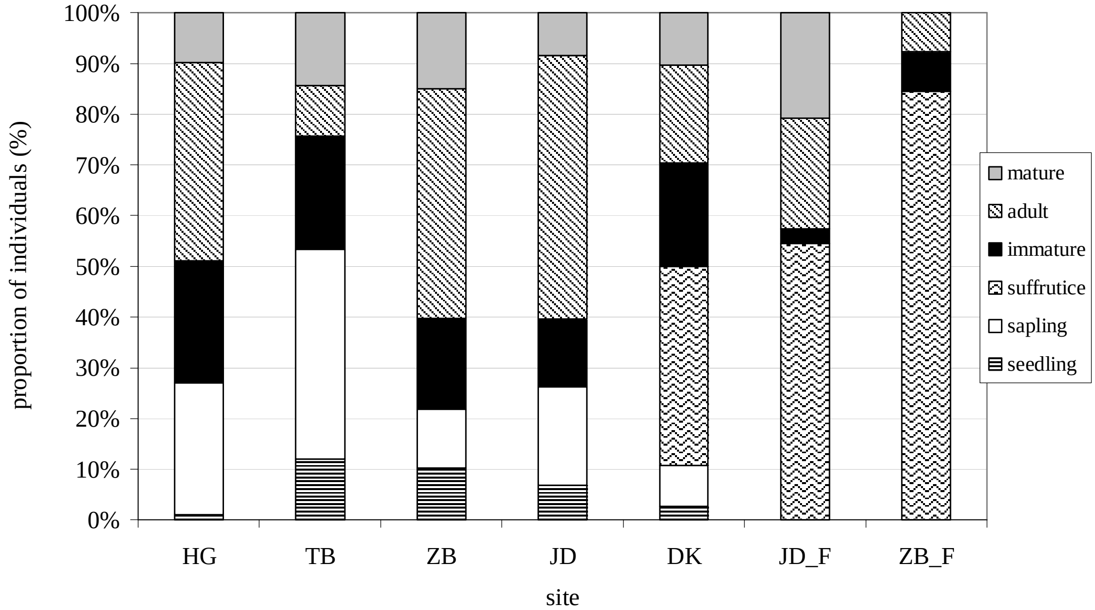


Figure 2.10 Stage structures of five sites (with 5 populations and 2 sub-populations) at different stages of recovery after fire in the first sampling year. HG: Heather Glen (n = 91); TB: Thomas Baines (n = 84); ZB: Suurberg (n = 78); JD: Jameson Dam (n = 88); DK: Dassie Krantz (n = 62); JD_F: Jameson Dam burnt site (n = 34); ZB_F: Suurberg burnt site (n = 13)

Stage structure and survival after a fire

Only one population burnt between two successive census years. The population at the Dassie Krantz site provides a good example of individual survival and sprouting ability after fire. The site was initially sampled in 2004 where the population not been burnt for at least 3 years. A fire had swept through the population between the first and second sampling year. With almost all of the tags still intact after the fire, each individuals mortality/recovery after fire could then be monitored.

The population structure before and after the fire (Figure 2.11) differed most for the suffrutice and immature stage classes. Only two individuals (a seedling and a mature plant) were destroyed as a result of the fire. Out of a total of 68 individuals, 23 % had all aboveground growth completely destroyed by the fire. Out of the remaining individuals whose canopy was still intact after the fire 49% had sprouting stems from the burnt base. The highest retrogression transition probability was seen in the immature stage at $a_{im,su} = 0.6522$. Adult stage transition retrogression probability after the fire was $a_{ad,su} = 0.1667$ and no mature stages retrogressed. It is impossible to say which suffrutice individuals retrogressed and which remained in the same stage so retrogression and survival was given by the transition probability $a_{su,su} = 0.3043$.

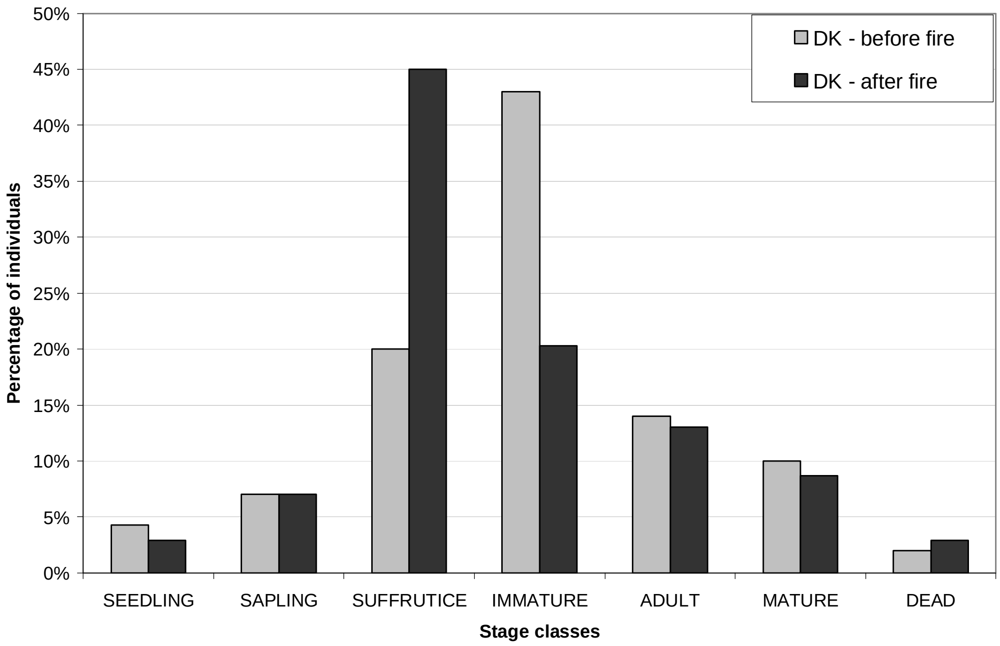


Figure 2.11 Population structure at Dassie Krantz before and after fire (n = 62)

<u>The role of rocky outcrops protecting individuals from fire</u>

Larger stage classes are associated with higher percentages of growing primarily on rock as opposed to soil, debris or with other types of vegetation (Figure 2.12).

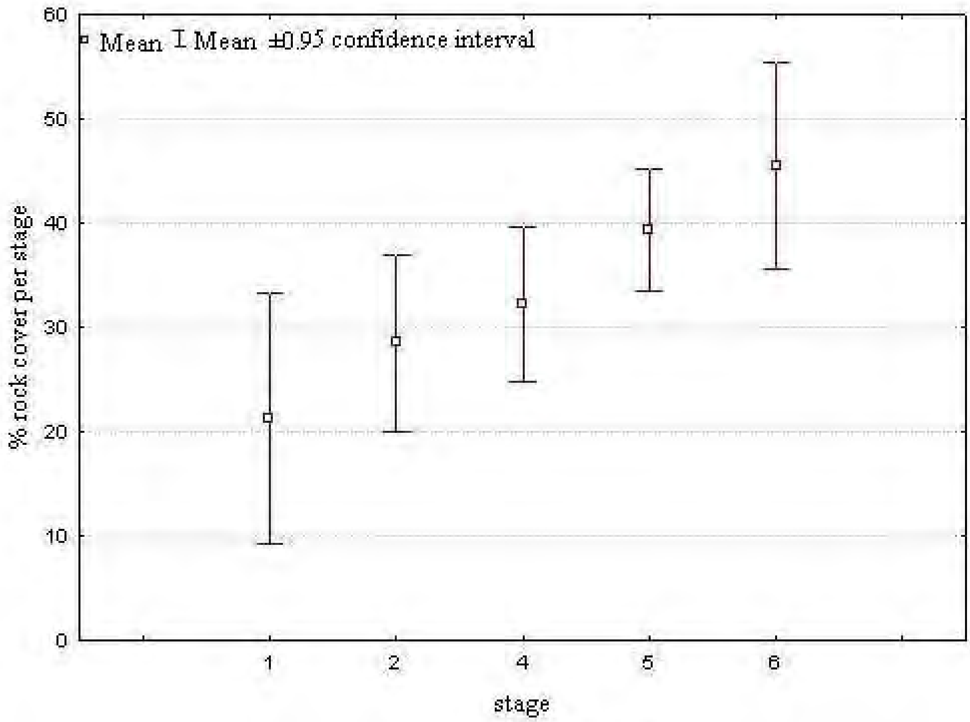


Figure 2.12 Percentage rock cover described as % substrate an individual is growing on, per stage for all sites not affected by fire for at least 10 years (Kruskal-Wallis 4.342) = 21.1711, p < 0.001))

Reproduction

Field observations showed flowering to be sporadic in *Oldenburgia grandis* acoss sites. This sporadic nature of flowering was also noted by Coates-Palgrave (1984). It was found that many plants only flowered every second year and the old flowering stalks often remained on the plant a few years after flowering. The flowering stalks were very slow to develop into a mature flowering capitulum. From the time the inflorescence emerges to full flowering can take up to a year. A peak in flowering was seen at all sites in the summer of 2004 and 2005 (Figure 2.13). Emerging flowering stalks in year one were not counted, but by year 2 the flower heads had fully developed. Those individuals that had flowered in year 2 did not flower again in year 3, and therefore the peak in flowering dropped again. The emergence of flower heads every second year would be mostly due to the slow development of growth of flower heads from emergence to seed set.

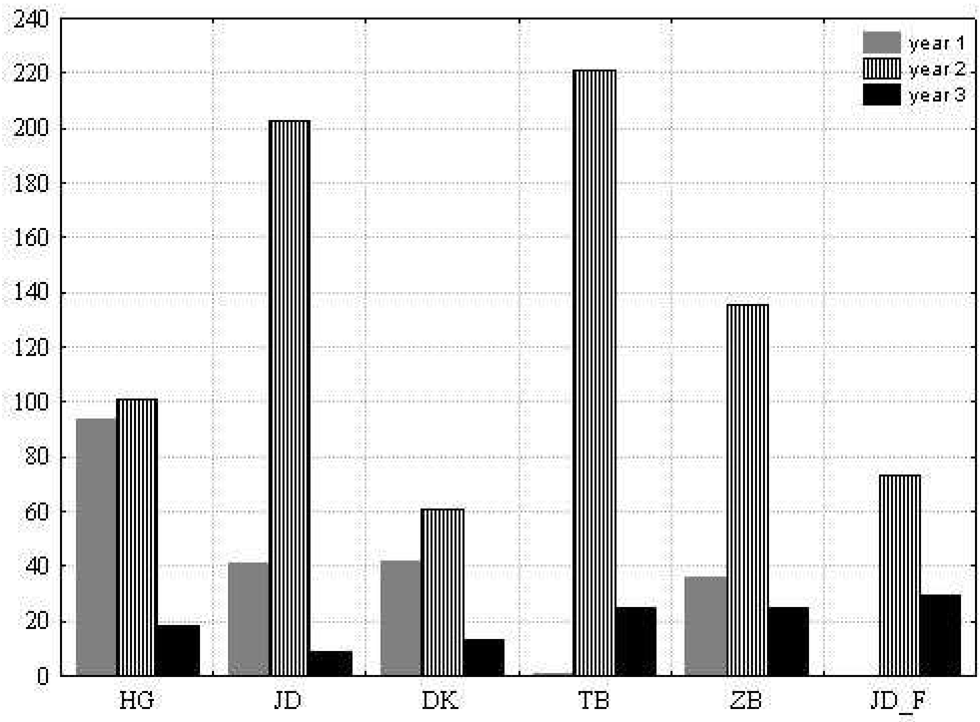


Figure 2.13 Number of developed flowering stalks (stage 5 and 6) on y-axis for each sampling year per site (x-axis)

A distinction can also be made between developed and aborted capitula where aborted captitula do not develop seeds (Figure 2.14). Not only are entire flower heads aborted but seeds often do not contain the endosperm and embryo necessary for germination.

Figure 2.14 Photo showing an example of a flowering stalk with a fully developed flowering capitulum at the far end and an aborted capitulum in the foreground

Aborted and fully developed capitula for stage 5 and 6 were summed and plotted for each site at each sampling year (shown in Figures 2.15 to 2.16). The DK site had a relatively high number of fully developed capitula before the fire, but these numbers dropped drastically in subsequent years. A peak in the number of fully developed capitula for the first and second sampling year was seen for the HG and JD sites with numbers dropping in the third year. The opposite was true for the TB and ZB sites where flowering peaked in the second year compared to the first and third years. In this study it was found that aborted capitula accounted for as much as 76% of all capitula sampled at all sites (n = 769). This differed between sites and between years. Production of aborted flower heads was the highest in the second sampling year for all sites, particularly for the JD, ZB and TB sites.

The number of both aborted and developed capitula coincided with the peak in flowering stalks in year 2. A high percentage of developed capitula were seen in the third year for most sites, but this was not reflected in the total percentage of flowerheads found at each site in the third year.

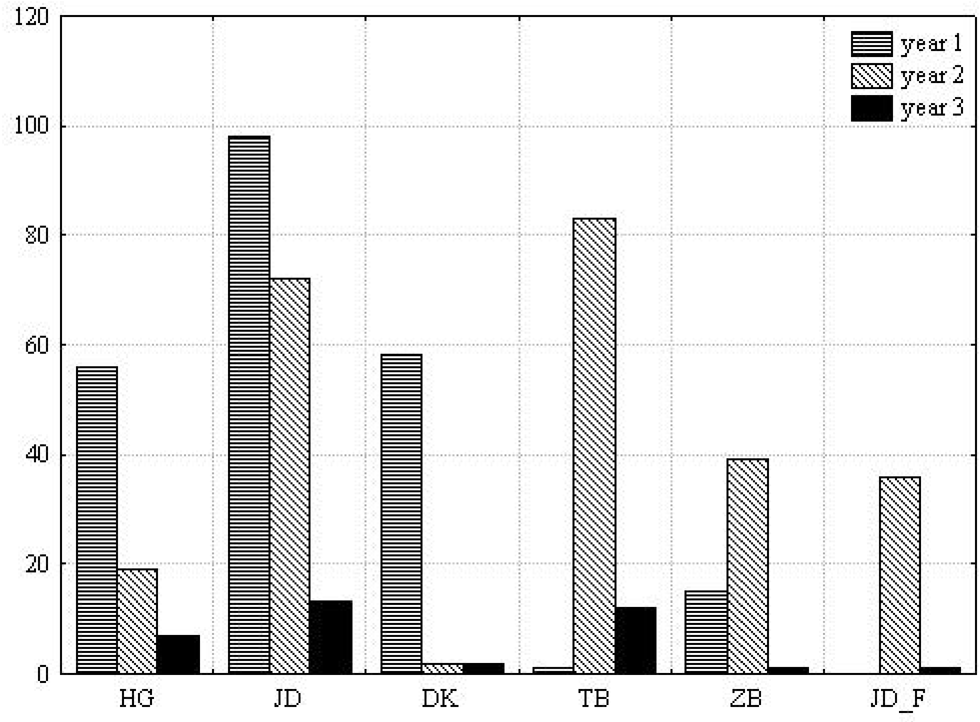


Figure 2.15 Number of fully developed capitula for stages 5 and 6 (y-axis) combined per site for each sampling year (x-axis)

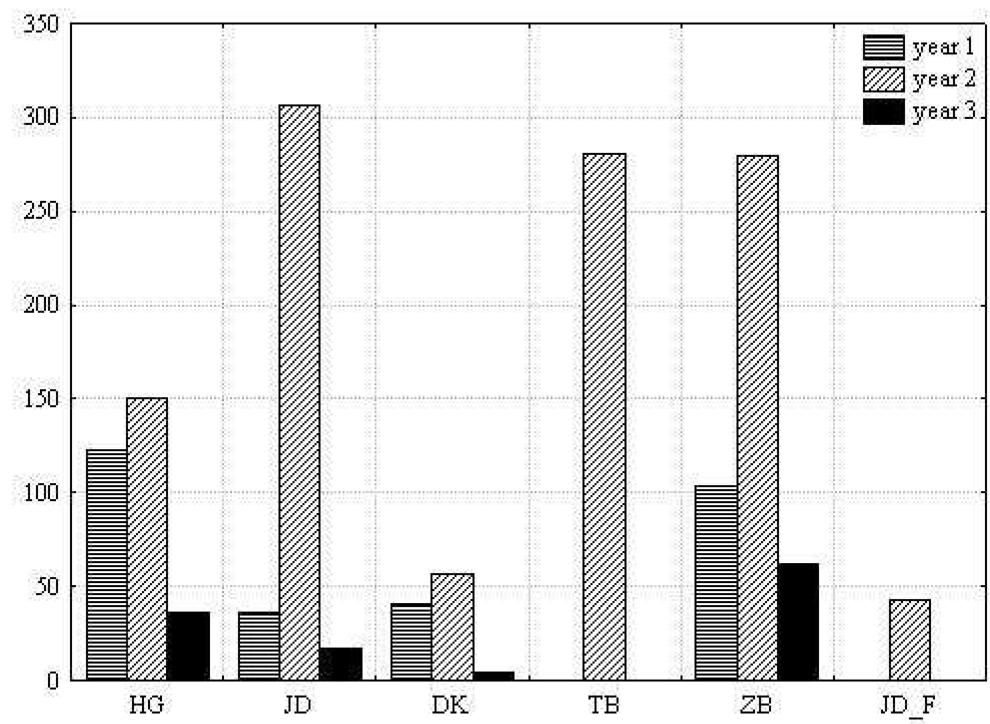


Figure 2.16 Number of aborted capitula combined for stages 5 and 6 (y-axis) per site for each sampling year (x-axis)

Work on seed viability by Hanel (1990) found that viable seeds with an endosperm were on average between 2.5mm – 3mm in width, 15mm in length and > 0.082g in weight. Hanel found unviable seeds to be on average between 0.9 – 1 mm wide, < 13.5mm and > 0.04g in weight. Aborted capitula accounted for 30% of all flower heads (n = 99) in the same study. Viable seeds (those with a developed endosperm with the potential to germinate) made up on average 4.1% of seeds contained in the seed head. Hanel's study also found that seed predation is the primary cause of seed damage, but the production of non-viable seeds (with no endosperm development) was also a contributing factor. Two species of *Anobiidae spp.* (Coloeptera Order) and *Tephritidae spp.* (Diptera Order) were found to be responsible for most seed damage.

Transition probabilities and population growth rate for each site

Population growth rate ranges between 0.9999 and 1.0006 for all sites. No decline in the growth rate of a population was seen for sites that had recently experienced fire, or that had burnt during the study period. Persistence of mature individuals does not differ between sites except at DK where some mortality occurred after the site burnt.

Adult persistence was more variable between sites where a reduction in the transition probabilities could be attributed to the JD and ZB sites that experienced low adult mortality, as well as the DK site after the fire burnt the population. Persistence of the immature stage classes is also slightly variable between sites with the lowest survival probability seen after the fire at DK. The low persistence transition probabilities of the immature individuals at the DK site was due to retrogression into the suffrutice stage. For all sites $a_{sa,sa}$ remained consistently 1, except at the Heather Glen site where the difference in the transition probability value was as a result of progression into the immature stage. The variation in seedling persistence is variable between sites and within sampling years for each site. Table 2.4 shows transition probabilities for each site.

A matrix was not constructed for the ZB_F site as it was considered that a sample size of 23 plants was too small to yield meaningful transition probabilities. This site was not completely excluded from the analysis because of the interesting results it contained. A fire had swept through the population less than a year from the time of sampling. Of the 23 plants sampled, 43% had not recovered from the fire all of which were once mature individuals. Suffrutices accounted for 48% of the sample, where it was not possible to determine previous stage, as there was 100% topkill. This was the only site sampled in Mountain Fynbos vegetation.

Fecundity transitions are considerably variable between sites and sample years. Highest fecundity transition probabilities were at the JD and TB sites. Other sites showed very low fecundity levels except for DK and DK_F where no new seedlings were found over the sampling period.

Table 2.4 Transition probabilities and population growth rates for all sites sampled between 2004 and 2006. Cells highlighted in grey indicate the probability of individuals remaining in the same stage (persistence). Elasticity transition probabilities are shown as P (persistence), F (fecundity), G (growth) and R (retrogression)

transition	Heather Glen (n = 91)		Jameson Dam (n = 88)		Suurberg (n = 78)		Thomas Baines (n = 84)		Jameson Dam Fire (n = 34)		Dassie Krantz (n = 62)	
year	1 - 2	2 - 3	1 - 2	2 - 3	1 - 2	2 – 3	1 - 2	2 - 3	1 - 2	2 - 3	1 - 2	2 - 3
$a_{se,se}$	1.0000	0	1.0000	0.6000	1.0000	0.8750	0.7500	1.0000	-	-	1.0000	0.5000
$a_{se,sa}$	0	1.0000	0	0.4000	0	0.1250	0.2500	0	-	-	0	0
$a_{sa,sa}$	0.9565	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	-	-	1.0000	1.0000
$a_{sa,im}$	0.0435	0	0	0	0	0	0	0	0	0	0	0
$a_{su,su}$	-	-	-	-	-	-	-	-	0.9524	0.7000	0.9286	0.9667
$a_{su,im}$	-	-	-	-	-	-	-	-	0	0	0	0.0333
$a_{su,ad}$	-	-	-	-	-	-	-	-	0	0	0.0714	0
$a_{im,su}$	-	-	-	-	-	-	-	-	-	-	0.6522	0
$a_{im,im}$	0.9565	1.0000	0.8462	1.0000	0.8125	1.0000	0.9500	1.0000	1.0000	1.0000	0.3043	1.0000
$a_{im,ad}$	0.0435	0	0.1538	0	0.1875	0	0.0500	0	0	0	0.0435	0
$a_{ad,su}$	-	-	-	-	-	-	-	-	-	-	0.1667	-
$a_{ad,ad}$	1.0000	1.0000	1.0000	0.9783	0.9706	1.0000	1.0000	1.0000	1.0000	0.7500	0.8333	1.0000
$a_{ad,ma}$	0	0	0	0.0217	0.0294	0	0	0	0	0.1250	0	0
$a_{ma,ma}$	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.8571	1.0000
$a_{ma,su}$	-	-	-	-	-	-	-	-	0	0	0	0
f_{ad}	0.0000	0.0117	0.0321	0.1141	0	0.0028	0	0.0080	0	0	0	0
f_{ma}	0.0000	0.0643	0.0792	0.2500	0	0.0748	0.3333	0.0773	0	0	0	0
λ	**0.9999**	**1.0000**	**0.9999**	**0.9999**	**0.9999**	**1.0006**	**1.0000**	**0.9999**	**1.0000**	**1.0000**	**1.0000**	**1.0000**
P	**1.0000**	**0.9998**	**1.0000**	**1.0000**	**1.0000**	**0.9992**	**0.9998**	**1.0000**	**1.0000**	**1.0000**	**0.9000**	**0.9998**
G	**0**	**0.0002**	**0**	**0**	**0**	**0.0007**	**0.0001**	**0**	**0**	**0**	**0.0500**	**0.0001**
F	**0**	**0**	**0**	**0**	**0**	**0.0002**	**0**	**0**	**0**	**0**	**0**	**0**
R	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.0500**	**0.0001**

Pooled transition probabilities and elasticity analysis

The transition matrix for the four sites show the highest probabilities for individuals remaining in the same stage (on the diagonal) except for the suffrutice stage where all suffrutices would have progressed to the immature stage (table 2.5).

Table 2.5 Transition probabilities based on census data from four sites that had no evidence of recent fire.

	1	**2**	**3**	**4**	**5**	**6**
1	0.7693	-	-	-	0.0227	0.1012
2	0.2307	0.9890	-	-	-	-
3	-	0.0000	0.0000	0.0000	0.0000	0.0000
4	-	0.0059	-	0.9156	0.0000	-
5	-	-	-	0.0570	0.9930	-
6	-	-	-	-	0.0070	1.0000

Elasticity analysis (Table 2.6) indicates that individuals remaining in the same stage class are the main contributor to population persistence.

Table 2.6 Elasticity matrix based on transition matrix from four sites that had no evidence of recent fire

	1	**2**	**3**	**4**	**5**	**6**
1	0.0154	-	-	-	0.0011	0.0037
2	0.0048	0.2331	-	-	-	-
3	-	0.0000	0.0000	0.0000	0.0000	0.0000
4	-	0.0048	0.0000	0.0470	-	-
5	-	-	0.0000	0.0048	0.2911	-
6	-	-	-	-	0.0037	0.3904

The results of the elasticity analysis confirm that sum of elasticities for persistence (97.7%) contributes to the population persistence and λ considerably more than growth (1.82%) or reproduction (0.48%). Persistence of saplings, adult and mature trees are most critical in contributing to the growth rate at 23.3%, 29.1% and 39.0%

respectively. Seedling (1.5%) and immature (4.7%) survival is not as crucial according to the results of the elasticity analysis.

The rate of population growth was calculated at 1.00989 as the dominant eigenvalue of the projection matrix. This suggests a stable population for sites not affected by fire for a number of years and is higher than the population growth rates calculated for individual sites in Table 2.4.

The relative abundance of individuals in the different stages remains constant over time when the SSD is reached (Caswell 2001). The Observed Stage Distribution (OSD) and Stable Stage Distribution (SSD) show a consistent pattern in the proportion of the different stages except for the sapling stage (Figure 2.17). A far higher proportion of saplings were predicted than observed.

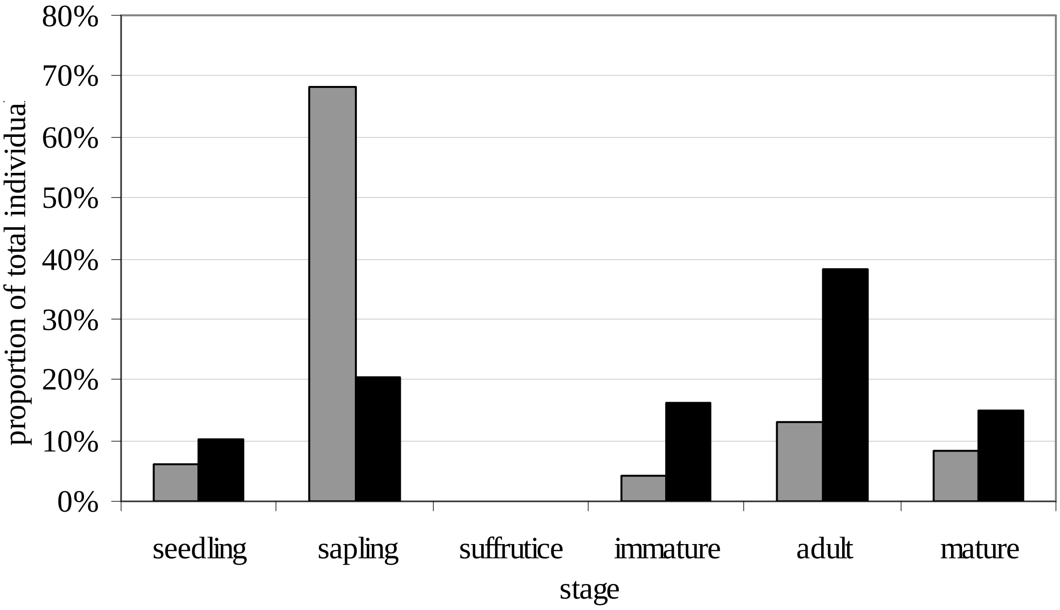


Figure 2.17 Observed stage distributions (dark shading) and stable stage distribution (light shading) derived from the matrix for *O. grandis* populations including census data from 6 sites (n = 472) for populations undisturbed by fire for a number of years

Discussion

The life-history strategy of *Oldenburgia grandis* is typical of a long-lived species that tends to allocate resources to persistence and resistance to disturbances rather than to growth or fecundity (Silvertown et al. 1993). This trade-off is confirmed by its relatively low fecundity levels, small proportion of seedlings established in the population and almost non-existent individual growth monitored over the duration of this study, while being relatively resilient to fire disturbance.

Stage structure and the effect of fire, land use and vegetation type

Fire can be considered to be the primary influencing factor in determining the stage structure of *O. grandis* populations, particularly for the smaller stage classes. Mature and adult stages show considerable resilience to fire. An exception is the one example in Mountain Fynbos where a burnt population had high levels of mortality due to an intense fire that had burnt the population. In comparison with other woody long-lived sprouters, the stage structure of *E. cycadifolius* (Raimondo and Donaldson 2003) is very similar to *O. grandis* where seedlings contribute the least to stage structure while adults make up the largest percentage of the population for sites not recently burnt.

Fire-induced mortality

Fire induced mortality can be compared to two Brazilian cerrado tree species (*Myrsine guianensis* and *Roupala montana*) where adult mortality was very low but seedling mortality very high after a fire (Hoffman 1999), a similar pattern seen in *O. grandis* at the DK site after fire. Morphological similarities between *O. grandis* and the two Brazilian species were also evident. The allocation of resources to producing a thick bark may explain the high levels of top kill and sprouting but low levels of actual mortality seen in the larger stages in *O. grandis*. Recovery after fire is extremely quick (as suffrutices) compared to the growth rate of seedlings, which makes it possible for individuals to occupy the same space as before the fire. It is this largely due to this adaptive trait that allows *O. grandis* to survive in a fire-prone environment.

Restriction to rocky outcrops

It could be argued that fire plays a large role in restricting populations to rocky quartzite outcrops. There is a clear relationship between the size of an individual and the probability that it is found growing on rock. It is likely that individuals that have not established themselves on primarily rocky substrate are more susceptible to fire damage either by mortality in the smaller stages or topkill in the larger stages. Individuals protected by rock are likely to survive fire as was seen at the DK site where a seedling growing on rock was completely undamaged while the surrounding vegetation was charred after the fire. This is particularly important for the smaller stage classes that do not have the ability to resprout. These individuals survive fire while they are small by being afforded protection from rock and continue to grow throughout the years in between fire events where they remain relatively unharmed. Not only does the outcrop provide some refuge against fire, but is likely to reduce inter-specific competition, particularly for the smaller stage classes more vulnerable to overtopping (Kruckeberg and Rabinowitz 1985). Species that sprout readily after a disturbance are often suppressed by taller seeders in fynbos as they concentrate their allocation of resources to maintaining a woody lignotuber while their multi-stemmed growth form limits their height (le Maitre and Midgley 1992). Growing on rocky outcrops would also limit competition between *Oldenburgia* individuals with taller seeders.

Reproductive success in *O. grandis*

A clear pattern emerges with other studies on long-lived sprouting species (Bond and Midgley 2001; Raimondo and Donaldson 2003) where it appears that allocation of resources into reproduction is limited in favour of allocation to underground reserves and bark but as Hoffman (1999) pointed out, sexual reproduction does have the advantage of dispersal to other habitable sites. It was observed on an occasion in this study that *O. grandis* is capable of vegetative reproduction by clonal growth. In many species where sexual reproduction is inhibited, clonal growth is common (Honnay and Bossuyt 2005) and often, vegetative reproduction is stimulated by fire (Hoffman 1999). Clonal growth was not frequently observed in this study, but the branching out of stems and the establishment of roots while still attached to the parent plant was observed.

Spatial variation in transition probabilities and population growth rate

The great similarity of λ between sites can be attributed to the very high levels of persistence, low mortality and low levels of fecundity. This resulted in a very constant population size and hence a stable population growth rate for all sites. It has been suggested that a stable population growth rate is indicative of invariability in habitats, especially in the frequency or intensity of disturbances (Desmet et al. 1996). Sites sampled in this study experienced variability in time since last fire that did not result in λ variability. Even for the DK site that experienced fire within the study period, did not result in significant a change in λ from the other sites. This is in contrast to other studies on plants with long life spans. Hoffman (1999) found that fire did produce variability in λ for two long-lived cerrado species. Fire exclusion resulted in a positive growth rate of between 1.05 and 1.10 for the two species while annual fire resulted in λ between 0.84 and 0.87.

Stability of *O. grandis* populations and life history stages contributing most to λ

If the sites sampled in this study are a true reflection of the majority of *O. grandis* populations, populations have a positive growth rate if the condition at the time of sampling remains constant over time (although this is clearly unrealistic). Long-lives species show a general trend in the importance of persistence in the larger stage categories as having the largest influence on λ (Desmet et al. 1996; Raimondo and Donaldson 2003). This is indicative of a life history strategy that evolved to deal with environmental stresses and unpredictable environments (Silvertown et al. 1993). A change in conditions that threaten the persistence of adult and mature stages will alter the current stability of the populations. If increased fire intensities in Mountain Fynbos areas result in high levels of adult and mature mortalities, the persistence of the critical life stages as seen at the ZB_F site would be detrimental to the persistence of the population. It has also been suggested (van Wilgen and Richardson 1985) that increased fire intensities have adverse effects on sprouting species in the Fynbos biome. The most favourable fire-burning season for Fynbos vegetation is between late summer and early autumn (le Maitre and Midgley 1992) but this is the season in which the fires are the most intense. Prescribed burning in these seasons with the additional effect of increased fuel loads could be detrimental to *O. grandis* persistence.

Observed and stable stage distributions

Stable stage distribution is described as the relative abundance of individuals in each stage remaining constant over time (Caswell 2001). Similarities between the stable stage distribution and the observed population structure may indicate the proximity of the model to reality. In this study, the model predicts stasis in a fire free environment, whereas in reality, a favourable year may result in an increased movement from saplings to the immature stage and therefore deviating from what the model predicts. Fire will also influence the number of saplings (in reality) where higher fire mortality is likely to be higher compared to the predictions of a fire free model. It is also possible that the higher number of immature individuals in the initial stage distribution is a result of retrogression from larger stages at times of fire disturbance. Silvertown and Charlesworth (2001) have noted that a peak in a certain stage does not necessarily imply a departure from the SSD of the matrix model where structure is determined by stage rather than age. Caswell (2001) noted that a peak in stable stage distribution of a particular stage is often observed in organisms with plastic growth patterns such as trees where the growth rate into a particular stage is relatively large and the probability of growing out the stage is relatively small.

Consequences for conservation

The importance of conserving existing populations, particularly ensuring the survival of adult and mature individuals is essential for the conservation of the species. *O. grandis* has very low reproductive capabilities and very slow rate of growth from seedling. It has been shown that for a species with a similar life history to *O. grandis*, such as *Banksia goodii*, hand-sowing seed in wild populations is a viable conservation strategy (Drechsler et al. 1999). Given the terrain and rocky outcrops to which *O. grandis* populations are restricted, restoration by means of hand-sowing seed would prove almost impossible. Protecting populations that are already established by targeting threats that put adult and mature stages at risk should be prioritised.

CHAPTER 3 DISTRIBUTION, POPULATION STRUCTURE AND IUCN STATUS OF *OLDENBURGIA GRANDIS*

Introduction

Stage structure of established populations

Oldenburgia populations are dominated by the adult stage with fairly equal numbers of sapling, immature and mature stages. The seedling stage makes up the lowest percentage of populations according to the observed stage distributions in Chapter 2.

It was necessary to extend the sampling of population structure to determine whether the results from the matrix model are confirmed by a larger sample size. Possible correlations between the structure of a population and time since last fire may reveal insight into changes in the levels of recruitment and seedling establishment and how these differ between sites at different times since last affected by fire. Stages with high persistence tend to be well represented in the structure of a population. Long-lived woody species with low levels of seedling establishment and high adult persistent tend to have j-shaped population structures, such as shown by *E. cycadifolius* (Raimondo and Donaldson 2003). In *O. grandis*, the matrix model predicts high percentages of sapling, adult and mature stages as these stages show the highest persistence (Chapter 2).

Distribution patterns of South African endemic plant species

Little emphasis has been placed on mapping distribution patterns of South African endemic plant species compared to other countries (van Wyk and Smith 2001). Literature on mapping the distribution of rare endemic species was sparse, specifically for South African plant species. To extend the detailed analysis of the five sites dealt with in Chapter 2, this part of the study aims to determine the spatial range of *O. grandis* and to assess the overall size and number of populations in the Eastern Cape Province. Capturing the spatial distribution of the populations at the time of this study will provide invaluable information to future studies on the species, which was lacking in the literature for this study.

This chapter deals with the distribution of *Oldenburgia grandis* over its geographic range as well as exploring population sizes, land use types associated with *Oldenburgia* populations and possible threats to the species across its distribution. A useful tool, not only for mapping species distribution but also for conservation planning and decision-making is a Geographic Information System (GIS). GIS has been widely used to assess suitable habitats for species or to estimate loss of habitat due to human developments and introduced threats (Salafsky and Margolius 1999; Theobald 2003; Rouget et al. 2003).

Distribution of existing *O. grandis* populations

A study undertaken by Croeser (1982) listed the occurrence of *Oldenburgia* populations from historical herbarium records and review of the available literature. A number of locations at the time of the study were also listed in an attempt to determine the limits of the distribution of *Oldenburgia* populations. Coordinates from the unpublished study confirmed that *O. grandis* is associated with the Suurberg Quartzite Fynbos (SQF) broad vegetation type. Suurberg Quartzite Fynbos vegetation distribution is available as a GIS layer of the VEGMAP project produced by the South African National Botanical Institute (Mucina et al. 2004). VEGMAP is a base vegetation map used for landscape, ecological and environmental studies in Southern Africa. The SQF vegetation type extends from the Kap River in the east to the Suurberg Mountains in the west and falls within the Albany Centre of Endemism (van Wyk and Smith 2001). *O. grandis* populations are restricted to outcrops of Witteberg Quartzite often growing directly on the rock surface which afford some protection from fire (Chapter 2).

Although Croeser (1982) undertook an extensive survey of historical sightings and records of *Oldenburgia* populations, a quantitative study including the size, land type and exotic vegetation densities associated with *O. grandis* populations did not form part of the study. No previous records of the population structure of *O. grandis* exist.

IUCN Red Data Assessments

An important consideration in the International Union for the Conservation of Nature (IUCN) Red Data List Assessment is to determine limits of the species distribution, actual threats to existing populations and which sectors (e.g. agricultural, urban, protected areas) to target for conservation recommendations.

An original assessment of most threatened plant species in South Africa was made in 1996 by Hilton-Taylor and was largely based on the IUCN Red List Criteria modified by Davis et al. (1986) where *O. grandis* was classified as a rare endemic. In re-assessing 25% of South Africa's threatened flora, based on IUCN version 2.3 criteria, *O. grandis* was classified as LR/nt (lower risk/near threatened) (Victor 2002). *Oldenburgia grandis* has not yet been assessed on the latest version 3.1 IUCN criteria (Figure 3.1). Lower risk is defined as a taxon that does not satisfy the criteria for any of the threatened categories (Figure 3.2). The category Near Threatened is a sub-category of lower risk, and includes taxa that do not qualify for Critically Endangered, Endangered or Vulnerable now, but is likely to qualify for the threatened category in the near future (IUCN 2001).

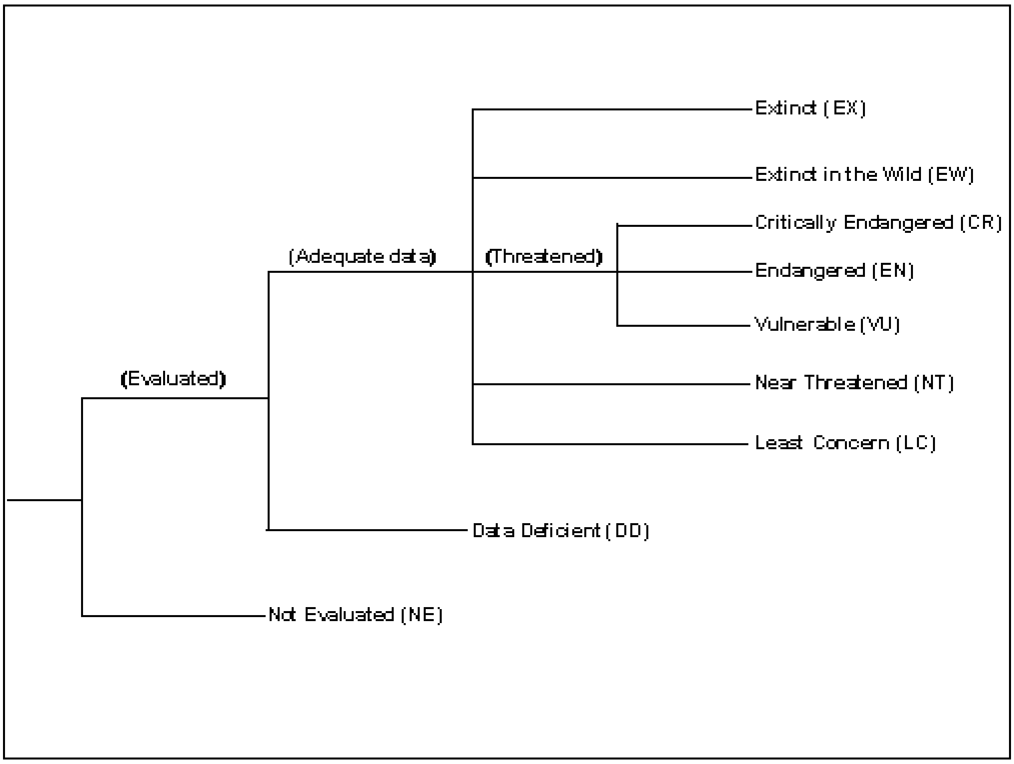


Figure 3.1 IUCN Red Data version 3.1 categories and criteria

In an attempt to assess the conservation status of *O. grandis*, criteria set out for the lowest threatened category (Vulnerable) were used as this is the next category up from lower risk. According to IUCN (2001) a taxon is Vulnerable when it is not critically endangered or endangered, but is facing a high risk of extinction in the wild in the medium term.

In order to be classified as Vulnerable, a set of criteria has to be met. These criteria either involve a reduction in population size over the last 10 years, geographic range, total number of mature individuals, how restricted or small the population is or an estimated probability of extinction within a given time frame (Figure 3.2).

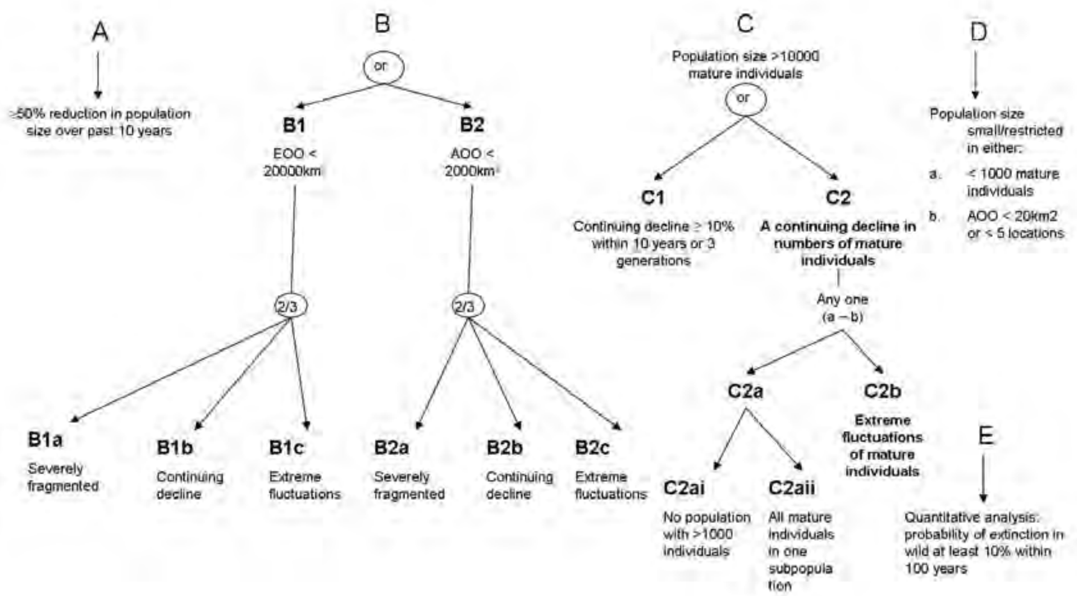


Figure 3.2 Diagrammatic representation of criteria to be met for a taxon to be classified as Vulnerable according to IUCN 3.1 criteria

A. Reduction in population size over the last 10 years

Criteria involving the population reduction over the last ten years could not be used to assess whether there has been a decline in population number or size as the time frame for this study was too short and baseline data for years preceding this study was not available.

B. Geographic range

Criteria for a projected or suspected reduction within the next 10 years included an assessment of the extent of occurrence and area of occupancy.

B1. *Extent of occurrence*

Extent of occurrence (EOO) is defined as the area encompassing all known individuals of the taxon concerned. The criterion will be met if the EOO determined for *O. grandis* is less than 20 000km^2.

B2. *Area of occupancy*

The area of occupancy (AOO) lies within the EOO but excludes unsuitable habitat where the taxon is unlikely to occur. The threshold value for this criterion is 2000km^2.

If either (or both) of these criteria (B1 and B2) is met, at least two of B1a to B1c or B2a to B2c are to be met for a taxon to be considered Vulnerable.

B1a and B2a. *Severely fragmented or known at no more than 10 locations*

A taxon is severely fragmented if most individuals are found in small and relatively isolated populations with little chance of recolonisation (IUCN 2001). The definition of severely fragmented refers to an increased risk of extinction due to the fact that most individuals are found in small, isolated populations. Location is defined as a geographically distinct area where a single threat can affect all individuals in an area (IUCN 2001).

B1b and B2b. *Continuing decline in mature individuals, habitat, locations or area of distribution*

An inferred or projected continuing decline in the EOO, AOO, area and/or quality of habitat, number of locations or number of mature individuals will meet this criterion. There is no prescribed threshold i.e. what percentage of decline is required to meet this criterion for a taxon to be considered Vulnerable.

B1c and B2c. *Extreme fluctuations*

Extreme fluctuations are defined by IUCN (2001) where population size or an area of distribution varies widely, rapidly and frequently particularly when the variation is greater than one order of magnitude. The definition of fluctuation in this sense suggests continous demographic changes rather than a once-off event i.e. an extreme fire that may affect *O. grandis* populations. Extreme fluctuations can be discounted for long-lived taxa such as *O. grandis*.

C. Total number of mature individuals

The total number of mature individuals includes individuals that are known (estimated or inferred) to be capable of reproduction. Potentially reproductive individuals in this study are classed as adult and mature. Senescent individuals have not been classed separately from reproductively active mature individuals in this study.

If criterion C is met, either C1 and/or C2 have to be satisfied for a taxon to be considered Vulnerable.

C1. *Estimated decline of 10% within 10 years or 3 generations*

It is not known what age *Oldenburgia grandis* trees can attain, or how long a generation is. A measure of decline can be estimated for reproductive individuals over 10 years.

Aims

There were two aims to this chapter:

1. To obtain information on population structure for 12 sites. This was done to extend the results from Chapter 2 on the life-history of *O. grandis* and to observe whether these results are confirmed by assessing a larger sample of population structure. The incidences of mortality in a larger sample were also investigated including whether any link between mortality and fire or other identified threats is apparent. It is predicted that populations would be dominated by the most persistent size classes (i.e. sapling, adult and mature).

2. To obtain baseline data for red data listing and future monitoring on the distribution of the species, population numbers and sizes. This included the

presence of certain threats and information on land use associated with established populations. The link between the distributions of observed populations to land use and potential threats may reveal where monitoring and possible conservation effort should be focussed.

Methods

<u>Determining population structure</u>

A total of seven populations were selected for sampling population structure (see Table 3.1 for a description of each site). Census data from the seven sites in Chapter 2 were also included in the analysis for this chapter and in the summary table.

All individuals were counted in a demarcated area taking care not to recount the same individuals. This was not difficult as trees usually occurred in scattered clumps, where all individuals in each clump were counted until the census included approximately 100 individuals. The same stage classes in Chapter 2 were used to determine population structures in order to compare the matrix model stage structure results.

<u>Single species ordination</u>

A multivariate approach was used to examine patterns in population structure at different sites to environmental factors. The technique of multivariate analysis which includes ordination (or multidimensional scaling) is most commonly used to analyse communities by arranging sites, together with species along environmental gradients (Larsen and Thorne 2001). Nonmetric multidimensional scaling (NMDS) is an ordination method based on ranking distances between points (Kenkel and Orlóci 1986) that arranges samples in a defined number of dimensions (Phillips et al. 2003) creating a similarity matrix across samples. For example, Phillips et al. (2003) used NMDS ordination techniques to find out to which extent Amazonian tree species distributions are determined by soil conditions or neutral processes.

In order to display the degree of similarity or dissimilarity of each site in relation to the structure of the population, an ordination plot was produced. By definition, multivariate data have attributes for more than one variable which are measured for each sampling unit within the context of a sample survey (Kenkel et al. 2002). In this case the variables are the stage classes and the sampling unit represents each site. Direct gradient analysis was not appropriate for this analysis as environmental data for each site consists of rough estimates and displayed within-site variation. For instance, cattle activity at each site varied depending on slope and accessibilty within the sample. Exotic tree densities tended to be patchy and therefore an average density for the area was estimated. Vegetation type and estimates of time since last fire were assigned categorical values.

Non-Metric Multidimensional Scaling (NMDS) ordination was chosen to configure the samples in such a way that their similarities in stage class distribution could be displayed. Samples were first standardised using percentages rather than absolute values. The PRIMER 6 software package (Clarke and Gorley 2006) was used for all ordination analysis. Before computing the similarity matrix, the data were square root transformed, reducing the difference between abundant and rare classes giving relatively greater weight to the rarer classes. This resulted in the lowest overall stress value of the NMDS ordination. A stress value of < 0.1 "corresponds to a good ordination with no real prospect of a misleading interpretation" (Clarke and Gorley 2006) The similarity matrix was calculated using the Bray-Curtis coefficient. The Bray-Curtis coefficient ensures that all stage classes contribute to the measure of similarity including the contribution of the less abundant classes negating the over-dominance effect by the very abundant size classes (Clarke and Gorley 2006). Sites that displayed clear groupings as a result of the analysis were assessed for stage class similarities i.e. to show which stage classes contribute most to within group similarity. For this, SIMPER analysis was perfomed on the ordination groups as well as groups categorised according to when last affected by fire. A Mantel-type Monte-Carlo analysis (ANOSIM) was performed to test for statistical differences between sites affected less than 1, between 2 to 5 and more than 5 years since fire.

Table 3.1 Description of 14 sites sampled to determine the structure of established *Oldenburgia* populations

ID	Co-ordinates	Description	Land Use	Aspect	Slope range (degrees)	Altitude (masl)	Population size (N)	Population density (% cover)	Alien vegetation density (% cover)	Approx. last fire (years from sample date)	Date sampled
BGR	26°6′0.0″ E 33°14′30.8″ S	Burchell's Game Reserve	Privately Conserved (game Farm)	S to SW	10 - 30	580 – 600	100 - 500	5 - 25	1 - 5	3 – 4	July 2005
BW	25°44′1.0″ E 33°16′36.6″ S	Barkley Wheat	Agricultural (cattle farm)	N to NW	30 - 40	760 – 800	100 – 500	50 - 75	0	≥ 5	July 2005
RH	25°39′42.6″ E 33°16′40.0″ S	Round Hill	Formally conserved (Addo NP)	N to NW	20 - 40	760 – 800	100 – 500	25 - 50	0	≥ 5	July 2005
FF	26°50′37.0″ E 33°17′31.2″ S	Fairview Farm	Agricultural (sheep farm)	N to NW	10 - 20	460 – 480	50 - 100	5 - 25	0	≥ 5	July 2005
GF	26°30′13.8″ E 33°21′9.0″ S	Glenstone Farm	Agricultural (cattle farm)	W to NW	10 - 40	590 – 715	> 500	5 - 25	50 - 75	3 – 4	July 2005
FK	26°30′35.0″ E 33°20′33.0″ S	Top part of Featherstone Kloof	Commonage	NW	20 - 40	700 – 714	50 - 100	5 - 25	1 - 5	≥ 5	July 2005
DK	26°29′54.3″ E 33°19′43.2″ S	Dassie Krantz	Formally conserved (part of Grahamstown Nature Reserve)	S to SW	20 - 30	720 – 730	100 - 500	5 - 25	1 - 5	3-4 ; 1-2	Jan 2004
HG	26°46′24.8″ E 33°18′33.0″ S	Heather Glen	Agricultural (cattle farm)	SW	30 - 40	600 – 640	> 500	25 - 50	5 - 25	≥ 5	Feb 2004
TB	26°29′42.5″ E 33°22′36.9″ S	Thomas Baines Nature Reserve	Formally conserved	S to SW	20 - 30	500 – 560	> 500	25 - 50	1 - 5	≥ 5	Mar 2004
JD	26°26′35.9″ E 33°18′47.3″ S	Jameson Dam	Commonage	S to SW	10 - 30	720 – 740	> 500	50 - 75	0	≥ 5	Jan 2004

		(Grahamstown)									
JD_F	26°26′5.6″ E 33°18′36.5″ S	Jameson Dam (portion of the population recently burnt)	Commonage	S to SW	10 - 30	720 – 740	50 - 100	5 - 25	0	1 – 2	Jan 2004
ZB	25°44′33.6″ E 33°18′42.1″ S	Suurberg Pass	Formally conserved	N to NW	30 – 40	620 – 660	50 - 100	5 - 25	1 - 5	≥ 5	Mar 2004
ZB_F	25°45′26.2″ E 33°19′18.3″ S	Suurberg Pass (site recently burnt)	Formally conserved	N to NW	30 - 40	620 - 660	1 - 10	1 - 5	0	1 – 2	Mar 2004
GH	26°46′24.8″ E 33°18′33.0″ S	Greenhills Farm	Agricultural (cattle farm)	SW	30 - 40	600 – 640	50 - 100	5 - 25	50 - 75	≥ 5	August 2006

Mapping *O. grandis* populations

A systematic approach to mapping was undertaken using the SQF vegetation type as an indication of where populations are likely to occur. The SQF vegetation data was superimposed on 1:50 000 topographical base maps that were partitioned into grids. Populations seen from roads that could be accessed by an off-road vehicle were then annotated in the field on the printed maps. Not all SQF areas could be accessed; these areas were annotated as "not explored" on the maps. Annotations included the following (see Table 3.2 for a summary of the categories used):

1. Population size defined as the estimated number of individuals per mapped area (i.e. number of individuals per polygon);
2. Population density defined as estimated percentage cover per area/polygon;
3. Landuse type per polygon includes conservation area, agricultural land or commonage;

   3.1. Conservation area consists of either *privately conserved* land defined as an area where no agricultural practices take place (i.e. private nature reserve, game farms have also been included in this category) or *formally conserved* land such as national and provincial parks;

   3.2. *Agricultural* areas where *O. grandis* populations are found consist mainly of grazing lands for cattle, as these fynbos areas with their rocky terrain are not suitable for cultivation;

   3.3. *Commonage,* a form of agricultural land owned by the state where the community has access to the land for grazing livestock. This land is often over-utilised and over-grazed except in areas where the terrain becomes inaccessible to livestock particularly cattle.
4. Density of exotic vegetation (if present) density is defined as estimated percentage cover of exotic individuals per polygon;
5. Approximate time since last fire. This could only be a rough estimate, as no fire records exist for the study area. Time since last fire was categorised into three classes: <1 year since last fire; between 2 and 5 years since last fire; > 5 years since last fire. If no fire evidence was observed either by charcoal in the soil, charred bark and newly sprouting grass tussocks and lack of a woody component of the surrounding vegetation, the site was estimated not to have been burnt by fire for at least 10 years;

6. Dominant vegetation type associated with the population either as Mountain or Grassy Fynbos.

Table 3.2 Categories used as field map annotations for each polygon mapped

Size (individuals)	Density (percentage cover)	Alien density (percentage cover)	Fire intervals (years)
1 – 10	Rare 1 – 5	None 0	Less than or equal 1
10 – 50	Scattered 5 - 25	Rare 1 - 5	Between 2 and 5
50 – 100	Medium 25 – 50	Scattered 5 – 25	Between 5 and 10
100 – 500	Dense 50 – 75	Medium 25 – 50	Greater than 10
> 500	Closed > 75	Dense 50 - 75	

Annotations were subsequently entered into a database and shapefile using ArcView 3.1 GIS software package with the digital 1: 50 000 topographical images as a base layer. All polygons digitised in the GIS were linked to an associated attribute table that included attributes 1 – 6 listed above as well as general notes about the site. Once the mapped data was in digital geo-referenced format, it was possible to overlay additional GIS datasets with the mapped data. GIS tools have been incorporated into PVA modelling packages (Akçakaya 1994) to include spatial aspects in population models. To determine if there is a relationship between population sizes of *O. grandis*, landuse and density of alien vegetation using the Kruskal-Wallis test (STATISTICA; StatSoft 2004).

To determine additional information for each polygon such as slope, aspect and altitude, 20m contours for the area were used. By creating a triangulated irregular network (TIN) from 2m contours it was possible to calculate aspect and slope for each polygon. To calculate the aspect of an area, ArcView identifies the steepest down slope direction from each cell (a grid cell size of 300m was used) to its neighbours with the values of the output grid theme representing the compass direction of the aspect. Slope values were extracted from the same TIN, but a grid cell size of 10m was used and the slope averaged out for each polygon.

Assessment of IUCN status of *O. grandis* based on version 3.1 criteria

The latest IUCN criteria (2001) were used in this study to determine the conservation status of *O. grandis*. A description of each criterion and the methodology used to assess whether *O. grandis* satisfies that criterion is detailed below. *Oldenburgia grandis* has not, until now, been assessed according to the latest criteria (version 3.1) which have been available since January 2001.

A. Reduction in population size over the last 10 years

This study forms part of the first in-depth study on *O. grandis*. Previous data is not available on the species to satisfy a method for this criterion.

B. Geographic range

It was possible to use the mapped data to calculate the geographic range of the species, both in extent of occurrence and area of occupancy.

B1. *Extent of occurrence*

To determine the EOO, a continuous boundary around all mapped polygons was digitised at a 1: 50 000 scale. The boundary was projected from decimal degrees using the Transverse Mercator Projection (central meridian: 25; datum: wgs84).

In order to meet this criterion at least 2 of B1a to B1c are to be met for *O. grandis* to be considered Vulnerable. It is possible, using mapped data and GIS analysis, to determine if populations are severely fragmented (B1a). It is difficult, without previous data sets to refer to, to determine whether there is a continuing decline (B1b) in the extent of occurrence. A decline in area, extent and/or quality (B1biii) may be inferred based on observed threats, but this is better described in specific detail under the area of occupancy (B2).

B1a. *Severely fragmented or known at no more than 10 locations*

The degree of fragmentation was determined using mapped populations including size and densities. The average population size and density as well as spatial distribution give a good indication of the level of fragmentation. Populations with between 1 to 10 individuals scattered within a small isolated population was considered fragmented.

In order to determine separate "locations" as defined by the IUCN (2001) criteria, a GIS analysis of each geographical area was completed to determine geographically distinct populations, and where possible, whether all individuals in the taxon would be affected by the same threatening event. For example: an area with a cluster of small populations was considered one location or a cluster of larger and smaller populations in an area were considered a single location.

B1b. *Continuing decline in mature individuals, habitat, locations or area of distribution*

To obtain a measure of continuing decline, more data over a longer time period would be necessary for any conclusive results. It was possible to determine whether populations may have declined over the short term based on observation. A descriptive analysis is included in the results.

B1c. *Extreme fluctuations*

Extreme fluctuations can be discounted for long-lived taxa such as *O. grandis*. By definition, population size or distribution would not vary widely, rapidly or frequently by one order of magnitude.

B2. *Area of occupancy*

To estimate the area of occupancy (AOO), the EOO was overlayed on the Suurberg Quartzite Fynbos vegetation type (for both checked and unchecked areas) and clipped to contain a single shapefile of the Suurberg Quartzite Fynbos vegetation within the EOO. The same projection as for the EOO was used to calculate the total area in km^2. It was not feasible to include only the mapped populations, as areas where populations could exist needed to be included. The AOO calculation may be an overestimation.

C. *Total number of mature individuals*

In order to calculate the total number of reproductive individuals, the estimated population size per polygon, number of polygons with similar population sizes and fraction of the population that is of reproductive age based on the initial stage distribution in Chapter 2.

Estimated population size per polygon: all mapped populations described in this chapter include an estimated size within a range. It was therefore possible to take the median for each range as well as the upper and lower estimates of the range where N_i is the number of individuals per polygon of size $_i$.

Number of polygons with similar population sizes: the number of polygons of size $_i$ was denoted as P_i.

The fraction of the population that is of reproductive age was denoted as F in the following calculation:

$$\Sigma\ N_i \times P_i \times F$$

C1. Estimated decline of 10% within 10 years of 3 generations

To calculate an estimated decline in the number of reproductive individuals, the short-term threats of mapped populations were assessed. Small populations are at the highest risk from the effects of fire. It has been observed that hot fires (such as in Mountain Fynbos areas in the Zuurberg) are likely to result in high mortality levels of reproductive individuals within a small, isolated population. Similar effects can be expected from a heavily invaded area within which a small population may exist. Small populations (between 1 and 50 individuals) were spatially selected using a GIS. Of these populations selected, those that occurred in Mountain Fynbos areas or those heavily invaded (alien density closed, dense or medium – see definitions of these categories) by exotic vegetation were selected (populations in mountain fynbos or those heavily invaded were identified when mapped). From the populations selected, the number of reproductive individuals were calculated in the same way it was done for criterion C above. From this, it was estimated that the number of reproductive individuals within these selected populations were likely to be threatened in the short term (calculated as a percentage of the total number of populations mapped).

Estimates for C2, D1 and D2 were based on mapped data and results from estimates of preceding criteria.

Results

<u>Distribution of *O. grandis*</u>

It was clear from field mapping that populations are concentrated along the lines of exposed quartzite, perhaps the most restrictive factor concerning possible habitat locations for the species. A total of 170 populations (a term used loosely here to describe a group of individuals of the same species and not necessarily genetically distinct entities) were identified. These included clusters of individuals separated by some distance (a few kilometres) or by a geographical area such as a mountain range.

These covered a total area of 861 hectares in varying densities. This calculation excluded the small populations mapped as point data, to indicate small clusters of less than 50 individuals, where it was not possible to calculate area. *Oldenburgia* populations were found on the following 1:50 000 topographic grid references: 3326AB (Piggott's Bridge); 3326AA (Riebeeck East); 3326AC (Alicedale); 3326AD (Salem); 3326BC (Grahamstown); 3325BC (Coerney); 3325BD (Paterson); 3326BD (Trappe's Valley).

From the mapping results, there exist three main centres where the majority of *Oldenburgia* populations occur. The first is along the *Oldenburgia* hiking trail, between Grahamstown and Thomas Baines Nature Reserve (26º 29´: 33º 20´). The second centre is along the Suurberg Pass (25º 44´: 33º 18´). The third location is toward the Kap River Mountains, 25 kilometres east of Grahamstown (26º 46: 33º 18´) (Figure 3.3 and Appendix 3.1). GIS analysis results show that *Oldenburgia* populations are restricted to low mountains as defined by Schulze (2001), at an altitude of between 450 and 900masl. The highest altitude at which a population was found at 800 masl and the lowest at 460 masl.

The majority of populations found were small and fairly isolated consisting of between 1 – 10 individuals. In some instances, population numbers may have been underestimated as they were mapped from a distance where the seedlings and smaller trees could not be seen, but this does allow the estimation of sexually mature individuals included in the IUCN assessment. Table 3.3 summarises the populations mapped according to size, density and associated alien vegetation density.

Table 3.3 Percentage population size, densities and alien cover mapped

Size as a % of total (n=170)		Densities as a % of total (n=170)		Exotic vegetation density as a % (n=169)	
1 – 10 individuals	33%	Rare 1-5% cover	63%	None	33%
10 – 50 individuals	22%	Scattered 5-25% cover	31%	Rare 1-5% cover	43%
50 – 100 individuals	22%	Medium 25-50% cover	5%	Scattered 5-25% cover	3%
100 – 500 individuals	15%	Dense 50-75% cover	1%	Medium 25-50% cover	17%
> 500 individuals	8%	Closed >75% cover	0%	Dense 50-75% cover	4%

Rare and scattered populations with trees making up less than 25% of the vegetation cover made up 94% of populations. Densities were difficult to estimate in some areas as clustered demes (a non-random clumped distribution) ranging in densities were scattered in an area. Difficulties in estimating densities of alien vegetation were also encountered, as exotic vegetation was usually not found amongst the *Oldenburgia* plants growing on the outcrops, but mostly in areas between the rocky outcrops where the soil tended to be deeper. Larger populations were found in areas that were less affected by exotic vegetation (Figure 3.4).

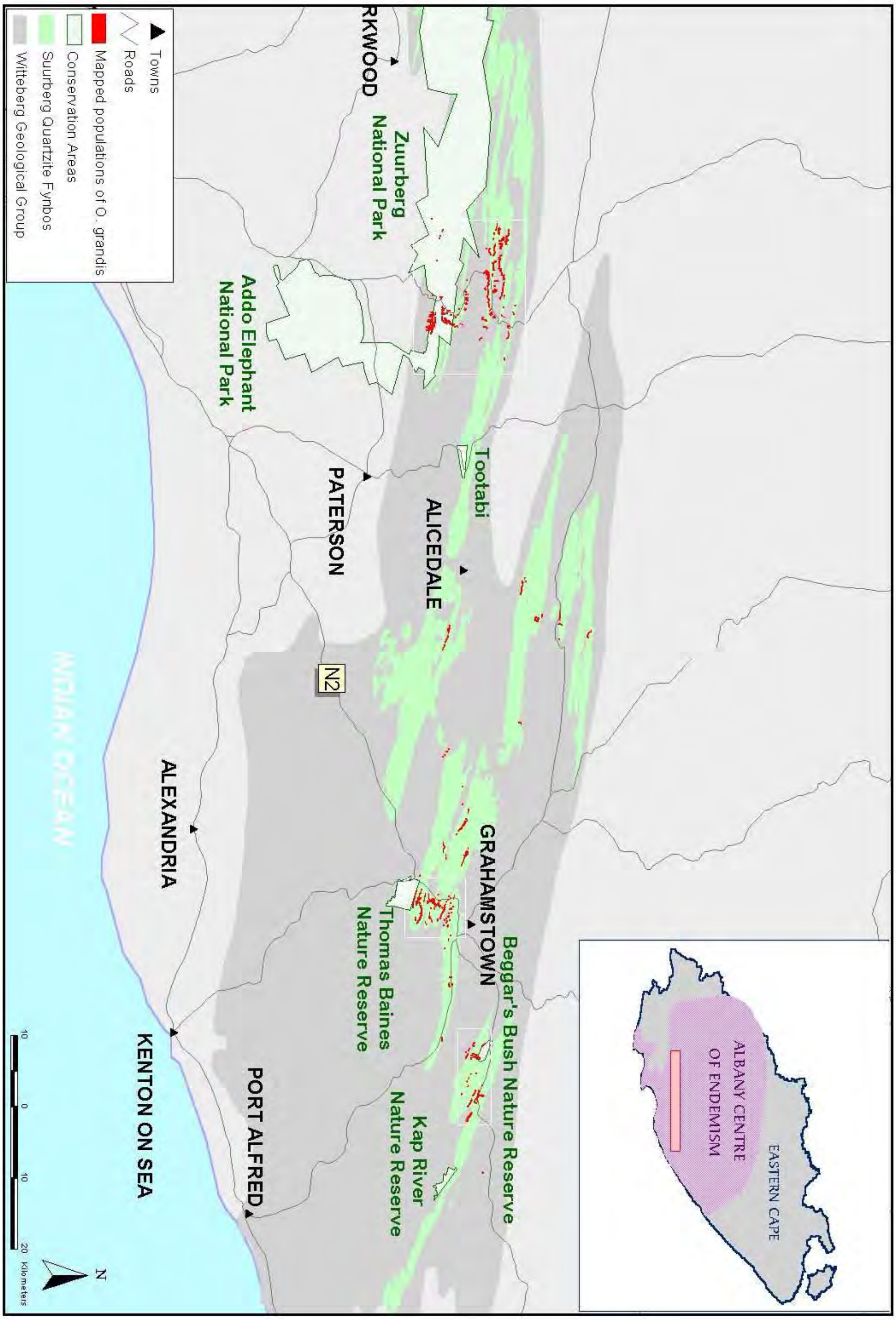


Figure 3.3 Overall distributions of *Oldenburgia grandis* populations mapped in this study closely associated to the Suurberg Quartzite Fynbos vegetation type. The pink shaded block in the inset map refers to the more detailed area shown on the larger map

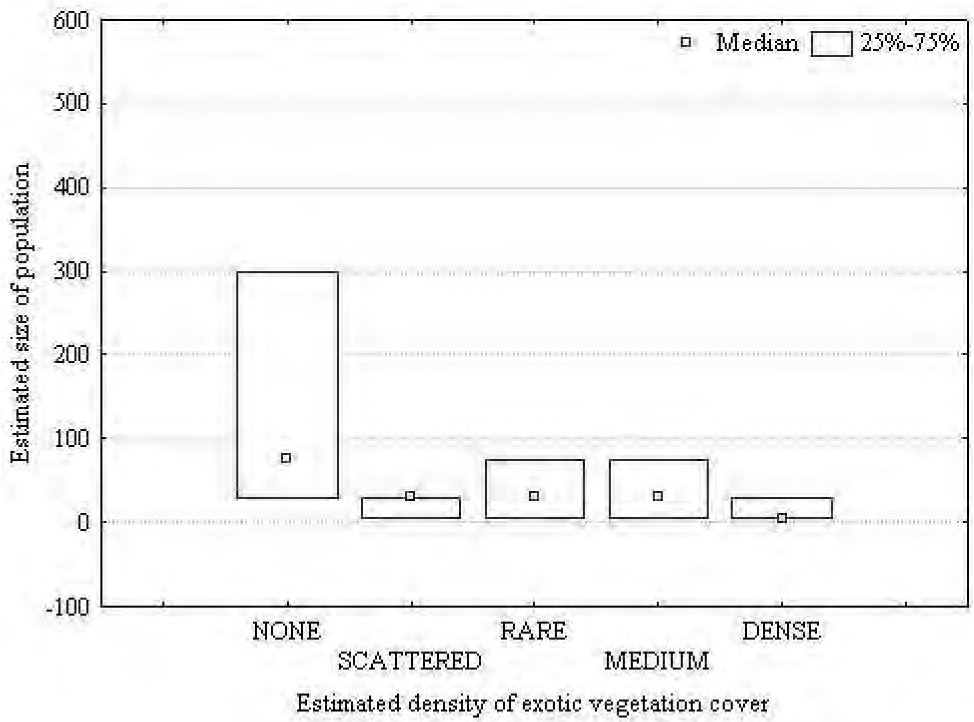


Figure 3.4 Estimated size of *Oldenburgia* populations grouped by estimated density of alien vegetation per mapped polygon (Kruskal-Wallis (4,169) = 9.95, p < 0.05))

Densities of exotic vegetation in the mapped areas may vary over time in certain areas due to clearing efforts by National Parks or Working for Water (WFW), therefore at some sites *Oldenburgia* populations may have been surrounded exotic trees in the past but which were recently cleared.

Population size plotted against land use type reveals that the larger populations were more commonly found on formally conserved land and agricultural land (Figure 3.5) than privately conserved and commonage areas.

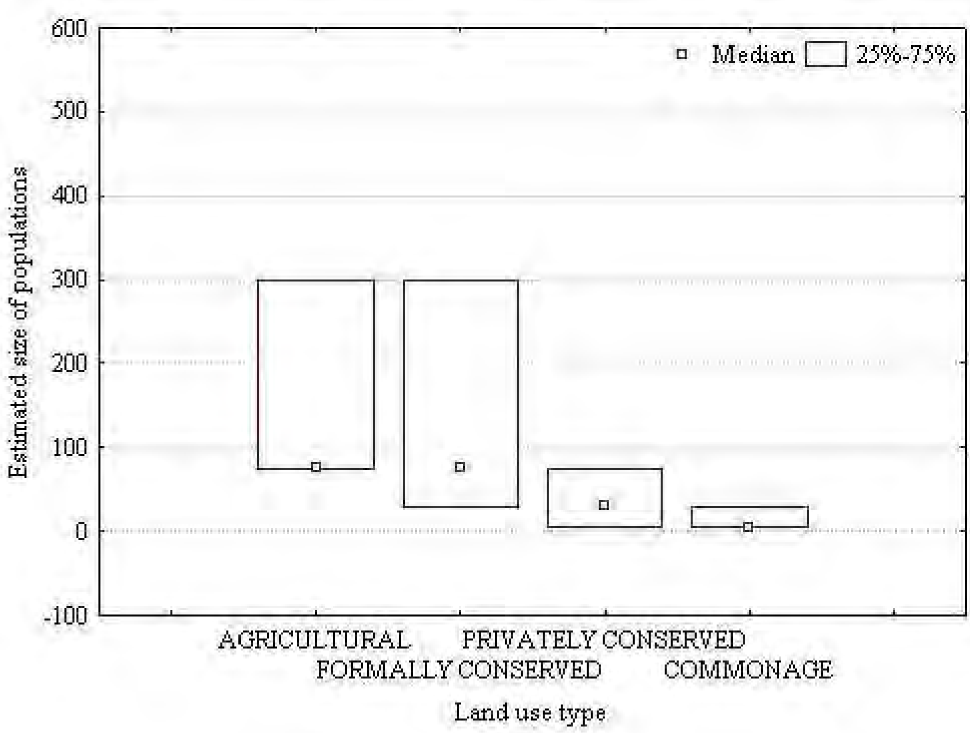


Figure 3.5 Estimated population size per landuse type (Kruskal-Wallis (3, 170) = 31.08, p < 0.000001)

Of all the mapped populations, 40% found were found on formally conserved land, which includes areas within the proposed boundary of the Greater Addo National Park. Populations found on state owned land made up 30% of all populations mapped, the majority of which is commonage, while 16% of populations occurred on land owned by cattle farmers. The remainder occurred on private land (other than cattle farms) on which relatively smaller populations occur. Cattle farms were distinguished here from other privately owned land to determine if cattle have an effect on populations by trampling seedlings and smaller plants.

<u>Population structure of sampled sites</u>

The 14 sites sampled to include a "snap-shot" of population structure are described in Table 3.1 under the Methods section. The population structure at the Dassie Krantz site before and after fire has been separated in the analysis.

Population structure of sites sampled in relation to time since last fire

NMDS results show that time since fire is the strongest grouping factor in the ordination plot (Figure 3.6). Sites more recently affected by fire (1 – 2 years ago) tended toward the left of the plot whereas sites that experienced fire over 5 years ago grouped to the right. Sites estimated to have experienced fire 3 – 4 years ago did not form a distinct group but are dispersed between the latter two groups. The outlier, ZB_F, on the far left of the plot was excluded from the SIMPER analysis. This site was dissimilar to the other sites, but was included in the NMDS analysis even though sample size was small at 23 individuals. After a fire that had recently burnt the site, 43% of the sample consisted of dead trees that had not resprouted during the period of this study, most of which were large mature trees that remained completely charred. The rest of the sample consisted of suffrutices. Within group 2, the only site with evidence of a fire (but not very recent) was that of Thomas Baines (TB) where some of the trees had blackened stems and which was therefore classed in the 3-4 year fire category. It is, however, possible that this fire could have occurred over 5 years ago where time since fire may have been underestimated. This site also had one of the highest seedling counts compared to the other sites.

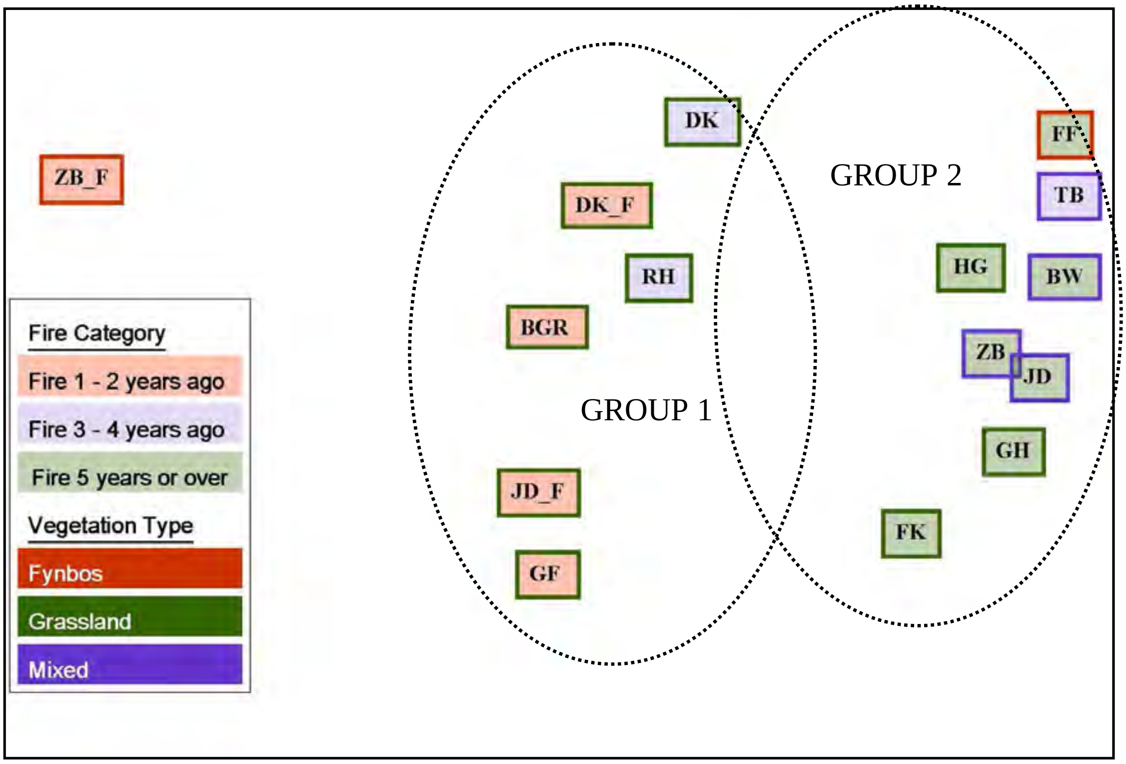


Figure 3.6 NMDS ordination plot showing similarities between sites (stress value = 0.09) based on their similarity in stage class distribution. Estimated last fire occurrence has been superimposed on the plot

Two distinct ordination groups (groups 1 and 2 in Figure 3.6) were used for the SIMPER analysis.

Table 3.4 shows the contribution of stage classes to within group similarity of groups 1 and 2 based on SIMPER analysis. It is clear that in ordination group 1 (more recently affected by fire) the stage category which contributes most to within-group similarity was the suffrutice stage followed by the adult, mature then dead stages, which reflects the mean abundance of each stage class in this group. Higher contributions to within-group similarity from the adult, sapling and immature stages are seen with group 2 where the sites had not been burnt for a number of years and again this correlated to the mean abundance of these stages found in the sites sampled.

ANOSIM analysis of the three groups categorised according to time since last fire show a significant difference in stage structure between groups separated according to last fire occurrence (global $R = 0.635$; $p < 0.01$; $N = 15$). Sites grouped according time since fire (Table 3.5) show that at sites which were not affected by fire for at least 5 years, adult stages contribute most to within group similarity followed by sapling, immature and mature stages. Again, these percentages reflect abundance of each stage class in these sites.

Group 2 where sites experienced intermediate time since last fire rank adults as both having the highest contribution to within group similarity as well as having the highest mean percentage abundance. In the group most recently affect by fire, the suffrutice stage class contributed most to within-group similarity and was also the most abundant. Dead stage contributions to both group similarity and abundance are equal to the adult stages.

Table 3.4 Contribution of the various stage classes to within group similarity between ordination groups 1 (recently burnt) and 2 (not recently burnt). Mean percentage abundance for sites sampled is also given to indicate average population structure for groups 1 and 2

Group	Average within group similarity (%)	Stage classes	Contribution to within group similarity (%)	Mean abundance in samples (%)
Group 1 recently burnt; < 5 years ago (n = 6)	64.0	Suffrutice	39.6	40
		Adult	27.7	18
		Mature	12.2	11
		Dead	5.5	18
		Immature	6.4	8
		Sapling	6.4	4
		Seedling	2.3	2
Group 2 burnt > 5 year ago (n = 8)	67.6	Adult	35.2	31
		Sapling	19.9	18
		Immature	17.1	18
		Mature	13.3	16
		Seedling	11.3	11
		Dead	3.3	3
		Suffrutice	0.00	4

Table 3.5 Percentage contribution of stage classes to within group similarity based on fire category groupings where fire > 1 year ago; fire between 2 and 3 years ago; fire between 5 and 10 years ago or greater

Group	Average within group similarity (%)	Characteristic stage classes	Contribution to within group similarity (%)	Mean abundance in samples (%)
Group 1 recently burnt; < 1 year (n = 4)	65.3	Suffutice	52.6	40
		Adult	19.2	18
		Dead	12.2	18
		Mature	7.4	11
		Immature	5.0	8
		Sapling	2.4	4
		Seedling	1.3	2
Group 2 burnt bet 2 to 4 years (n = 3)	48.4	Adult	22.0	25
		Immature	20.0	23
		Mature	18.3	10
		Sapling	17.9	17
		Suffrutice	13.8	14
		Seedling	4.2	8

Group	Average within group similarity (%)	Characteristic stage classes	Contribution to within group similarity (%)	Mean abundance in samples (%)
		Dead	3.9	2
Group 3 burnt ≥ 5 years (n = 7)	68.8	Adult	41.7	34
		Sapling	17.4	18
		Immature	15.3	15
		Mature	12.8	18
		Seedling	9.7	11
		Dead	3.0	3
		Suffrutice	0.0	0

Sites more recently affected by fire had the lowest abundance of the smaller stage classes. Suffrutice contribution to population structure is appreciably higher in sites most recently affected by fire. This percentage contribution drops for sites not disturbed by fire between 2-3 years and does not occur in sites estimated to have been affected by fire over 5 years ago. Sites in the > 5 year category have a higher contribution of adult trees whereas sites in the more recent category have a higher percentage of dead trees in the sample. The outlier (ZB_F) was included in the SIMPER analysis and exclusion of this site from the analysis resulted in a lower contribution of dead trees for the most recent fire groups.

Population structure in relation to population density

Populations of different densities were found to differ in their size class distribution. It is interesting to note that the dense sites of Jameson Dam and Suurberg are very similar in their stage class distribution (Figure 3.7) compared to the other sites. From observations in the field, individuals from these two sites tended to occur in clumped demes, and it is within these demes that seedlings were usually found sheltered by the older trees. There was usually very little vegetative cover under the canopies of the larger trees and in many cases mosses are often associated with seedlings.

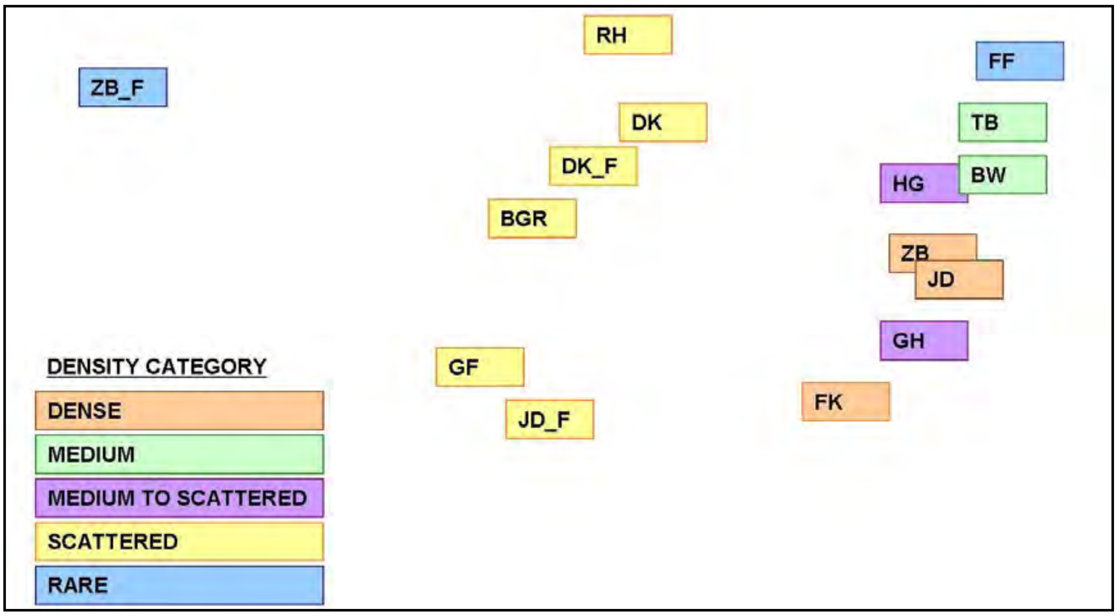


Figure 3.7 NMDS ordination of sites grouped according to stage class distribution where density has been superimposed

<u>IUCN version 3.1 criteria assessment</u>

B1. Extent of occurrence was calculated at 895.2 km^2. This is less than the 20 000km^2 required by the IUCN criteria that defines the Vulnerable category.

B1a. The GIS analysis revealed that *O. grandis* could be considered severely fragmented and is known from only 9 locations (Table 3.6).

Table 3.6 Locations identified by GIS analysis based on possible threatening events

Location	*Description*	*Possible threats*
Zuurberg Mountains 1	North and South Eastern sections of the distribution	These populations are large and often dense. Not threatened by Mountain Fynbos fires except on the periphery of populations
Zuurberg Mountains 2	South-Western section	Populations are small and isolated. Threat from hot fire in Mountain Fynbos

		areas is high
Highlands 1	Eastern section of the distribution in the area	Aliens infest this area. A likely threat to small populations is increased fire intensity
Highlands 2	Western section of the distribution in the area	Populations are large and no threat in the short term envisioned
Alicedale / Riebeek East	Populations existing between these two towns	Small populations are isolated. Threat from hot fire in areas where alien density is high
Grahamstown	Populations between Grahamstown and Thomas Baines Nature Reserve	Small isolated populations in some sections are surrounded by heavy alien infestations and are threatened
Glengarry	Population situated on the Willowfountain Farm south of Alicedale	Population fairly isolated from other populations but alien densities do not pose a threat
Heather Glen / Greenhills	Populations situated between Grahamstown and Heather Glen Farm	Populations are large but the Greenhills farm is so heavily invaded that it may threaten all individuals in the populations should they be allowed to spread.
Coombs	A small, isolated population in the Coombs Valley	A single fire is likely so threaten the population

B1b. A decline in area, extent and/or quality of habitat (B1biii) may be inferred from development and agricultural potential of the vegetation in the area as well as the expansion of alien vegetation. As previously mentioned, the vegetation associated with *O. grandis* populations has poor development prospects due to the rocky nature of the terrain. Agricultural potential is limited for similar reasons and grazing (although practised) is not ideal in grassy fynbos areas. There are two areas where transformation due to alien invasions and therefore habitat transformation for *O. grandis* is likely to be a real threat and may contribute to population decline in these areas. It is rare but in these two areas evident that the alien infestation is so severe, that certain sections of the population are being smothered. The first area is between Grahamstown and Thomas Baines along the *Oldenburgia* hiking trail. The second area is the population on the Greenhills Farm. The true nature of the threat is not obvious, and if the aliens are cleared, recovery may be possible such as the population at Dassie Krantz. It can be stated that there is a continuing decline in quality of habitat, but whether this directly affects *O. grandis* populations as a major threat cannot be ascertained without further study. Based on this assessment, criterion B1b is not met until further studies have been completed.

B1c. Due to their slow-growing nature, extreme fluctuations can be discounted for *Oldenburgia grandis.* Long-lived species are unlikely to experience fluctuations in population size due to low fecundity, mortality and vegetative growth.

B2. The area of occupancy was calculated at 16.0km^2. This is below the 2000km^2 to satisfy the Vulnerable criterion.

B2a – same as B1a

B2b – same as B1b

B2c – same as B1c

C. The maximum, minimum and median number of mature individuals was calculated to be 15 231, 5 463 and 10 311 respectively in all mapped populations. This is more or less at the 10 000 mark and satisfies this criterion for a taxon to be considered Vulnerable. Estimated population decline within the short-term is estimated to be between 2 and 3%, lower than the 10% required by criterion C1 for a taxon to be considered Vulnerable. Continuing decline (as with B1b) cannot be determined without further studies and extreme fluctuations (as with B1c) can be discounted for *O. grandis*. It is possible from the mapped populations to state that *O. grandis* does not satisfy criterion C2a where some populations are estimated to contain over 1000 mature individuals (C2ai) and not all mature individuals are in one subpopulation (C2aii).

Table 3.7 Estimated numbers of total and reproductive individuals for different sized populations

Population size			N (populations)	N (individuals)			N (reproductive)		
lower	mid	upper		lower	mid	upper	lower	mid	upper
1	5	10	56	56	280	560	30	151	302
10	30	50	37	370	1092	1850	200	589	999
50	75	100	37	1850	2757	3700	999	1489	1998
100	300	500	26	2600	7787	13000	1404	4205	7020
500	750	1000	14	7000	10500	14000	3780	5670	7560
Total			**170**	**11876**	**22415**	**33110**	**6413**	**12104**	**17879**

The data does not suggest that the taxon satisfies the criteria for D or E (Chapter 4). Populations were found to be not made up of fewer than 1000 mature individuals (D1) or with an AOO of less than 20 km^2 or less than 5 locations (D2).

Table 3.8 Summary of the results for each IUCN version 3.1 criteria

Criteria		Results
A taxon is considered to be Vulnerable if evidence that meets any of the following criteria (A – E)		
A	Reduction in population size over the past 10 years by ≥ 50%	Not known
B	Geographic range in the form of either B1 (extent of occurrence) or B2 (area of occupancy) or both	
B1	Extent of occurrence estimated to be less than 20 000 km^2 and estimates indicating at least 2 of the following:	895.2 km^2
B1a	Severely fragmented or known to exist at no more than 10 locations	9 locations
B1b	Continuing decline, observed, inferred or projected, in any of the following:	
B1bi	Extent of occurrence	B1biii)

B1bii	Area of occupancy	continuing decline in habitat but direct threat to populations is uncertain
B1biii	Area, extent and/or quality of habitat	
B1biv	Number of locations or sub-populations	
B1bv	Number of mature individuals	
B1c	Extreme fluctuations in any of the following:	
B1ci	Extent of occurrence	Discounted for *O. grandis* based on life history information
B1cii	Area of occupancy	
B1ciii	Number of locations or subpopulations	
B1civ	Number of mature individuals	
B2	Area of occupancy estimated to be less than 2000 km^2, and estimates including at least 2 of the following:	16.0 km^2
B2a	Severely fragmented or known to exist at no more than 10 locations	See B1a
B2b	Continuing decline, observed, inferred or projected, in any of the following:	
B2bi	Extent of occurrence	See B1b
B2bii	Area of occupancy	
B2biii	Area, extent and/or quality of habitat	
B2biv	Number of locations or subpopulations	
B2bv	Number of mature individuals	
B2c	Extreme fluctuations in any of the following:	
B2ci	Extent of occurrence	See B1c
B2cii	Area of occupancy	
B2ciii	Number of locations or subpopulations	
B2civ	Number of mature individuals	
C	Population size estimated to number fewer than 10 000 mature individuals and either:	10 311 (5463 – lower estimate; 15 231 – upper estimate)
C1	An estimated continuing decline of at least 10% within 10 years or 3 generations, whichever is longer (up to a maximum of 100 years in the future) OR	2% to 3%

C2	A continuing decline, observed, projected or inferred in numbers of mature individuals AND at least one of the following (a-b):	
C2a	Population structure in the form of one of the following:	
C2ai	No population estimated to contain more than 1000 mature individuals OR	No
C2aii	All mature individuals are in one subpopulation	No
C2b	Extreme fluctuations in number of mature individuals	No
D	Population very small or restricted in the form of either of the following:	
D1	Population size estimated to number fewer than 1000 mature individuals	No
D2	Population with a very restricted area of occupancy (typically less than 20 km^2) or number of locations (typically five or fewer) such that is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future, and is thus capable of becoming Critically Endangered or even Extinct in a very short time period	No
E	Quantitative analysis showing the probability of extinction in the wild is at least 10% within 100 years	Chapter 4

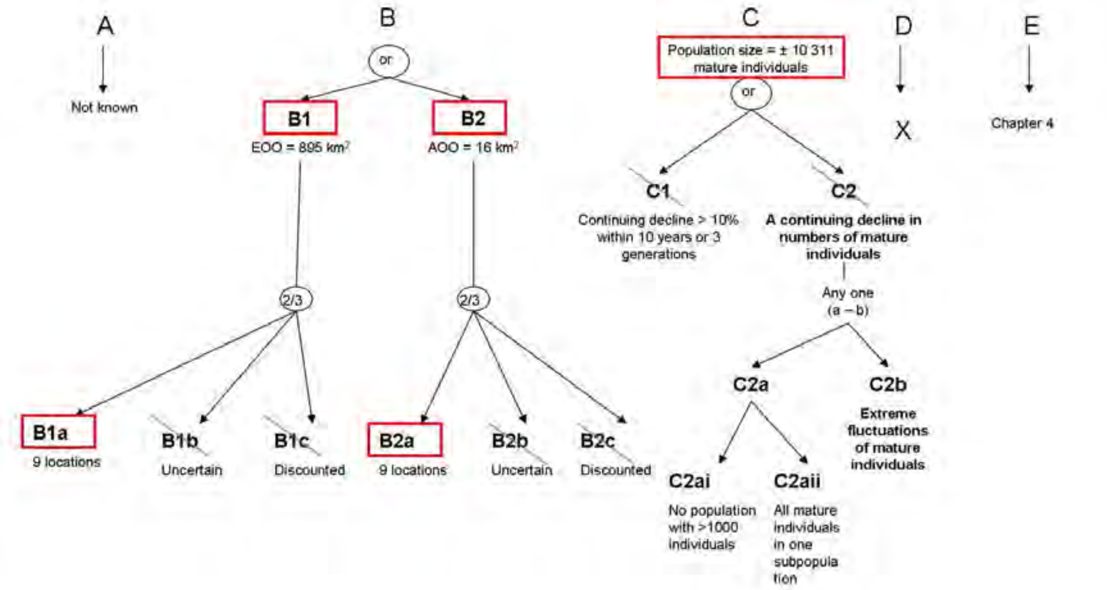


Figure 3.8 Diagrammatic representation of version 3.1 criteria met by *O. grandis* (square box) and not met (\)

The results show that *Oldenburgia grandis* should remain in the LR category. The furthest criteria met are B1 and B2, but subsequent criteria (i.e. 2 out of three for B1 a to c and B2a to c) are not met.

Discussion

<u>Distribution of *O. grandis* and the focus of conservation efforts</u>

The findings of this chapter reveal that there are three areas where the majority of *O. grandis* populations are found. A large percentage of *O. grandis* populations fall within a formally conserved area (Addo National Park) in the western part of its distribution. Conservation efforts should therefore be focussed in the eastern limits of its distribution, particularly in areas where exotic vegetation densities are high and where *O. grandis* populations are small. The best strategy for the conservation of rare endemic species postulated by Oostermeijer (2003) is to keep their natural habitat as free from any human-induced disturbances including livestock grazing, alteration of fire regimes and exotic invasions. Areas should be prioritised for clearing of alien vegetation where care should be taken not to leave wood piles close to populations after clearing, as this would pose a threat by increasing the intensity of a fire that might occur. Holmes et al. (2000) recommend that the optimal management of exotic vegetation in the fynbos biome would be a "burn standing" rather than a "fell and burn" clearing strategy. "Burn standing" method involves the burning of alien stands prior to clearing. These stands will have high levels of biomass but not high loads of dead material close to the ground as when the "fell and burn" method is used. Landowner awareness regarding the near-threatened status of the species should be encouraged, particularly for clearing alien vegetation. Initiatives such as the *Oldenburgia* conservancy should be encouraged, where stakeholders such as the municipality and private landowners can in a combined effort plan to control the invasion of aliens in areas where they co-exist with rare and endemic species in high densities.

Population structure and the influence of fire

Time since fire disturbance has the largest influence in determining similarities between populations according to their stage structure. The population structures at sites that had not recently been affected by fire show similar stage distribution to the projected stable stage distribution from Chapter 2 using transition matrices from sites also not recently disturbed from fire. Saplings are predicted to have higher abundances at a stable stage than the adult stages that were the most abundant stage for sites not affected by fire for a number of years in this chapter. Stages with high elasticity values for persistence (Chapter 2) are well represented in the population structures presented in this chapter for sites not recently affected by fire. The population structure of sites recently burnt have the suffrutice stage in the highest abundance, with the number of dead trees being the third most abundant stage suggesting that there was a high rate of retrogression and mortality after the fire.

It is unlikely that land use has a major effect on the structure of a population, particularly as the rocky outcrops where most *Oldenburgia* are found are often inaccessible to grazing cattle due to the rocky terrain. It is possible however that land disturbances such as overgrazing may open areas up to invasions by woody exotic vegetation. Not only does the rocky habitat on which *O. grandis* grows provide some protection from fire (Chapter 2), but may buffer larger populations from displacement by woody exotics.

Population structure in relation to population density

In very dense populations, the accumulation of leaf litter under the canopies of the larger trees is notable compared to the less dense sites. A higher percentage of adults were found in denser populations while an increased number of suffrutices were found in more scattered populations. The extent of the rock outcrops and the colonisation of this rock may have an impact on whether the population is exposed to fire. Scattered populations tended to be isolated suggesting that populations may be more exposed to fires that occur than populations that have colonised a larger rock surface area which may be better protected against a fire. Exotic vegetation tends to occur in the patches between the rock outcrops, resulting in a certain spatial segregation between the *Oldenburgia* populations and the stand of alien vegetation.

The IUCN status of *O. grandis*

Although *O. grandis* is severely restricted by its area of occupancy and extent of occurrence, its habitat preference for rocky outcrops is likely to be an advantage for its survival as a species. Rocky outcrops provide many advantages to species restricted to them. Outcrops are not likely to experience human-induced impacts such as urban development or intensive agricultural activities. Although most of the privately, non-conserved land on which the larger *Oldenburgia* populations exist are cattle farms, grazing within the populations is often difficult due to the nature of the terrain. *O. grandis* is also an unpalatable species, and no direct grazing impact was observed in this study. Land mismanagement and over-grazing may open up areas to invasions by exotic trees, particularly in a susceptible environment such as the Fynbos Biome to these invasions (van Wilgen and Richardson 1985). This may have an indirect effect on the smaller *Oldenburgia* populations that may be at a greater risk of intense fires fuelled by this woody biomass.

Adult and mature numbers approximately equal the threshold prescribed for a taxon to be considered Vulnerable. It is therefore imperative that the persistence of adult and mature individuals remains the focus of any conservation efforts for the species (Chapter 2). The recommendation is that *O. grandis* remains in its current lower risk/near threatened category but continued monitoring of populations is recommended.

Conclusion

A cause for concern is that most *O. grandis* populations are small. In addition to this, only 33% of *O. grandis* populations were found in vegetation free of aliens. Small populations, which form the majority of populations mapped, are not protected and exposed to exotic species. On the other hand, a large proportion of *O. grandis* populations are found in protected areas and areas generally free from alien vegetation where 40% of populations are formally conserved.

The burnt population on the Suurberg Pass (ZB_F) where a high percentage of dead trees were found after a fire shows that there can be high adult and mature mortality. An interesting question to then consider is does occasional high recruitment compensate for this? If the answer to this question is negative, small populations threatened by hot fire will decline steadily with each mortality event. The ZB_F being in a conservation area suggests that it is part of a natural dynamic but highlights the need for monitoring and further attention to the effect of fire regime on *O. grandis* survival.

CHAPTER 4 POPULATION VIABILITY ANALYSIS

Introduction

Population models are quantitative methods that make it possible to project future population numbers over time (Akçakaya et al. 1999), evaluate threats to a species and determine risks of extinction (Akçakaya and Sjögren-Gulve 2000). Population viability analysis (PVAs) is a modeling approach used to assess population persistence based on quantitatively sampled species-specific data and modeling scenarios (Menges, 2000).

Higgins et al. (2000) have postulated that the rate of population growth determined in a PVA analysis should take into account the interactions of the life-history of a species (chapter 2) and stochastic changes in the environment in which it exists. Assessing the outcome of stochastic population growth rates (λs) for different environmental scenarios is not sufficient without taking into account the effects of storage mechanisms certain species have evolved (Warner and Chesson 1985). The storage effect refers to the ability of plants to store reproductive output so that in years that favour reproduction, plants with this mechanism can maximise their reproductive ability (Higgins et al. 2000). Populations may therefore be seen to decline (especially over short study periods) during unfavourable years but recover during periods that favour reproduction and seedling establishment (Warner and Chesson 1985). *O. grandis* has two ways of storing reproductive output between years that favour reproduction: by reprouting after fire, this ensuring persistence of the reproductive stages (Chapter 2) and by having a persistent sapling bank (Chapter 3). What implications does this have for determining extinction risks? For plants with storage mechanisms, such as *O. grandis*, an increase in the variance in recruitment should promote population persistence whereas an in increase in the variance of mortality should increase the risks of extinction (Higgins et al. 2000). The opposite is true for species with low or no storage mechanisms where an increase in the variance of recruitment would promote extinction (Higgins et al. 2000).

The primary use of PVAs is to assess the extinction risk of a population under current conditions or various management scenarios (Reed at al. 2002). PVAs are highly dependent on the quality of the data and structure of the model. PVA for plants are particularly dependent on sufficient data for parts of the life cycle of the plant, episodic recruitment events and environmental variation during the time of sampling (Reed at al. 2002). Concerns with regards to the precision of PVAs have been well documented and discussed (Ellner et al. 2002; Reed at al. 2002, Ludwig 1999; Fieberg and Ellner 2001). Important considerations of a matrix model are the associated assumptions including: that the life cycle model on which the model is based is an accurate reflection of the model, that the vital rates of the population do not change and that there are enough sampling years to accurately account for the range in environmental variability. Studies (Bierzychudek, 1999; Lindborg and Ehrlén 2002) have revealed that these assumptions can be serious drawbacks particularly for density dependent populations. On the other hand Vandermeer et al. (2003) suggests that density-independent models are sufficient in order to estimate current population growth rate for conservation purposes as these species tend to occur at low densities. *O. grandis* populations occur mostly at low densities (Chapter 2).

Limitations and benefits to using PVA methods in demographic studies have been investigated (Heppel et al. 2000; Fieberg et al. 2001; de Kroon et al. 2000; Akçakaya and Sjögren-Gulve 2000). PVAs require sufficient data, often over numerous years to provide accurate estimates of transition probabilities for life history stages and to account for both spatial and temporal variability populations experience (Bierzychudek 1999; Akçakaya and Sjögren-Gulve 2000). Uncertainties can often be incorporated into the PVA study and do not necessarily affect the overall results (Akçakaya and Sjögren-Gulve 2000). PVAs are useful when comparing management options, for answering specific questions regarding the management of a rare species such as *O. grandis* and aid in identifying what the primary research focus should be for reaching sound management decisions (Akçakaya and Sjögren-Gulve 2000). Akçakaya and Sjögren-Gulve 2000 have suggested that the level of detail of the PVA must be consistent with the data available and that comparative results regarding risks of decline rather than fixed predicted times to extinction. PVAs should also be treated as adaptive assessments including continued re-assessments and monitoring of management strategies once in place (Coulson et al. 2001). Akçakaya and Sjögren-Gulve 2000 listed four important aspects PVAs address in the assessment of management for rare or threatened species: PVAs can guide research by highlighting factors that most affect probabilities of extinction, estimate the relative vulnerability of populations to extinction, assess the impact of human activities and ranking management options.

A component of PVAs is the use of elasticites to determine the relative contribution of G, S and L to population growth rate (Silvertown et al. 1993). Elasticity analyses are very useful in understanding the life history of a species (de Kroon at al. 2000) and have been regarded as relatively accurate in predicting changes in population growth rate with changing transition probabilities (Mills et al. 1999). They have also been considered as robust analytical tools for initial model building scenarios and supposition testing for demographic studies (Benton and Grant 1999).

In order to perform a PVA, a demographic analysis needs to be completed for the species concerned. This will determine the current status of the population and the vital life-cycle stages of a population (Caswell, 2001). Data from the demographic analysis are used to project population numbers over a specified time period by changing certain parameters that may affect future population dynamics. In this way, population responses to environmental stochasticity can be projected to determine which management scenarios or environmental conditions are optimal or detrimental for population persistence. Pfab and Scholes (2004) for example successfully used a stochastic population model to determine if the harvesting of the endangered *Aloe peglerae* was sustainable from the wild while numerous authors (Silva et al. 1991; Canales et al. 1994 and Gross et al. 1998) have modelled the effects of fire on plant populations using stochastic matrix models. Silvertown and Charlesworth (2001) have listed four factors that determine the impact of stochastic variation on λ: how much the various vital rates vary i.e. how much seedling persistence varies compared to adult persistence; the sensitivity of λ to the vital rates that vary the most; the temporal correlation between vital rates and environmental autocorrelation.

Various PVA methods are used to model environmental stochasticity (Menges 2000; Caswell, 2001). One method used is to randomly select transition probabilities that vary independently of each other, but still within limits of transitions observed from census data. Variations within observed limits represent a demographic response to environmental variation. But this does not take into account correlations among certain vital rates where there is often a positive correlation (Oostermeijer et al. 1996; Fieberg and Ellner 2001) that has to be incorporated into the model. An alternative method is to randomly select entire matrices containing elements of the original matrix and applying this to the model (Menges 2000). Using this method, the transitions keep their correlations as observed in field. This method was not used in this study, as there were not enough transition data to generate a large set of matrices that could be randomly selected. Environmental autocorrelation is a measure of whether there is a predictable pattern of good and bad years or whether these are random events. Environmental autocorrelation was not factored into the modelling in this study. Not only has environmental autocorrelation been considered less important than temporal correlation between vital rates but the conclusion of a study is often not affected by the exclusion of environmental autocorrelation (Fieberg and Ellner 2001).

Oldenburgia grandis is found in areas where fire plays a role in determining vegetation type and structure. The key environmental factor used in modelling population responses was therefore fire regime. The two effects of fire modelled were frequency and intensity. From the results of Chapter 2 it is clear that the effects of fire include loss of reproduction, loss of seedling establishment, reduced individual growth, mortality and retrogression into smaller stage classes. The effects of fire on all the stages of the life cycle can therefore have a profound effect on the population growth rate.

Population responses to environmental factors excluding fire are also modelled. Life history analysis of *O. grandis* (Chapter 2) reveals that survival of adults and mature trees is crucial to population survival whereas fecundity and growth had comparatively low elasticity values. To test this result, fecundity levels and seedling survival were dramatically reduced and population responses to this modelled.

Aims

The overall aim of this chapter was to perform a PVA for *O. grandis* and to model population responses to variation in climate and fire regime. More specifically, the following three aims describe the objectives of this chapter:

1. To model population responses to environmental stochasticity. Environmental stochasticity included environmental effects that did not involve fire such as unfavourable or favourable climatic conditions. This was done to compare random stochastic changes reflected in changes in the vital rates to compare with the effects of fire.

2. To determine which fire regime (in terms of fire frequency and fire intensity) had the largest influence on stochastic population growth rate. Fire is an important environmental influence in Fynbos vegetation and responses to fire could determine how well adapted a plant is to the environment in which it lives. This adaptation is reflected in the life history of the species and may give insight into the possible threats facing established populations.

3. To test whether life strategies found not to be critical to the persistence (e.g. fecundity in Chapter 2) of the species have an effect on population growth and stability. This was done by factoring in low and occasional high fecundity and levels of recruitment and monitor population responses into the model.

4. To investigate the implications of the storage effect on the stochastic population growth rate.

Methods

Transition probabilities used in this chapter were based on those recorded in Chapter 2. In addition, plausible scenarios not encountered in the study were simulated using predicted transition probabilities that were incorporated into the model.

<u>Correlated and uncorrelated transition probabilities</u>

To simulate environmental variation between fires, transition probabilities were set to vary randomly between their minimum and maximum values recorded. Two approaches were used to simulate environmental stochasticity. The first approach was the use of uncorrelated random transition probabilities. Random transitions were set to vary independently of one another by selecting the RandReal function in Microsoft Excel (2000). The range within which the random transitions were set to vary was calculated from the standard deviation derived from observed transitions probabilities.

It is expected that environmental influences that affect survival of one stage will affect survival in another stage. In reality, it is therefore expected that stasis and growth transitions should be correlated as environmental factors positively affecting growth would have a positive effect on survival and vice versa. It is therefore unrealistic to allow transition probabilities to vary independently without including a correlation coefficient. Both correlated and uncorrelated transition probabilities were included in this chapter. Strong positive correlation, although more realistic, results in more variable predictions of population growth and accentuates differences between growth rates in favourable and unfavourable years (Brigham and Thompson, 2003). Results from both uncorrelated and correlated transitions may therefore return likely population responses between the two sets of results. It is expected that actual population dynamics are likely to lie between extremes of 100% correlation and complete lack of correlation.

To build correlated transition probabilities into the model, the first step was to determine which transitions are likely to correlate, and whether the correlation is positive or negative. All survival and growth transitions were set to correlate positively when simulating years without fire. To get the transition values to correlate, a random environmental variable was generated between -1 and 1. This represents positive and negative changes in environmental conditions affecting demographic parameters. The environmental variable was then linked to transition rates using the following formula:

correlated transition probability = mean + (standard deviation x environmental variable)

where the mean and standard deviation are the same as used in uncorrelated transition probabilities to represent the range in variation of transition probabilities.

A fundamental problem in the matrix occurs where negative values or values exceeding 1 may be returned. To ensure that each transition did not exceed 1 or go below 0, the following Microsoft Excel (2000) "IF" statement was used:

$$\mathbf{=IF\ (a_{i,j} > 1, 1, IF\ (a_{i,j} < 0, 0, a_{i,j}))}$$

For any value exceeding 1, 1 would be returned; any negative value will remain zero. If neither of these conditions were satisfied, the original random transition variable is returned.

It is also possible for the sum of persistence and growth (for example $a_{i,j} + a_{i,j+1}$) to be either negative or greater than 1. This is biologically impossible. The following Microsoft Excel (2000) formula was used to ensure that the sum of two transitions in the same stage do not exceed 1. This was not applied to fecundity transition probabilities as the sum may exceed 1.

$$\mathbf{= IF\ ((a_{i,j} + a_{i,j}+1) > 1, a_{i,j} - (ABS\ (1 - (a_{i,j} + a_{i,j+1}))/2), a_{i,j})}$$

Using the above equation, if two transition values in the same stage exceed 1, the values were reduced by the same amount until their sum equals 1.

Stochastic growth rate

Averaging the population growth rate derived directly from the projection matrix does not sufficiently describe the growth rate of a population when subject to stochastic variation. This is best calculated directly from population sizes (McPeek and Kalisz 1993). Stochastic fluctuations affect the growth rate of a population due to unpredictable environmental influences (Dennis et al. 1991) therefore it was appropriate to calculate the stochastic growth rate of the simulated population. Stochastic growth rate (λs) for correlated and uncorrelated transition probabilities was calculated using the following formula (McPeek and Kalisz 1993; Caswell, 2001):

$$\mathbf{\log \lambda s = \log ((N_t / N_0)^{1/t})\ \therefore\ \lambda s = e^{\log \lambda s}}$$

Where N_t was taken as the total population number at 500 years (t), N_0 was the population number in the first year.

Monte-Carlo Analysis

Monte-Carlo analysis makes it possible to estimate demographic parameters in a stochastic environment. Random numbers were generated with each worksheet calculation resulting in different transition probabilities and therefore changes in λs. Monte-Carlo analysis makes it possible to recalculate a worksheet over a specified number of times and summarise the results for analysis. Monte-Carlo analysis (PopTools *ver.* 2.7, Hood 2006) was used to iteratively generate random transition probabilities a specified number of times and output static results used in the analysis. To save computational time, the sample size was kept at 500 as increasing it to 1000 did not change the output of the analysis. To determine upper and lower confidence limits, upper and lower percentiles were set to 0.025 and 0.975 respectively.

Elasticity analysis

Elasticity for sites not affected by fire was analysed. Elasticities for scenarios including the effects of fire were not determined as the modelling procedure switched between transition matrices depending on whether fire was included or not. Elasticies are calculated directly from the transition matrix that would only determine the elasticies for the years that included either fire or no fire and would not take into account frequency fire or years with increased fecundity.

Simulation of stochastic scenarios

Ten scenarios were modelled simulating the effects of stochastic variation excluding fire, various fire regimes such as changes in fire frequency and intensity, and variation in reproductive outputs in the absence of fire.

Modeling the effects of fire

The effects of fire include mortality as a result of burning, retrogressing into the suffrutice stage and survival without sprouting. Retrogression of individuals into the suffrutice stage after fire is likely to be specific to the substrate type on which an individual grows (i.e. the proportion of protection from rock an individual receives) particularly for the seedling, sapling and immature stages. The substrate type on which an individual grows is likely to vary greatly between populations. Transition probabilities based solely on the Dassie Krantz population (where before and after fire transition values were available) were not considered to be a true reflection of the effects of fire on the general structure for the model as different levels of protection individuals stages receive from rock are likely to differ between sites. Data used to construct the model to include the effects of fire were extracted from three sources. Transition values for the first year after fire were based on data collected before and after the fire at Dassie Krantz (DK) as well as from the sites that had been affected by fire less than a year before the time of sampling (JD_F and ZB_F) and from substrate data collected for each site. Retrogression transition probabilities from the site at DK were used to model the effects of fire on the suffrutice and immature individuals. These stages were the most affected by fire displaying the highest levels of retrogression. It is likely that these individuals remain longer in the suffrutice and immature categories due to the lack of protection from rock seen in chapter 2. Transition probabilities reflecting the persistence of the adult and mature stages were based on the observed transition probabilities from the DK, JD_F and ZB_F sites. It cannot be assumed that protection of seedlings by rock can be extrapolated from the DK site to represent the general survivorship probabilities of seedlings after a fire. Transition probabilities for seedling persistence were therefore divided into two categories: High and low levels of protection from rock during a fire. The level of rock protection saplings receive are higher than seedlings (chapter 2) and therefore persistence probabilities for saplings during a fire were set to be the same as the higher range for seedling persistence.

Not all transition probabilities are expected to correlate positively. Retrogression parameters were correlated separately from growth and survival parameters by using a separate randomly correlated environmental value. In this way it was taken that growth and survival parameters do not correlate positively or negatively with retrogression parameters.

a. Seedling persistence

Survival transition probabilities before and after a fire for the smaller stage classes were derived from the potential vulnerability to mortality during a fire. This is based on the percentage rock protection an individual might experience during a fire. The range of seedling survival ($a_{se,se}$) was divided into two possible categories. If between 0 to 40% of seedlings in a population were growing on rock rather than directly on soil or amongst other vegetation, the models assumes that survival of seedlings is between 0 to 0.4 in other words, survival is directly proportional to whether an individual is protected by rock. On the other hand, if seedlings have a higher percentage of rock protection of between 60 to 100%, survival probability would then range between 0.6 and 1. If completely damaged by fire, saplings and seedlings do not re-sprout.

b. Sapling persistence

Sapling persistence ($a_{sa,sa}$) was set higher than seedling survival after a fire. The assumption here is that saplings were seedlings that have survived previous fires (because of their position in the population mostly sheltered by rock during a fire) and have more of a chance of surviving a fire compared to seedlings. Saplings are extremely slow growing and it is likely individuals have survived previous fires to get to this stage. Sapling persistence was set at between 0.6 – 1.

c. Persistence of immature and suffrutice stages

Retrogression from immature to suffrutice stage ($a_{im,su}$) after a fire was set between 0.25 and 0.75. Results from the Dassie Krantz site before and after a fire suggest that it is likely that a proportion of the immature individuals had burnt in previous years, resprouted and have progressed into the immature stage. It is likely that a fraction of the individuals in immature stage are recovering from retrogression. These will be more likely to burn than adult or mature stages that had not retrogressed in the previous fire(s). Persistence of immature individuals ($a_{im,im}$) after a fire was set at between 0.15 and 0.25. This is low due to the likelihood that a large percentage of immature individuals retrogress to the suffrutice stage during a fire.

Suffrutice individuals resprouting after a fire are included as suffrutice persistence ($a_{su,su}$). The likelihood of suffrutice individuals retrogressing is likely to be similar to retrogression of immatures and therefore has the same transition probabilities. No data exists for transition probabilities from suffrutice to immature; these transition probabilities are expected to be higher than from sapling to immature due to stored carbon in the burnt stem available to it (Bond and Midgley 2001). Progression of suffrutice to the immature stage ($a_{su,im}$) was estimated to have the same range as progression from immature to adult ($_{asu,im}$ to $a_{im,ad}$).

d. Persistence of adult and mature stages

For the first year after a fire, transition values from the site at Dassie Krantz were taken as an indication of adult ($a_{ad,ad}$) and mature ($a_{ma,ma}$) persistence. This was accordingly set to be high at between 0.95 – 1. Retrogression after fire was set to between 0 and 0.05. Adult and mature trees have significantly higher substrate protection as they are mainly found on rock (Chapter 2) compared to the younger stage classes. Transition probabilities from the sites not affected by fire (Scenario 1) were used for subsequent years after a fire.

Scenario 1

In order to model transitional changes due to environmental stochasticity (excluding the effects of fire) the transitions from four sites that had not experienced fire for approximately 10 years were used. Eight transitions (two transitions from each of four sites) were averaged and correlated and uncorrelated random transitions were generated in an Excel spreadsheet (2000) to vary between the standard deviation from the mean using the RandReal function. Both transition matrices were then used to project population numbers over 500 years. Flowering for every second year (as observed in chapter 2) using the same transition rate was also modelled, as this would be more realistic for *O. grandis* (Table 4.1).

Scenario 2

Fire was not modelled here, but the effects of low recruitment due to factors such as fungal infestation of seed, high seed predation, low levels of flowering or high percentages of aborted flower heads were modelled to predict population response and growth rate. Fecundity transitions were altered to be low at f_{ad} = 0 – 0.01 and f_{ma} = 0 – 0.01. The matrix transitions for stochastic changes without fire remained the same as in Scenario 1.

Scenario 3

Using the probabilities described in 'modeling the effects of fire', a cool fire was modelled to burn every 5 years. This was reflected in the high probabilities of adult and mature trees surviving the fire. Suffrutice and immature stages have a moderate to high probability of retrogression with a low probability of staying in the same stage. Seedlings were set to have higher probabilities of staying in the same stage by surviving fire as a result of higher levels of rock protection (0.6 – 1). The same procedure to calculate λs and to sample for 500 years as in Scenario 1 was used.

Scenario 4

A cool fire is modelled every 5 years using the same probabilities as in Scenario 3, except seedlings have higher probabilities of mortality due to the lower protection from rock.

Scenario 5

The same transition probabilities were used in this scenario as in Scenario 3, except that the frequency of fire was decreased to every 10 years instead of 5. The fire temperature was modelled to be cool with relatively high seedling survival due to a high level of rock protection.

Scenario 6

The same transition probabilities were used in this scenario as in Scenario 4, except that the frequency of fire was decreased to every 10 years instead of 5. The fire temperature was modelled to be cool with relatively low seedling survival due to a low level of rock protection.

Scenario 7

The frequency of fire was decreased further to a 20-year interval. The assumption is that a relatively high fuel load may have built up during this fire interval resulting in a hot fire. This could be caused by bergwind conditions in an area where there was a high build up of biomass. This scenario is more likely to negatively impact smaller populations by high levels of adult and mature stage mortalities, possibly in Mountain Fynbos areas or in areas where alien vegetation is dense. Seedling mortality is likely to be high regardless of levels of rock protection as it is likely that seedlings growing on rock will not survive the hot flames. High adult and mature stage mortality is modelled using probabilities between 0 – 0.3. Table 4.1 shows all the transition values for this scenario. This would be the worst-case scenario, and example of which was sampled at the Suurberg National Park (ZB_F) where 43% of adult and mature trees sampled in the population were dead as a result of a hot fire that had swept through the site.

Scenario 8

A moderately hot fire is modelled every 20 years, not as intense as scenario 6 (perhaps a fire in a wetter season or where not as much biomass has accumulated in Grassy Fynbos area), but where the fire is still hot enough to cause moderately high levels of mortality. Seedling survival is relatively low, whereas adult survival is moderate.

Scenario 9

To determine if higher fecundity can in some years counteract the effects of fire, fire at an interval of 5 years was modelled with low intensity and high levels of seedling protection. Fecundity levels were set to vary between the observed highest and second highest from the sites sampled. For adult fecundity, the highest transitions were seen for JD at year 2 (f_{ad} = 0.1141) and second highest for JD at year 1 (f_{ad} = 0.0321). The fecundity transitions for mature plants were taken from observed rates for TB in the first sampling year (f_{ma} = 0.3333) and for JD in the second year (f_{ma} = 0.25).

Scenario 10

Frequency of fire was decreased to 10 years using the same fecundity values and transition probabilities as in scenario 9 where seedling protection received from rock remained high.

Table 4.1 gives a summary of transitions for all scenarios used in the matrix model.

Table 4.1 Transition probabilities used for modelling the effects of fire for each scenario. Transition probabilities for scenario 1 and were used for all years; for scenarios that included the effects of fire (3 – 10) the transitions shown in this table were used for the first year after a fire where scenario 1 transitions were used for subsequent years after the fire. Scenarios 3 – 5 had either high or low levels of seedling refuge from fire. The asterisk * depicts transitions probabilities in the years in which fire does not occur

	SCENARIO 1	SCENARIO 2	SCENARIOS 3 - 6		SCENARIO 7	SCENARIO 8	SCENARIO 9	SCENARIO 10
$a_{se,se}$	0.4616 – 1	0.4616 – 1	0 – 0.4	0.6 – 1	0 – 0.4	0 – 0.1	0.6 - 1	0.6 - 1
$a_{se,sa}$	0 – 0.5384	0 – 0.5384	0		0	-	0	0
$a_{sa,sa}$	0.9687 – 1	0.9687 – 1	0.6 - 1		0 – 0.1	0.6 – 1	0.6 - 1	0.6 - 1
$a_{sa,im}$	0 – 0.02	0 – 0.02	0		0	-	0	0
$a_{su,su}$	0.7230 – 1	0.7230 – 1	0.25 – 0.75		0 – 0.15	-	0.25 – 0.75	0.25 – 0.75
$a_{su,im}$	0 – 0.0304	0 – 0.0304	0		0	-	0	0
$a_{su,ad}$	0	0	0		0	-	0	0
$a_{im,su}$	0	0	0.25 – 0.75		0 – 0.25	0.25 – 0.75	0.25 – 0.75	0.25 – 0.75
$a_{im,im}$	0.8567 – 0.9745	0.8567 – 0.9745	0.15 – 0.25		0 – 0.15	0.15 – 0.25	0.15 – 0.25	0.15 – 0.25
$a_{im,ad}$	0 – 0.1223	0 – 0.1223	0		0	-	0	0
$a_{ad,su}$	0	0	0 – 0.05		0 – 0.01	0 – 0.05	0 – 0.05	0 – 0.05
$a_{ad,ad}$	0.9824 - 1	0.9824 - 1	0.95 - 1		0 – 0.3	0.4 – 0.7	0.95 - 1	0.95 - 1
$a_{ad,ma}$	0 – 0.0176	0 – 0.0176	0		0	-	0	0
$a_{ma,ma}$	1 - 1	1 - 1	0.95 - 1		0 – 0.3	0.4 – 0.7	0.95 - 1	0.95 - 1
$a_{ma,su}$	0	0	0 – 0.05		0 – 0.01	0 – 0.05	0 – 0.05	0 – 0.05
f_{ad}	0 – 0.0601	0 – 0.0601	0		0	0	0.0321 – 0.1141*	0.0321 – 0.1141*
f_{ma}	0 - 0.2072	0 - 0.2072	0		0	0	0.25 – 0.3333*	0.25 – 0.3333*

Results

Scenarios 1 and 2: no fire

Populations unaffected by fire (Scenario 1) show a steadily increasing population. When using correlated transition probabilities, λs is 1.00, whereas λs is marginally lower at 1.0122 when using uncorrelated transition probabilities (Figure 4.3). *Oldenburgia grandis* populations are thus predicted to increasing without the effects of fire. For populations where flowering occurred every second year, the correlated matrix transition resulted in λs of 1.0123. A reduction of fecundity levels (Scenario 2) shows that population growth is still positive for correlated transitions (1.0022) but it declines below 1 for uncorrelated transitions (0.9998). Both correlated and uncorrelated transitions show positive growth rate at low fecundity levels at the upper confidence limits (Table 4.1).

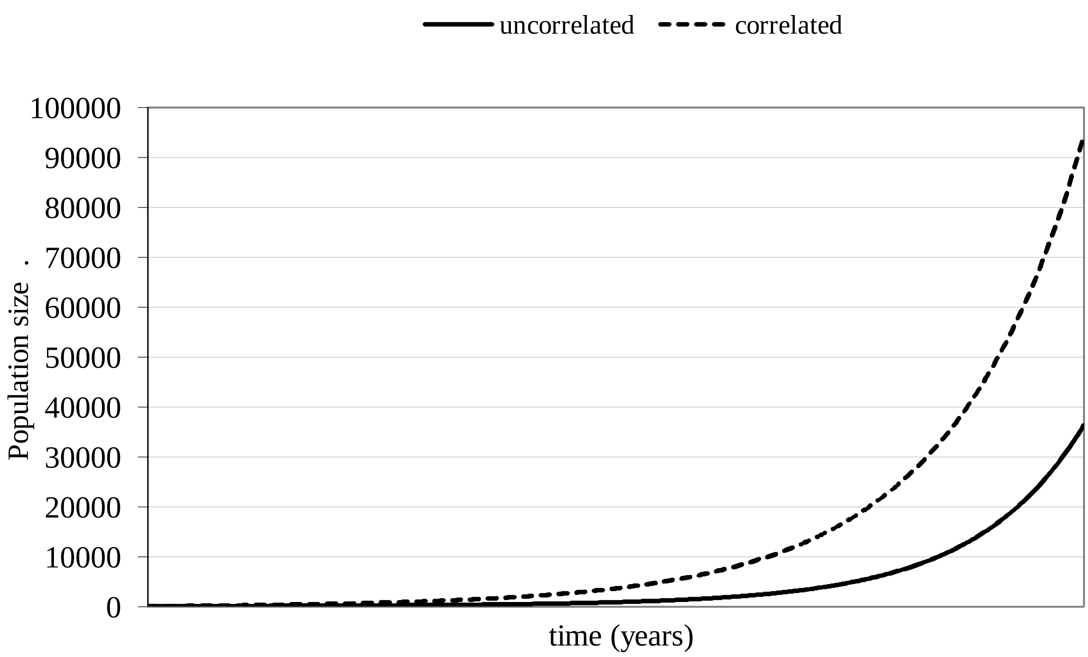


Figure 4.1 Population numbers for Scenario 1 projected over 500 years with correlated and uncorrelated transition probabilities (Monte-Carlo iterations = 500)

The population structure for Scenario 1 at 500 years for models using both correlated and uncorrelated transition probabilities show that saplings dominate population structure (Figure 4.2; only correlated transition probabilities are shown). Seedlings make up a small proportion of individuals while mature and adult trees contribute almost equally to population structure. For Scenario 2, mature individuals dominate the structure of the population, while only 1% of the population consists of seedlings.

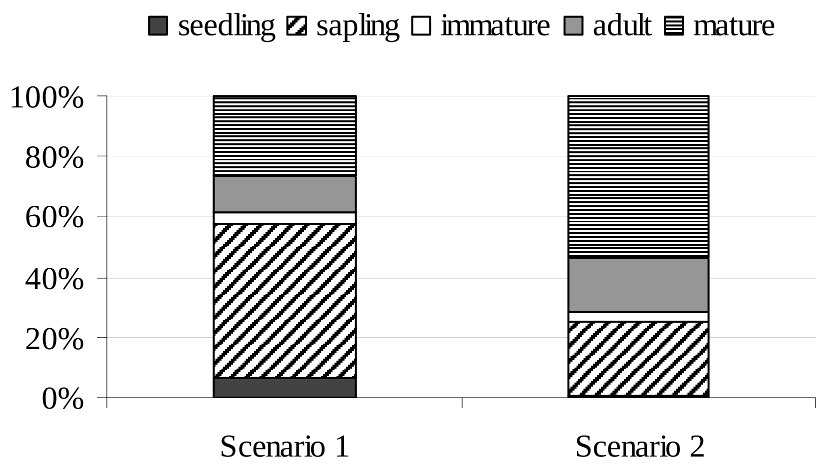


Figure 4.2 The proportion of individuals in each stage for Scenario 1 and Scenario 2 (no fire) at 500 years from model. Models using correlated transition probabilities are only shown. Transition probabilities are based on the range of observed data from 5 sites

Elasticity results show persistence to be the highest contributor to population growth rate at 98.44% for uncorrelated and 98.16 % for correlated transition probabilities (Table 4.2). The results show that population growth rate is least sensitive to changes in fecundity.

Table 4.2 Survival, growth and fecundity elasticities for correlated and uncorrelated transition probabilities modelled for sites unaffected by over 500 years

	persistence	**growth**	**fecundity**
uncorrelated	98.44	1.16	0.33
correlated	98.16	1.42	0.37

Persistence elasticities were highest for the mature stage (65.40% uncorrelated and 59.00% correlated) followed by the adult stage for uncorrelated transition probabilities (16.65%) but by the sapling stage for correlated transition variables

(17.34%) (Figure 4.3). The sapling stage ranks third highest using uncorrelated transition probabilities (12.63%) where adult persistence is marginally lower than sapling persistence at 17.24%. Seedling persistence ranks to lowest at 0.61% for uncorrelated and 1.13% for correlated transition probabilities. Suffrutice individuals do not contribute at these are sites as no plants had recently retrogressed as a result of damage by fire.

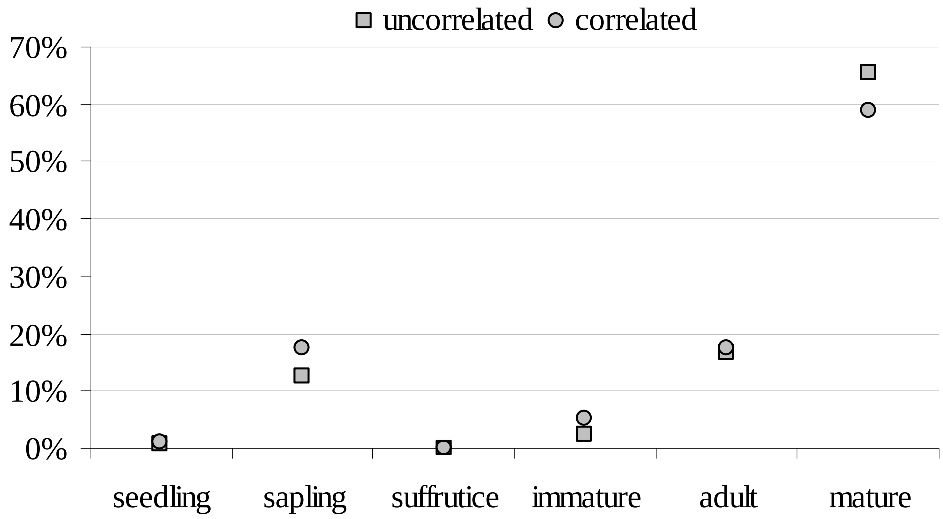


Figure 4.3 Persistence elasticities for each stage class (Scenario 1 – no fire)

The effects of fire

Table 4.3 gives a summary of the fire regime, fecundity and levels of seedling protection from rock for all scenarios as well as whether the resultant λs was above or below zero. The two scenarios that resulted in a positive rate of population growth, irrespective of whether uncorrelated or correlated transition probabilities were used suggest that the optimal prescribed fire frequency for *O. grandis* is 10 years. It is clear that populations have higher growth at sites where seedlings are well protected from fire by rock refuges. Different population growth rates (but still close to 1) for uncorrelated and correlated transition probabilities result when fire frequency is increased to 5 every five years and seedling persistence is high (Scenario 9) and when the opposite is true (fire frequencies are at 10 years but seedling persistence is high – Scenario 6) meaning that seedling protection from fire does to some degree have a positive influence on the rate of population growth. The major threat to populations is an increase in fire intensity resulting in high adult and mature mortality (Scenario 7) where both upper and lower bound confidence levels resulted in negative stochastic population growth. In areas where the vegetation is tall such a Mountain Fynbos areas combined uncharacteristic weather conditions such as hot strong winds would increase the intensity of a fire and pose a threat to population persistence, particularly if there are high adult and mature mortalities as seen at the ZB_F site. The combination of a frequency of a fire every 5 years with low seedling persistence (Scenario 4) may also have a slight negative effect on population growth rate where using uncorrelated and correlated transition probabilities resulted in negative λs.

Table 4.3 A summary of scenarios used in modeling effects of environmental influences on *Oldenburgia* populations. Stochastic population growth rate for uncorrelated and correlated transition probabilities are shown where they are positive (λs >1) or negative (λs <1)

scenario	fire	fire frequency (years)	fire intensity	levels of seedling protection	fecundity	λs correlated	λs uncorrelated
1	no	-	-	-	observed min and max	1.0179	1.0122
2	no	-	-	-	low	1.0022	0.9998
3	yes	5	low	high	observed min and max	1.0005	0.9967
4	yes	5	low	low	observed min and max	0.9986	0.9938
5	yes	10	low	high	observed min and max	1.0054	1.0010
6	yes	10	low	low	observed min and max	1.0038	0.9996
7	yes	20	hot	low	observed min and max	0.9403	0.9661
8	yes	20	moderate	low	observed min and max	0.9992	0.9956
9	yes	5	low	high	high	1.0015	0.9989
10	yes	10	low	high	high	1.0066	1.0049

All scenarios resulted in negative lower bound confidence limits for stochastic population growth rate. The upper bound confidence intervals were positive for both correlated and uncorrelated transition probabilities in all for scenarios 1, 2, 3, 5, 6, 9 and 10 except Scenario 7. In Scenario 7 both upper and lower bound confidence limits were negative because fire intensity resulted in high mortality rates of mature and adult stages (Table 4.4).

Table 4.4 Upper and lower confidence limits for stochastic growth rate using uncorrelated and correlated transition probabilities

Scenario	*Correlated λs*		*Uncorrelated λs*	
	Upper CL	Lower CL	Upper CL	Lower CL
1	1.0223	0.9959	1.0165	0.9986
2	1.0039	0.9958	1.0010	0.9984
3	1.0054	0.9865	1.0001	0.9911
4	1.0032	0.9870	0.9760	0.9879
5	1.0102	0.9910	1.0048	0.9928
6	1.0076	0.9912	1.0016	0.9967
7	0.9433	0.8129	0.9682	0.9302
8	1.0047	0.9546	0.9972	0.9832
9	1.0063	0.9874	1.0020	0.9897
10	1.0111	0.9918	1.0091	0.9944

Population numbers projected over 500 years for each scenario reveal that four scenarios resulted in a positive trend with the population not becoming extinct within the 500-year projection. Modeling scenarios using correlated and uncorrelated transition probabilities show the same trends, therefore projected population numbers over time using correlated transition probabilities only are shown in Figure 4.5. For the purposes of comparing populations, a population with less than 10 mature and adult trees combined was considered extinct. Populations tolerate fire better at a 10-year interval (Scenarios 5 and 6) than at 5 years (Scenarios 3 and 4). Levels of seedling protection have an effect on the overall population growth rate in comparison between Scenario 3 and 4. If fecundity levels are high every year with fire frequency at between 5 and 10 years (Scenarios 9 and 10) the rate of population growth is positively influenced. However, high fecundity every year appears to be unrealistic when one considers data on Chapter 2.

The greatest detrimental effect on *O. grandis* populations is the high levels of adult and mature mortality associated with high fire intensities. Predicted population numbers crash at 17 years (Scenario 7) and at 71 years for moderate fire intensities (Scenario 8).

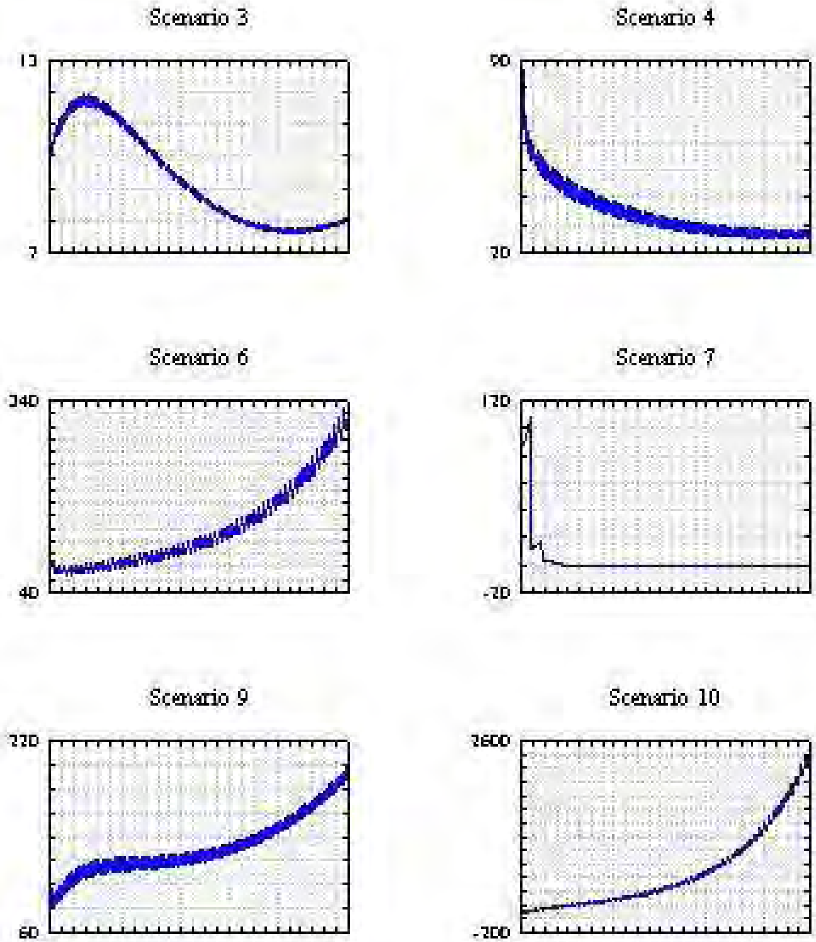


Figure 4.4 Projected population numbers over 500 years using correlated transition probabilities for all scenarios including fire (Scenarios 3 to 10)

Discussion

The use of positively correlated transition probabilities produces more variable differences between population growth rates in good and bad years (Brigham and Thompson 2003). Population increase, decline and structure show similar trends for correlated and uncorrelated transition probabilities. Positive and negative influences tend to be exaggerated for correlated transitions in this study, and the range (upper and lower limits) of stochastic growth rate is larger than for uncorrelated transitions. It is likely that the results from the correlated transitions are closer to reality as individuals experiencing the certain environmental conditions will be similarly influenced and additive effects will have an effect on the overall population growth rate but also result in an exaggeration of upper and lower confidence limits compared to uncorrelated transition probabilities.

<u>Population responses to stochastic environmental influences excluding fire</u>

Oldenburgia grandis is fairly insensitive to random stochastic events excluding fire such as adverse climatic conditions or low fecundity and seedling establishment although it is unlikely that results over the duration of this study could encompass all possible negative and positive environmental stochastic influences on the population. For long-lived species, the number of sampling years have to be sufficient to include fluctuations in recruitment levels, seedling growth rate etc (Brigham 2003). The model however does confirm the importance of persistence, particularly of the mature stages. Even when fecundity levels were decreased to below the observed minimum levels, the stochastic growth rate was not dramatically affected as long as there was no fire that resulted in high adult and mature stage mortalities.

<u>Population responses to stochastic effects including the effects of fire</u>

It was shown that the optimal frequency favouring *O. grandis* populations was an interval of 10 years. Populations are resilient to fire at shorter intervals but the protection of seedlings during a fire becomes an important consideration for population persistence. The model confirms the prediction that fire intensity (Chapter 2) resulting in high mortalities promotes extinction. Fires in late summer and early autumn are beneficial for most Fynbos species (le Maitre and Midgley 1992) but it is at these times when the intensities are the highest. Higher fire intensities can have adverse effects on sprouting species as seen in this study and other studies (van Wilgen and Richardson 1985). Lower fire intensities also favour species with shallow seed banks such as other Asteraceae species of the Fynbos Biome (le Maitre and Midgley 1992).

Model responses to changes in levels of fecundity

Fecundity in *O. grandis* has the lowest contribution, with growth to the population growth rate (Chapter 2). The stochastic model confirms that increasing fecundity for years with different fire intervals (Scenarios 3,4 and 9, 10) did not improve the stability of the rate of population growth.

Implications of the storage effect

This study has taken into account variation in mortality of the reproductive stages as well as variation in recruitment and reproduction often not separated out in PVA studies (Higgins et al. 2000). Variances have been simulated beyond the minimum and maximum observed transition probabilities. In this way, potential effects of the storage mechanism of *O. grandis* have been taken into account. Increasing the variance of recruitment does not result in increased population persistence although increasing the survivorship of seedlings after a fire results in increased stochastic rate of population growth when correlated rather uncorrelated transition probabilities are used. Increasing the variance of mortality of the reproductive stages does have a detrimental effect on the rate of population growth. If reproductive plants aren't able to persist after a fire, they cannot take advantage of good reproductive years.

Conservation implications based on the projections from the stochastic model are mirrored in the comparison between *Widdringtonia cedarbergensis* (Manders 1987) and *Oldenburgia grandis*. *O. grandis* has adapted to a fire-prone environment by the ability to store reproductive potential whereas *W. cedarbergensis* does not have this ability. *O. grandis* is therefore able to cope with frequent fires by persistence of the reproductive stages whereas an increase in fire frequency is likely to promote the extinction of *W. cedarbergensis* (Manders 1987). The opposite is true for fire intensity. Increased fire intensity is likely to promote extinction of *O. grandis* populations, but would not have a detrimental effect on *W. cedarbergensis* populations as reproductive individuals are easily killed by fire regardless of the intensity (Manders 1987).

CHAPTER 5 CONCLUSION AND FURTHER RESEARCH

Life history strategy of *O. grandis* and implications for conservation

The results of this study show that persistence of established populations is important for the persistence of the species. *O. grandis* has evolved life history traits that enable it to survive in a fire-prone environment where the investment of resources to the persistence of adult, mature and sapling stages is traded off against investment in growth and fecundity. In terms of the categories suggested when assessing the risks of extinction to a species suggested by Caswell (2001), the following applies to *O. grandis*:

Assessment

Oldenburgia grandis populations are capable of increasing in environments that experience climatic and environmental fluctuations including and excluding the effects of fire. This is provided that the stochastic variations are within the limits observed in this study. The resilience of the adult and mature stages to fire is high (Chapter 3) and the smaller stages are protected to some degree by the rock outcrops. Populations are capable of increasing in an environment with fire frequencies at a 10 year interval that have low intensities and the when seedlings in the population have high levels of protection from the rock substrate (Chapter 4).

Diagnosis

The population viability analysis in Chapter 4 shows that fire, while clearly a factor *O. grandis* has evolved with and typical of the vegetation type it inhabits is also a potential threat. Adult and mature mortalities are expected to be high as a result of high fire intensities. The cause of high fire intensities is dependent on deterministic and stochastic forces (Figure 5.1). Deterministic forces include the increase of biomass accumulation in two ways. 1) Mountain Fynbos vegetation that has accumulated biomass by not having burnt for a number of years. An example of this was seen at the Suurberg site where a population that had burnt in a Mountain Fynbos area had high numbers of dead adult and mature trees present in the sample. 2) The increase in biomass is due to the increase in densities of woody alien tree species. This increase may be due to overgrazing and poor land management practises in areas where *O. grandis* populations are found. Stochastic forces that could increase the intensity of a fire are hot, dry, bergwind climatic conditions. These two forces combined are likely to generate such fire intensities that completely destroy resources *O. grandis* individuals have stored to survive fires resulting in high adult and mature mortalities.

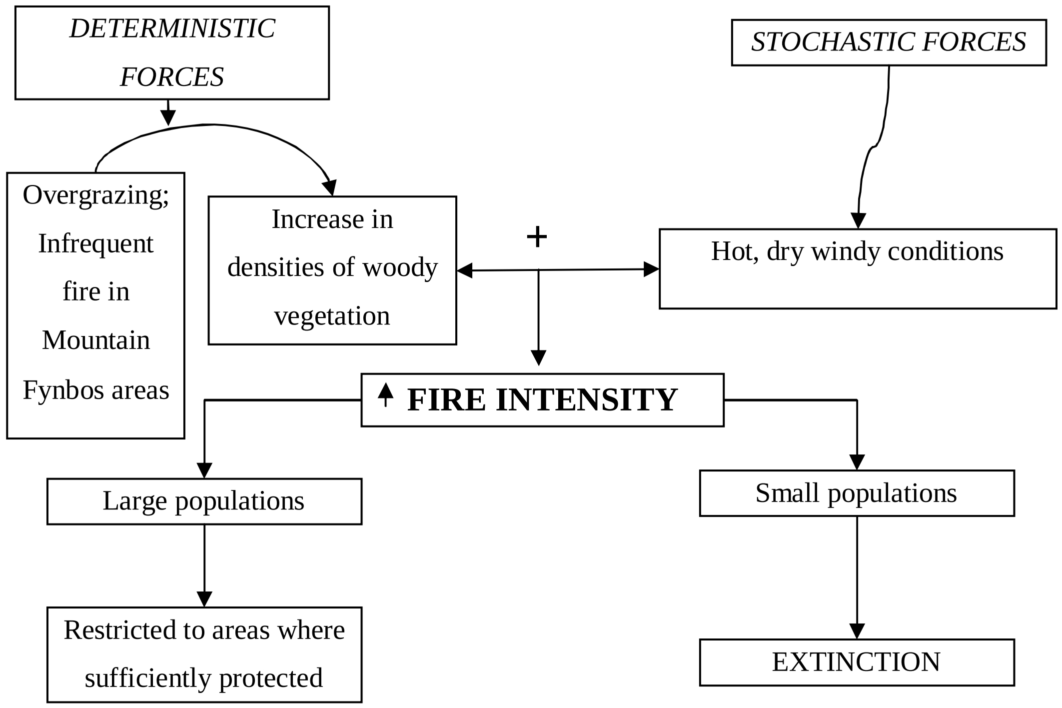


Figure 5.1 Diagram showing deterministic and stochastic forces that may threaten *O. grandis* populations. The combination of deterministic forces such as invasions of exotic vegetation increasing the woody biomass surrounding populations and adverse random stochastic environmental influences such as hot, dry, windy conditions may in turn result in fires with high intensities elevating levels of mortality in the adult and mature stages.

Small populations are likely to be at a higher risk of extinction compared to larger populations (Kruckeberg and Rabinowitz; Matthies et al. 2004). Low fecundities and scattered populations make it very unlikely that if a small population is wiped out it is able to re-establish itself.

Prescription

The focus of conservation for *O. grandis* should be on preserving and ensuring the persistence of populations, particularly the adult and mature stages in populations. The monitoring of small, scattered populations in Mountain Fynbos areas is particularly important. This should be incorporated into the vegetation management plan of the Suurberg Section of the Addo Elephant National Park. The locations of the smaller mapped populations from this study are available in GIS format and can be used in monitoring programs. It is imperative that monitoring programs include the keeping of accurate fire records, including spatial extent of fire preferably mapped at a suitable scale, season and climatic conditions at the time of fire.

Conservation focus should also be directed in the Eastern part of the range of *O. grandis*. It is in these areas that most *O. grandis* populations are not formally conserved. It is also in these areas where the invasions by woody aliens are the most prevalent. Prescribed alien vegetation clearing plans around *O. grandis* populations on private farms should be included in planning documents such as the *Oldenburgia* conservancy management plan. Emphasis should be placed on ensuring the persistence of established populations that cannot be restored or replaced if destroyed.

Prognosis

According to the IUCN assessment in Chapter 3, it is recommended that *O. grandis* remain in the lower risk, near-threatened category. This means that although not yet threatened, it is likely to become threatened in the future. Even though *O. grandis* is not yet considered threatened, landowners can still employ strategies to ensure the threatened status is not realised in the near future.

Further research recommendations

It is difficult to design management strategies for rare species where data on direct threats are not incorporated into the PVA. More extensive sampling is needed to determine the direct threats to *O. grandis* populations as well as information on the frequency of events that cause mortality in the adult and mature stages. Detailed analysis of the effects of exotic vegetation through increased fire intensities or inter-specific competition could be used to fine-tune conservation management recommendations for the species. It would be essential to determine if there are any correlations between the density of exotic vegetation surrounding a population and increased variance in mortality levels of the adult, mature and sapling stages.

A more detailed conservation assessment should include more samples to capture temporal variation in vital rates and to increase the number of observed transition probabilities between the life history stages. Rather than simulating environmental stochasticity by using a randomly generated environmental variable to generate correlated transition probabilities, more data years would determine observed correlations between vital rates. In this way, entire matrices could be randomly selected where the observed correlations between vital rates are maintained.

The digital GIS data collected during this study has been submitted to the Threatened Species Programme (a research division of the South African National Biodiversity Institute). It is therefore available to be used in the public domain for spatial planning projects. The GIS data from this study also serves as a source of baseline data for future monitoring efforts. Lindborg and Ehrlen (2002) suggest that PVA is a much more powerful tool when combined with long-term historical information. These data could be used for a historical assessment by locating historical photographs of *O. grandis* populations to determine population changes using repeat-photograph techniques.

Conclusion

Restriction of scattered *O. grandis* populations to rocky outcrops is a function of their ability to survive in particular microhabitats. *O. grandis* is also likely to be confined to Grassy Fynbos vegetation due to the risks associated with high fire intensities in areas with a higher woody biomass such as Mountain Fynbos areas. As a result, the distribution of *O. grandis* does not extend further west into the Fynbos biome. Restriction of the distribution of *O. grandis* in the east is likely to be linked to the limits of the fynbos biome and in particular the limits of the Suurberg Quartzite Fynbos vegetation.

REFERENCES

Acocks, J.P.H. (1988) Veld types of South Africa, *Memoirs of the Botanical Survey of South Africa* No 57 3rd Edition. Botanical Research Institute, South Africa.

Akçakaya, H.R. & Sjögren-Gulve, P. (2000) Population viability analysis in conservation planning: an overview. *Ecological Bulletins,* **48**: 9 – 21

Akçakaya, H.R., Burgman, M.A. & Ginzburg, L.R. (1999) Applied population ecology: principles and computer exercises using RAMAS EcoLab 2.0 2nd Edition – Sinauer, Sunderland, Massachusetts.

ArcView GIS Version 3.1. 1992 – 1998. Environmental Systems Research Institute, Inc.

Barbour, M.G., Burk, J.H. & Pitts, W.D. (1987) Terrestrial plant ecology. The Benjamin/Cummings Publishing Company, Inc.

Bellingham, P.J. & Sparrow, A.D. (2000) Resprouting as a life-history strategy in woody plant communities. *Oikos,* **89**: 409 – 416.

Benton, T.G. & Grant, A. (1999) Elasticity analysis as an important tool in evolutionary and population ecology. *Trends Evol. Ecol*., **14** (12): 467 – 471.

Bevill, R.L. & Louda, S.M. (1999) Comparisons of related rare and common species in the study of plant rarity. *Conservation Biology,* **13**: 493 – 498.

Bierzychudek, P. (1999) Looking backwards: assessing the projections of a transition matrix model. *Ecology,* **9**: 12781 – 287.

Bond, P. (1987) A revision of *Oldenburgia* (Asteraceae – Mutisieae). *South African Journal of Botany,* **53** (6): 493 – 500.

Bond, W.J. & Midgley, J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Evol. Ecol.*, **16** (1): 45 – 51.

Brigham, C.A. (2003) Factors affecting persistence in formerly common and historically rare plants. *In*: Population viability in plants. Brigham, C.A. & Schwartz, M.W. (eds*). Ecological Studies*, **165**: 59 – 97.

Brigham, C.A. & Thompson, D.M. (2003) Approaches to modelling population viability in plants: an overview. *In*: Population viability in plants. Brigham, C.A. & Schwartz, M.W. (eds*). Ecological Studies*, **165**: 145 – 171.

Cao, Y., Larsen, D.P. and Thorne, R.St-J. (2001) Rare species in multivariate analysis for bioassessment: some considerations. *J. N. Am. Benthol. Soc*. **20**: 144-153.

Caswell, H. (1989) Matrix population models: construction, analysis and interpretation. First Edition. Sinuaer Associates, Sunderland, Massachusetts.

Caswell, H. (2001) Matrix population models: construction, analysis and interpretation. Sinauer Associates, Sunderland, Massachusetts.

Clarke, K.R. & Gorley, R.N. (2006) PRIMER ver 6. User manual/tutorial, PRIMER-E, Plymouth UK.

Coulson, T., Mace, G.M., Hudson, E. & Possingham, H. (2001) The use and abuse of population viability analysis. *Trends Evol. Ecol.*, **16** (5): 219 – 221.

Cowling, R. (ed) (1991) The ecology of fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Cowling, R. & Richardson, D. (1995) Fynbos: South Africa's unique floral kingdom. Fernwood Press, Vlaeberg.

Cowling, R.M., Richardson, D.M. & Pierce, S.M. (1997) Vegetation of South Africa. Cambridge University Press.

Croeser, P.M.C. (1982) The conservation status of *Oldenburgia arbuscula* DC. (Compositae) Unpublished report for the Plant Science Department, Rhodes University.

D'Antonio, C. & Meyerson, L.A. (2002) Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis *Restoration Ecology,* **10** (4): 703–713.

Dennis, B., Munholland, P.L. & Scott, J.M. (1991) Estimation of growth and extinction parameters for endangered species *Ecological Monographs,* **61**: 1 15-1 43

de Kroon, H., van Groenendael, J. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology,* **81** (3): 607 – 618.

Drechsler, M., Lamont, B.B., Burgman, M.A., Akçakaya, H.R., Witkowski, E.T.F. & Supriyadi. (1999) Modelling the persistence of an apparently immortal *Banksia* species after fire and land clearing. *Biological Conservation* **88**: 249 – 259.

Desmet, P.G., Shackleton, C.M. & Robinson, E.R. (1996) The population dynamics and life-history attributes of a *Pterocarpus angolensis* DC. Population in the Northern Province, South Africa. *S. Afr. J. Bot*., **62** (3): 160 – 166.

Ellner, S.P., Fieberg, J., Ludwig, D. & Wilcox, C. (2002) Precision of population viability analysis. *Conservation Biology,* **16** (1): 258 – 261.

Enright, N.J., Franco, M. & Silvertown, J. (1995) Comparing life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. *Oecologia,* **104**: 79 – 84.

Enright, N.J., Marsula, R., Lamont, B.B. & Wissel, C. (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for resprouting shrubs. *Journal of Ecology,* **86**: 960–973.

Fieberg, J. & Ellner, S.P. (2001) Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters*, **4**: 244 – 266.

Fiedler, P.L. (1987) Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: LILIACEAE). *Journal of Ecology***,** **75**: 977 – 995.

Funk, V.A., Bayer, R.J., Keeley, S., Chan, R., Watson, L., Gemeinholzer, B., Schilling, E., Panero, J.L., Baldwin, B.G., Garcia-Jacas, N., Alfonso, S. & Jansen, R.K. (2005) Everywhere but Antartica: Using a supertree to understand the diversity and distribution of the Compositae. *Biol. Skr*., **55**: 343 – 374.

Gilpin, M.E. & Soulě, M.E. (1986) Minimum viable populations: the processes of species extinctions. *In*: Conservation Biology: the Science of Scarcity and Diversity. Soulě, M.E. (ed). Sinauer, Sunderland, Massachusetts. pp 13 – 34.

Given, D.R. (1994) Principles and Practice of Plant Conservation. Timber Press, Portland, Oregon.

Gledhill, E. (1981) Eastern Cape Veld Flowers. The Department of Nature and Environment Conservation of the Cape Province Administration, Cape Town.

Goldblatt, P. (1987) Chromosome cytology of *Oldenburgia* (Asteraceae – Mutisieae). *Annals of the Missouri Botanical Gardens*, **74** (2): 331 – 332.

Golding, J. (2002) Southern African Plant Red Data Lists. *South African Botanical Diversity Network Report* No. **14**. pp 2 – 11.

Grime, J.P. (1977) Evidence of the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169 – 1194.

Haigh, L. & Illgner, P. (2001) The Featherstone Kloof wetland: history, environment and rehabilitation. *Unpublished report*. Water Research Commission, Grahamstown.

Hanel, C. (1990) An ecological study on the germination and viability of *Oldenburgia grandis* seeds. *Unpublished 3rd year project*, Rhodes University.

Harper, J.L. (1977) Population Biology of Plants. Academic Press. London.

Harper, J.L. (1981) The meaning of rarity. *In*: The Biological Aspects of Rare Plant Conservation. Synge, H. (ed). John Wiley & Sons Ltd, Chichester pp 189 – 203.

Heppell, S.S., Caswell, H. and Crowder, L.B. (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81: 654 – 665.

Higgins, S.I., Pickett, S.T.A & Bond, W.J. (2000) Predicting extinction risks for plants: environmental stochasticity can save declining populations. *Trends Evol. Ecol.*, **15** (12): 516 – 520.

Hilton-Taylor, C. (1996) Red Data List of southern African Plants. *Strelitzia* **4**. National Botanical Institute, Pretoria.

Hoffman, W.A. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology*, **80** (4): 1354 – 1369.

Holmes, P.M., Richardson, D.M., van Wilgen, B.W. & Gelderblom, C. (2000) Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration *Austral Ecology*, **25** (6): 631–639.

Honnay, O. & Bossuyt, B. (2005) Prolonged clonal growth: escape route or route to extinction? *Oikos*, **108** (2): 427 – 432.

Hood, G. M. (2005) PopTools version 2.6.6. URL http://www.cse.csiro.au/poptools

Hunt, L.P. (2001) Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology*, **38**: 238 – 252.

IUCN. (1994) IUCN Red List Categories. Prepared by the Species Survival Commission. IUCN, Gland, Switzerland.

IUCN Red List Categories and Criteria, version 3.1 (IUCN Species Survival Commission, Gland, Switzerland, 2001)

Jones, S.B. & Luchsinger, A.E. (1987) Plant Systematics. McGraw-Hill.

Kaneko, Y., Takada, T. & Kawano, S. (1999) Population biology of *Aesculus turbinate* Blume: A demographic analysis using transition matrices on a natural population along a riparian environmental gradient. *Plant Species Biology*, **14**: 47 – 68.

Kenkel, N.C. & L. Orlóci. (1986) Applying metric and non-metric multidimensional scaling to ecological studies: some new results. *Ecology*, **67**: 919-928.

Kenkel, N.C., Derksen, D.A., Thomas, A.G. & Watson, P.R. (2002) Multivariate analysis in weed science research. *Weed Science*, **50**: 281 – 292.

Kleynhans, CJ, Thirion, C and Moolman, J (2005) A Level I River Ecoregion classification System for South Africa, Lesotho and Swaziland. Report No. N/0000/00/REQ0104. Resource Quality Services, Department of Water Affairs and Forestry, Pretoria, South Africa.

Kruckeberg, A.R. & Rabinowitz, D. (1985) Biological aspects of endemism in higher plants. *Annual Review of Ecology and Systematics*, **16**: 447 – 479.

Lacy, R.C., Borbat, M. & Pollack, J.P. (2003) VORTEX A stochastic simulation of the extinction process. Manual for Version 9. Chicago Zoological Society, Brookfield, Illinois.

Lande, R. (1988) Genetics and demography in biological conservation. *Science,* **241**: 1455 – 1460.

le Maitre, D.C. & Midgley, J.J. (1992) Plant reproduction ecology. *In*: The ecology of fynbos: nutrients, fire and diversity. Oxford University Press.

Lefkovitch, L.P. (1965) The study of population growth in organisms grouped by stages. *Biometrics,* **21** (1): 1 - 18.

Lennartsson, T. & Oostermeijer, J.J. (2001) Demographic variation and population viability in Gentianella campestris: effects of grassland management and environmental stochasticity. *Journal of Ecology,* **89**: 451 – 463.

Lindborg, R. & Ehrlén, J. (2002) Evaluating the extinction risk of a perennial herb: demographic data versus historical records. *Cons. Biol*., **16** (3): 683 – 690.

Lubke, R.A. & van Wijk, Y. (1998) Terrestrial plants and coastal vegetation. *In*: Field Guide to the Eastern & Southern Cape Coasts. Lubke, R.A. & de Moor, I. (eds). University of Cape Town press. Cape Town.

Ludwig, D. (1999) Is it meaningful to estimate a probability of extinction? *Ecology* **80**: 298 – 310.

Manders, P.T. (1987) A transition matrix model of the population dynamics of the Clanwilliam Cedar (*Widdringtonia cedarbergensis*) in natural stands subject to fire. *Forest Ecology and Management*, **20**: 171 – 186.

Matthies, D., Bräuer, I., Maibom, W. & Tscharntke, T. (2004) Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos,* **105**: 481 – 488.

McCarthy, T. & Rubidge, B. (2005) The story of earth and life: A southern African perspective on a 4.6-billion-year journey. Struik Publishers. South Africa.

McPeek, M.A. & Kalisz, S. 1993. Population sampling and bootstrapping in complex design: demographic analysis. Design and analysis of ecological experiments. Scheiner, S. & Gurevitch, J. (eds). Chapman and Hall, New York. Pp

Menges, E.S. (2000) Population viability analysis in plants: challenges and opportunities. *Trends Evol. Ecol*., **15**: 51 – 56.

Menges, E. & Dolan, R.W. (1998) Demographic viability of populations of *Silene regia* in Midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. *Journal of Ecology,* **86**: 63 – 78.

Menges, E.S. & Quintana-Ascencio, P.F. (2003) Modeling the effects of disturbance, spatial variation and environmental heterogeneity on population viability of plants. *In*: Population viability in plants. Brigham, C.A. & Schwartz, M.W. (eds). *Ecological Studies*, **165**: 289 – 307.

Microsoft ® (2000) Microsoft Corporation. Microsoft Office Professional.

Mills, L.S., Doak, D.F. & Wisdom, M.J. (1999) Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biol*., **13**: 815 – 829.

Moloney, K.A. (1986) A generalised algorithm for determining category size. *Oecologia*, **69**: 176 – 180.

Mucina, L., Rutherford, M.C. & Powrie, L.W. (eds) (2005) Vegetation map of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria

Murray, B.R., Thrall, P.H., Gill, A.M. & Nicotra, A. B. (2002) How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology*, **27**: 291 – 310.

Ojeda, F., Brun, F.G. & Vergara, J.J. (2005) Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. *New Phytologist*, **168**: 155 – 165.

Olivieri, E.T. (1977) An ecological study of the establishment of *Oldenburgia arbuscula* DC. On Witteberg Quartzite derived soils. *Unpublished Honours Thesis*. Rhodes University.

Oostermeijer, J.G.B. (2003) Threats to rare plant persistence. *In*: Population viability in plants. Brigham, C.A. & Schwartz, M.W. (eds*)*. *Ecological Studies*, **165**: 18 – 58.

Oostermeijer, J. G. B., Brugman, M.L., DeBoer, E. R and DenNijs, H.C.M. (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology,* **84**:153–166.

Coates – Palgrave, K. (1984) Trees of southern Africa. C. Struik Publishers, Cape Town.

Panero, J.L. & Funk, V.A. (2002) Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae). *Proc. Biol. Soc. Wash*., **115** (4): 909-922

Pfab, M.F. & Scholes, M.A. (2004) Is the collection of *Aloe peglerae* from the wild sustainable? An evaluation using stochastic population modelling. *Biological Conservation*, **118**: 695 – 701.

Pfab, M.F. & Witkowski, E.T.F. (1999) Fire survival of the Critically Endangered succulent, *Euphorbia clivicola* R.A. Dyer – fire-avoider or fie tolerant? *Afr. J. Ecol.*, **37**: 249 – 257.

Pfister, C.A. & Stevens, F.R. (2003) Individual variation and environmental stochasticity: implications for matrix model predictions. *Ecology*, **84** (2): 496 – 510.

Phillips, O., Vargas Nuñez, P., Monteagudo Lorenzo, A., Cruz Peña, A., Zans Chuspe, M.-E., Sánchez Galiano, W. (2003) Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology*, **91**: 757–775.

Primack, R.B. (1993) Essentials of Conservation Biology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Rabinowitz, D. (1981) Seven forms of rarity. *In*: The Biological Aspects of Rare Plant Conservation. Synge, H. (ed). John Wiley & Sons Ltd, Chichester pp 205 – 217.

Raimondo, D.C. & Donaldson, J.S. (2003) Responses of cycads with different life histories to the impact of plant collecting: simulation models to determine important life history stages and population recovery times. *Biological Conservation,* **111**: 345 – 358.

Ramula, S. & Lehtila, K. (2005) Matrix dimensionality in a demographic analysis of plants: when to use smaller matrices? *Oikos,* **111**: 563 – 573.

Reed, J.M., Scott Mills, L, Dunning Jr, J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S.R., Anstett, M-A. & Miller, P. (2002) Emerging issues in population viability analysis. *Conservation Biology,* **16** (1): 7 – 19.

Richardson, D.M., MacDonald. I.A.W., Holmes, P.M. & Cowling, R.M. (1992) Plant and animal invasions. *In*: The ecology of fynbos: nutrients, fire and diversity. Oxford University Press.

Ricklefs, R.E. and Schluter, D. (eds) (1993) Species Diversity in Ecological Communities. University of Chicago Press.

Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003) Current patterns of habitat transformation and future threats of biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation* 112: 63 – 85.

Salafsky, N. & Margoluis, R. (1999) Threat reduction assessment: a practical and cost-effective approach to evaluating conservation and development projects. *Conservation Biology,* **13** (4): 830 – 841.

Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwillie, C., Parker, I.M. & Bishop, J.G. (1994) Evaluating approaches to the conservation of rare and endangered plants. *Ecology*, **75**, 584 – 606

Schulze, R.E. (2001) South African Atlas of Agrohydrology and Climatology. Beta 1.002. Water Research Commission Publication. South African Department of Agriculture.

Schwartz, M.W. (2003) Assessing population viability in long-lives plants. *In*: Population viability in plants. Brigham, C.A. & Schwartz, M.W. (eds). *Ecological Studies*, **165**: 239 – 266.

Shea, K. & Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications,* **8** (3): 824 – 832.

Silva Matos, D.M., Freckleton, R.P. & Watkinson, A.R. (1999) The role of density dependence in the population dynamics of a tropical palm. *Ecology,* **80** (8): 2635-2650.

Silvertown, J. & Charlesworth, D. (2001) Introduction to plant population biology. 4th Edition. Blackwell Science Ltd.

Silvertown, J., Franco, M. & Harper, J.L. (eds) (1997) Plant life histories: ecology, phylogeny and evolution. Cambridge University Press.

Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. (1993) Comparative plant demography: relative importance of demographic components to the finite rate of increase in perennial plants. *Journal of Ecology,* **81**: 465 – 476.

Spellerberg, I.F. (1992) Evaluation and assessment for conservation. Ecological guidelines for determining priorities for nature conservation. *Conservation Biology Series.* Chapman and Hall, London.

South African National Biodiversity Institute (SANBI) 2007 http://www.sanbi.org/frames/researchfram.htm

StatSoft, Inc. (2004) STATISTICA (data analysis software system). Ver 7. www.statsoft.com

Theobald, D.M. (2003) Targeting conservation action through assessment of protection and exurban threats. *Conservation Biology*, **17** (6): 1624 – 1637.

van Wilgen, B.W. & Richardson, D.M. (1985) The effects of alien shrub invasions on vegetation structure and fire behaviour in South African fynbos shrublands: A simulation study. *The Journal of Applied Ecology*, (22) 3: 955-966.

van Wyk, A.E. & Smith, G.F. (2001) Regions of floristic endemism in southern Africa: a review with emphasis on succulents. Umdaus Press, Hatfield, South Africa.

van Wyk, B-E., Novellie, P.A., & van Wyk, C.M. (1988) Flora of the Suurberg National Park. 1. Characterization of major vegetation units. *Bothalia*, **18** (2): 211 – 220.

Vandermeer, J.H. & Goldberg, D.E. (2003) Population ecology: first principles. Princeton University Press

Vesk, P.A. & Westoby, M. (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology*, **92**: 310 – 320.

Victor, J.E. (2002) South Africa. *In*: Southern African Plant Red Data Lists. Golding, J. (ed). *South African Botanical Diversity Network Report* No. **14**. pp 93 – 94.

Warner, R.R. & Chesson, P.L. (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *The American Naturalist*, **125** (6): 769 – 787.