

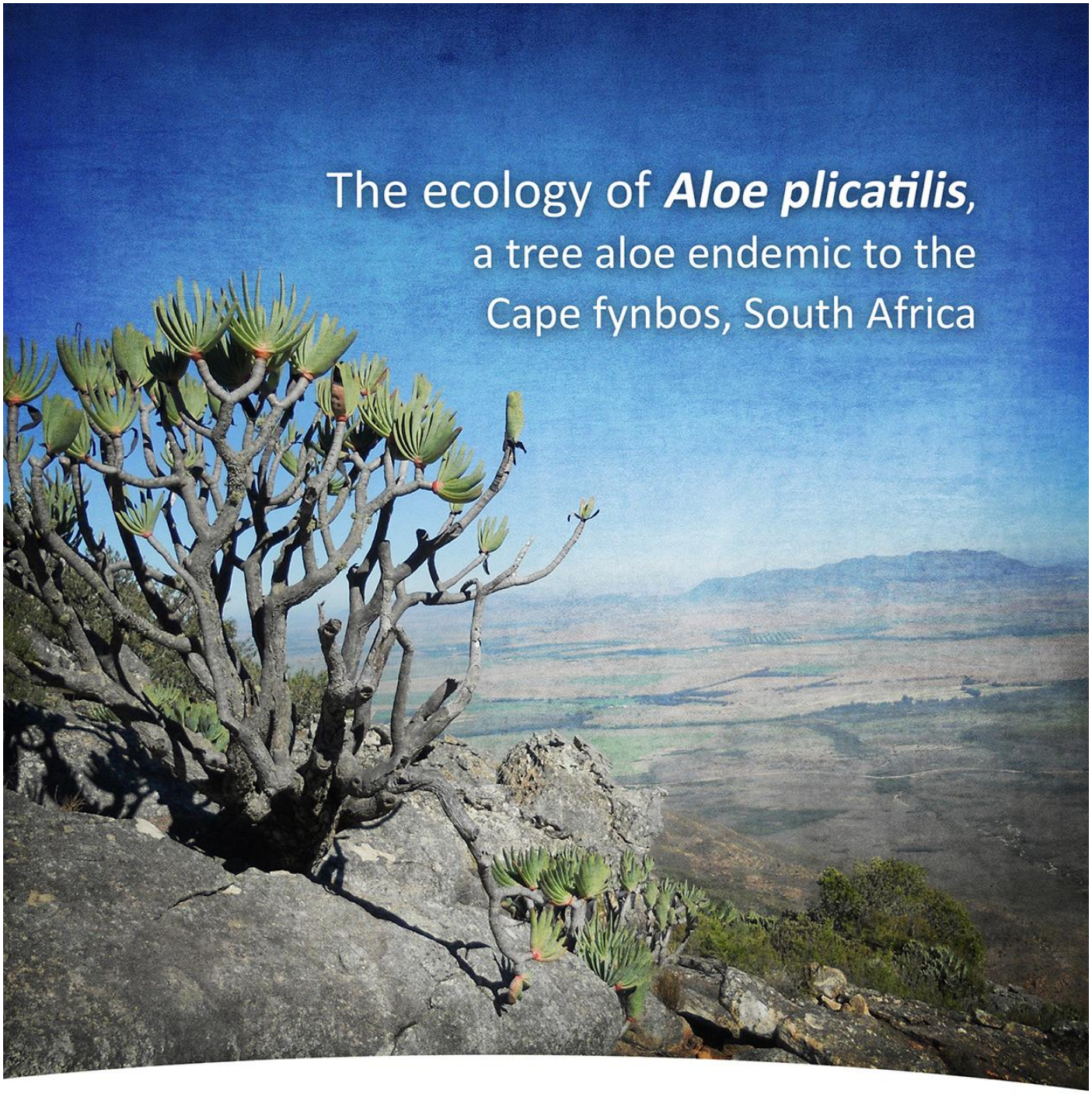
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The ecology of *Aloe plicatilis*, a tree aloe endemic to the Cape fynbos, South Africa

Master of Science Dissertation

Stephen Ross Cousins

UNIVERSITY OF THE WITWATERSRAND JOHANNESBURG

SANBI Biodiversity for Life

NRF National Research Foundation

CTI-B

THE ECOLOGY OF *ALOE PLICATILIS*, A TREE ALOE ENDEMIC TO THE CAPE FYNBOS, SOUTH AFRICA

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

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19 July 2013

School of Animal, Plant & Environmental Sciences
The Biology of a Changing World: Conserving African Biodiversity

DECLARATION

I, Stephen Ross Cousins, hereby declare that this dissertation is my own work. It is being submitted for a Master of Science degree at the University of the Witwatersrand, Johannesburg and has not been submitted before for any degree or examination in any other university.

Signature of candidate



Signed at_____Johannesburg_____ on the ___19th_____ day of ____July_____ 2013

ABSTRACT

Plant ecological studies at the population level on carefully selected single species provide key insights into their structural and functional ecology, but may also be extrapolated to enhance ecologists' understanding of other similar taxa, which ultimately contributes to the conservation and management of the group as a whole. Long-lived, slow-growing plants such as succulents and cycads, which are popular among plant collectors and often threatened as a consequence, are prime candidates for research owing to the considerable benefits to their conservation and management. *Aloe plicatilis* is a unique and charismatic arborescent succulent monocot that is endemic to the Cape Floristic Region, South Africa. It is restricted to mountainous areas in the Cape Winelands in the south-western Cape, and is the only tree aloe that occurs in the Cape fynbos. *Aloe plicatilis* is a prized species in the horticultural trade in succulent plants, and a recent spike in exports of the species from South Africa, including consignments of reportedly wild-collected plants, has raised concerns about its persistence in the wild.

Potential threats to *A. plicatilis* combined with a dearth of knowledge on the species' ecology prompted a broad-scale ecological study on the species, and an assessment of how potential threats may be affecting its survival in the wild. The primary aim of this study was to investigate three key elements of the ecology of *A. plicatilis*, viz. (1) demographic trends across the species' distribution, (2) the reproductive ecology of the species, and (3) its fire ecology. The study was first contextualized by compiling a comprehensive review of the ecology of African aloes. The objectives specific to *A. plicatilis* then involved determining the species' habitat profile, its geographical distribution, number of populations, and estimations of the sizes thereof. Further objectives entailed an assessment of the population size structure and density of a large proportion of *A. plicatilis* populations across the species' distribution, studies of its pollination and seed ecology, and an investigation of the species' fire survival and the impacts of fire on population structure. The study concludes with a synthesis that highlights and extrapolates the findings of the research and the implications these have for other *Aloe* species and similar long-lived, slow-growing plant taxa. Threats to the persistence of *A. plicatilis* in the wild are discussed, and recommendations are made for management, population monitoring and directions for future research.

Several of the knowledge gaps in aloe ecology highlighted in the review were investigated for *A. plicatilis* in this study, notably seed ecology, resprouting and fire ecology. The demographic study on *A. plicatilis* uncovered 14 previously undocumented populations, bringing the total currently known to 30. Fifty percent of the 19 populations surveyed for size structure, density and spatial extent exhibited bell-shaped size class distributions (SCD), which are hypothesized to indicate an adult-persistence

population survival strategy, typical of many long-lived, slow-growing plant taxa. This trend was reflected in the apparent lack of persistent seed banks in *A. plicatilis*, which suggests minimal 'drib-drab' recruitment over time as opposed to mass episodic recruitment. There appears to be a positive relationship between *A. plicatilis* population size and reproductive success. Quantification of natural fruit and seed set at three *A. plicatilis* populations revealed that large, dense populations exhibit higher seed production/plant relative to smaller and sparser ones, suggesting an Allee effect. Pollinators of the species (insects and specialist avian nectarivores) are probably attracted in greater numbers to large, dense populations where prolific food rewards and short inter-plant distances facilitate efficient floral visitation, and hence effective pollination.

Recruitment in *A. plicatilis* appears to depend on the alignment of numerous biotic and abiotic factors such as slope, aspect, temperature, quantity and timing of rainfall, fire occurrence, and the availability of suitable rocky microsites. These sites are of particular importance as they serve as fire refugia and provide nurse objects (nurse plants and/or nurse rocks), which create cool, shady conditions, where organic matter and moisture may accumulate, all of which appear to be essential to germination and establishment in *A. plicatilis*. As with most plant species, the large majority of *A. plicatilis* seeds are dispersed close to parent plants (estimated 1.3 – 15.3m for 0.8 and 4.0m in height respectively). However, the occurrence of *A. plicatilis* on Paarl Mountain and the Paardeberg, which are completely isolated from other mountain ranges where the species occurs, suggests the possibility of long-distance dispersal by strong, persistent and gusty summer winds that blow during the peak seed dispersal season.

Size structure analyses and detailed field observations suggest that *A. plicatilis* displays the 'bonsai effect', whereby plants growing in very rocky sites with restrictive rooting space and/or sites where they are exposed to persistent strong winds, are maintained as stunted individuals termed 'suppressed juveniles' or 'reproductive dwarfs'. However, rocky sites also act as fire refugia and provide nurse rocks, both of which are necessary for recruitment and persistence. Hence, there appears to be a trade-off between plant size and fire survival probability: individuals in very rocky sites are well-protected from fire, but often remain stunted and unreproductive, while plants in less rocky sites with more rooting space can attain larger sizes but are more vulnerable to fire damage. *Aloe plicatilis* is unique in that it is the only *Aloe* species that possesses thick, corky bark, which affords it additional fire protection. Its stems, leaves and bark also contain large water reserves, which may act as a fire retardant. Fire survival is heavily reliant on the prevention of hydraulic failure by the thick insulating bark and the protection of apical meristems, which facilitates onward apical growth, since *A. plicatilis* is incapable of epicormic or basal resprouting post-fire. Despite the species' fire survival adaptations,

A. plicatilis population size structure may be dramatically altered by fires, especially at sites where they have been excluded for periods longer than appropriate for the vegetation type.

The very recent name change from *Aloe plicatilis* to *Kumara plicatilis* has important conservation implications for the species. Recognition of the species' uniqueness by ascribing it to a monotypic genus may result in greater conservation efforts to preserve its sole genetic lineage; nonetheless, the inadvertent and unwanted consequence may be increased perceived rarity and desirability, and concomitant threats to the species' persistence in the wild. Illegal wild-harvesting of *A. plicatilis* does not appear to be posing a major threat to the species at present; however, monitoring of small and/or low-lying and easily-accessible populations is advised. The four smallest surveyed populations are also recommended for long-term monitoring due to poor or absent recent recruitment and vulnerability to climate change at the species' distribution edge. Appropriate management actions are recommended for twelve *A. plicatilis* populations that are under potential threat by invasive alien plant species encroachment.

The baseline data presented in this study serve as a foundation for future studies, which will build on current understanding of the ecology of *A. plicatilis*, other aloe species, and long-lived, slow-growing plant taxa in general. Opportunities for future research on *A. plicatilis*, (which also apply to other *Aloe* species) include: (1) a study on the long-term population dynamics of the species, which includes population modelling; (2) further studies on the species' pollination ecology, seed dispersal and recruitment patterns; (3) investigations into the physiological role that bark properties and plant tissue water content play in fire survival and (4) a predictive species distribution modelling study that models the current distribution of *A. plicatilis*, and how this might change under different climate change scenarios. Modelling Cape fynbos species distributions using climate change predictions is vital for adaptation and mitigation in the south-western Cape, where severe climate change impacts are forecast. Furthermore, deepened insight into the ecology of long-lived, slow-growing and potentially threatened plant species will contribute to predicting and understanding their responses to threats including climate change, which will ultimately lead to better management and conservation practises.

Key words: *Aloe plicatilis*, conservation, density, ecology, fire, fynbos, geographical distribution, horticultural trade, long-lived, pollination, reproduction, size class distribution, seeds, slow-growing

DEDICATION

This dissertation is dedicated to my grandmother,

Grace Muriel Miller,

(23rd November 1917 – 20th August 2012)

who played an integral and dearly-cherished role in my life.



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The person who undoubtedly deserves first mention in this section is my principal supervisor, Professor Ed Witkowski in the School of Animal, Plant & Environmental Sciences (AP&ES) at the University of the Witwatersrand, Johannesburg. The job he has done of supervising my Masters degree has been beyond outstanding and I truly cannot thank him enough for his excellent, excellent work. He has been extremely supportive academically, financially and on a personal level, and not once has he displayed any unwillingness to help. His enthusiastic and accommodating attitude has created a highly positive and conducive environment in which to work – something I believe will be difficult to match elsewhere. I express my deepest and most sincere gratitude to Prof. Witkowski and look forward to further collaborative projects with him in the future.

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CHAPTER ONE

1. Introduction

1.1. Study rationale

Succulent plants should be considered as priorities for conservation, since they are extremely popular with both local and international plant collectors and are often threatened as a consequence thereof (Pfab, 1997). Aloes are highly sought-after among succulent plant collectors (Smith et al., 2000), with the most desirable species including rare, morphologically distinctive and difficult-to-grow taxa (Grace, 2011). Prized species include the rare Lesotho endemic *Aloe polyphylla* Schönland ex Pillans, which has an unusual spiral-shaped leaf arrangement, and the Western Cape endemics *Aloe plicatilis* L. Miller and *Aloe haemanthifolia* A.Berger & Marloth, which are favoured for their atypical distichous leaves with rounded apices (Grace, 2011).

Aloe plicatilis is artificially propagated in South Africa and traded locally, but is also exported to several countries such as Australia, Japan and Italy primarily for use in the horticultural industry (CITES Trade Database). Although most *A. plicatilis* plants exported are reportedly artificially propagated, there is concern that illegal collection from the wild is also taking place. The trade statistics for *A. plicatilis* between 1980 and 2008 indicate that relatively few plants were exported from South Africa between 1980 and 2002 (most consignments comprised ≤20 plants) (Fig. 1). However, the period between 2003 and 2007 saw a major increase in the number of plants exported (Fig. 1). The recent spike in exports of the species including consignments of wild-collected plants has raised concerns about the persistence of *A. plicatilis* in the wild. Since the species has a limited distribution, and some of the populations are very small (<50 mature individuals), increases in wild harvesting are likely to have a deleterious effect on the species.

In light of the threats posed to *A. plicatilis* due to illegal wild harvesting, the species was flagged as a species of special conservation concern by the South African National Biodiversity Institute (SANBI) Scientific Authority. *Aloe plicatilis* was therefore listed as a priority species for research, which prompted an investigation into the trade in the species as well as its general ecology. The trade analyses are important to determine whether trade in *A. plicatilis* is detrimental to its survival in the wild and will also help establish harvesting quotas and develop a management plan for the species. Hence, this information, combined with data on the ecology of *A. plicatilis*, will contribute towards a Non-Detriment Finding (NDF) for the species.

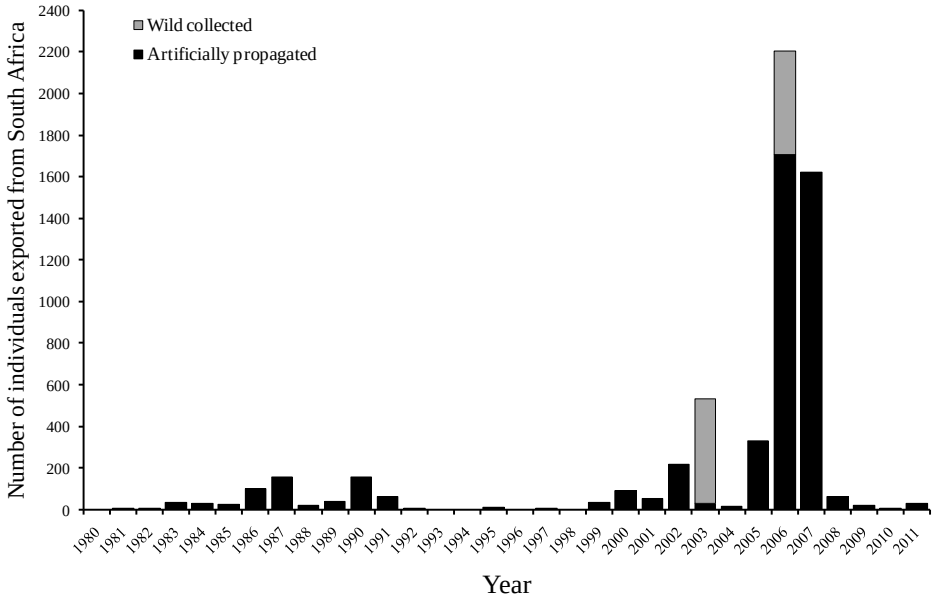


Fig. 1.1. Quantities of artificially propagated and wild collected *Aloe plicatilis* individuals exported from South Africa between 1980 and 2011. Data sourced from the CITES Trade Database 13/02/2013.

The primary motivation for this study was to gain an understanding of the ecology of *A. plicatilis* to provide baseline data on population counts, demographic trends, reproductive biology, the impacts of fire and harvesting and to assess other possible threats to persistence. This information will be useful for improved management and long-term monitoring and it will lay the foundation for future research on the species' ecology. In addition, it is important that the results from a study on an individual species can be extrapolated to benefit the conservation of other species (Hall et al., 1984). To this end, the study not only includes a review of aloe ecology, but also provides insights into important under-researched aspects of aloe ecology such as population structure, fire survival and resprouting, which will make a valuable contribution to our understanding of the ecology of the genus as a whole, as well as that of other long-lived, slow-growing taxa similar to *A. plicatilis*.

1.2. Literature review: General Plant Ecology

Plant ecological studies take place at various scales, from assessing ecophysiology at the individual plant level, to the ecology of populations, communities, ecosystems and landscapes, and ultimately to global patterns and processes (Schulze et al., 2002; Gurevitch et al., 2006). Ecophysiology explores the physiological and morphological adaptations of plants to their environment and includes studies on photosynthesis and the light environment, plant water relations, energy balance, below-ground interactions, and nutrient acquisition (Gurevitch et al., 2006). Of particular interest to plant ecologists who study ecophysiology is the ability of plants to tolerate stress. Plants are constantly subjected to

external influences, or environmental factors, which may be biotic (e.g. infection or herbivory) or abiotic (e.g. temperature or light intensity) (Schulze et al., 2002). When these environmental factors deviate from the optimal quantity or intensity suitable for growth, they become stress factors (Schulze et al., 2002). A researcher may, for instance wish to investigate the genes and regulatory mechanisms that govern cold acclimation in plants (e.g. Thomashow, 1999), or the effects of heat stress on a particular species (e.g. Lafta and Lorenzen, 1995). Ecophysiological studies may also seek to unravel the relationships between plant responses to stress at the cellular level and larger scale ecological phenomena, for example, the effects of freeze events on the demography of a plant population (e.g. Whitecross et al., 2012).

Studies at the population level typically investigate aspects such as plant life histories, population structure, population growth and decline, phenology, impacts of disturbance and strategies for reproduction (Schulze et al., 2002; Gurevitch et al., 2006; Crawley, 2007). A pollination ecologist, for example, may want to test whether small, isolated populations of a certain species exhibit compromised reproductive success compared to larger populations (e.g. Groom, 1998). Keystone plant species in reserves require effective population management, which necessitates an understanding of the way biotic and abiotic factors, e.g. herbivory and fire, affect plant population dynamics (e.g. Helm and Witkowski, 2012). Plant populations from which material is harvested for human use (e.g. Non-Timber Forest Products such as traditional medicine) require assessments of the impacts of harvesting on population health in order to ensure sustainable utilization (e.g. Botha et al., 2004). Studies that involve population modelling are particularly useful for predicting the impacts of harvesting different numbers of individual plants and/or plant parts from species that are popular either as Non-Timber Forest Products or collectors' items, e.g. cycads and succulents (e.g. Raimondo and Donaldson, 2003; Pfab and Scholes, 2004). The results from these studies can then be used to make recommendations regarding harvesting quotas for sustainable off-take.

Plant population ecology studies on rare and threatened species are crucial for determining population number and size (e.g. Pfab, 1997; Knowles and Witkowski, 2000). Information on changes in population statistics can then be used to update species' Red List statuses and implement relevant conservation measures such as population augmentation *in situ* (e.g. Tarlton, 2011) and population monitoring programmes. In addition, knowledge of plant species' distributions and abundances enables the identification of biodiversity hotspots for focussing conservation efforts (Myers et al., 2000). The questions and methods of population biology also hold promise for understanding and managing invasive alien plant species (Sakai et al., 2001). Studies on attributes of the population biology of invasive alien species such as flowering season and duration, seed production and dispersal, and potential for vegetative propagation, combined with demographic models, may be helpful for

identifying life history stages where management will be most successful (Sakai et al., 2001; Lloret et al., 2005). Furthermore, systems in which invasive alien species have pervasive affects on ecosystem level properties provide the basis for integrating the methods and approaches of population and ecosystem ecology (Vitousek, 1990).

At the levels of communities, ecosystems and landscapes, plant ecologists attempt to understand processes such as nutrient cycling, trophic dynamics, plant-herbivore interactions and mechanisms of plant competition, invasion, disturbance and succession (Chapin et al., 2002; Schulze et al., 2002; Gurevitch et al., 2006; Crawley, 2007). Knowledge of plant-herbivore interactions is key to the development of effective management plans in reserves, where large herbivores may have profound impacts on landscape vegetation structure, especially when present in large numbers and high densities (e.g. Teren and Owen-Smith, 2010). These impacts may include population declines in certain plant species, necessitating population monitoring studies to provide data for making management decisions. Other natural disturbances such as fire are important in shaping the vegetation patterns in fire-prone ecosystems, and anthropogenically-driven alterations to fire regimes (e.g. fire suppression) can lead to marked changes in population structure, vegetation structure and species composition (e.g. Luger and Moll, 1993).

Another field in which plant ecological research plays a pivotal role is ecosystem restoration. The global problem of biodiversity loss, primarily due to habitat destruction and non-native alien species invasions, renders ecosystem restoration an essential part of the survival strategy of humankind, which demands that restoration ecology provide effective conceptual and practical tools for this task (Hobbs and Harris, 2001). Careful native species selection is an important part of the restoration process, especially when alien species invasions must be constrained (Abella et al., 2012). Selection of the appropriate indigenous species for reintroductions requires a thorough understanding of the traits of the native and alien species concerned as well as the interactions between them (Abella et al., 2012). Similarly, surveys of the floristic composition of permanently anthropogenically-modified landscapes such as mine tailings and their surrounds help to determine which species are best adapted for colonizing these areas (Weiersbye et al., 2006), while germination and establishment trials are useful for identifying which of these species are suitable for introductions for stabilization and phytoremediation purposes (Weiersbye and Witkowski, 2002). Follow-up studies on the performance of (re)introduced native plants are essential for the success of restoration projects (e.g. Gómez-Aparicio et al., 2004).

Finally, plant ecological studies at the broadest scale assume global dimensions and examine trends in global biogeochemical cycles, human influences on these cycles, and global change (Chapin et al., 2002; Schulze et al., 2002; Gurevitch et al., 2006). With increasing awareness and concern about the impacts of climate change on biodiversity, considerable attention is being focused on the current and predicted changes in species distributions and the implications these changes have for conservation (e.g. Midgley et al., 2003; Fitzpatrick et al., 2008; Yates et al., 2010). Studies on shifting geographical distributions and changes in the abundance of so-called 'indicator species' help test hypotheses relating to climate change and its impacts on vegetation dynamics (e.g. Foden et al., 2007; Jack, 2012). By determining which species adapt easily to change and are therefore capable of range shifts, and which species are less adaptive and likely to go extinct, conservation efforts can be focused accordingly.

1.3. Context and relevance of this study in the field of Plant Ecology

This study focuses on a charismatic arborescent monocot succulent plant, *Aloe plicatilis*, at the population level. The core content of the study covers three major fields within the discipline of Plant Ecology, viz. population, reproductive and fire ecology. While the study examines the ecology of a single species, the results have a wider application within the field, especially to other long-lived, slow-growing plant species. Furthermore, the broad review of African aloe ecology that precedes the chapters that are specific to *A. plicatilis* makes a substantial contribution to the field of Plant Ecology by synthesizing current knowledge on the eminent and ecologically important genus *Aloe*.

1.4. Study species

Aloe plicatilis (L.) Mill. (Asphodelaceae: Alooideae) is one of six tree aloes indigenous to South Africa, and is the only tree aloe that occurs in the Cape fynbos (Van Wyk and Smith, 2008). It is a long-lived, slow-growing shrub to small tree, with dichotomously branching stems, each ending in a set of 12–16 alternate strap-shaped leaves displayed in a fan-shaped arrangement, hence its common name, the fan aloe (Fig. 1.2.) (Reynolds, 1969; Van Wyk and Smith, 2008; Carter et al., 2011). Most adult *A. plicatilis* individuals average 1.5–2 m in height, but exceptionally large plants may reach up to 5 m (Van Wyk and Smith, 2008). The species grows in well-drained, acidic soils on steep rocky slopes and rocky outcrops in areas of high winter rainfall (Van Wyk and Smith, 2008; Carter et al., 2011). *Aloe plicatilis* occurs at altitudes of 200–950 m, with average annual rainfall and temperatures of 420–1900 mm/year and 14–18°C, respectively (Mucina and Rutherford, 2006; Schulze, 1997). *Aloe plicatilis* is unique in that it is the only aloe that possesses thick, corky bark that offers protection against fires (Van Jaarsveld, 1989). Flowering takes place from August–October, with 25–30 tubular scarlet-coloured

flowers produced on laxly-flowered cylindrical racemes (Reynolds, 1969; Van Wyk and Smith, 2008). Between December and January longitudinally dehiscent capsules release relatively small, winged seeds which are wind-dispersed (Van Wyk and Smith, 2008). For more details on the species' description refer to the methods sections in chapters three, four and five, where photographs of the species are also presented.

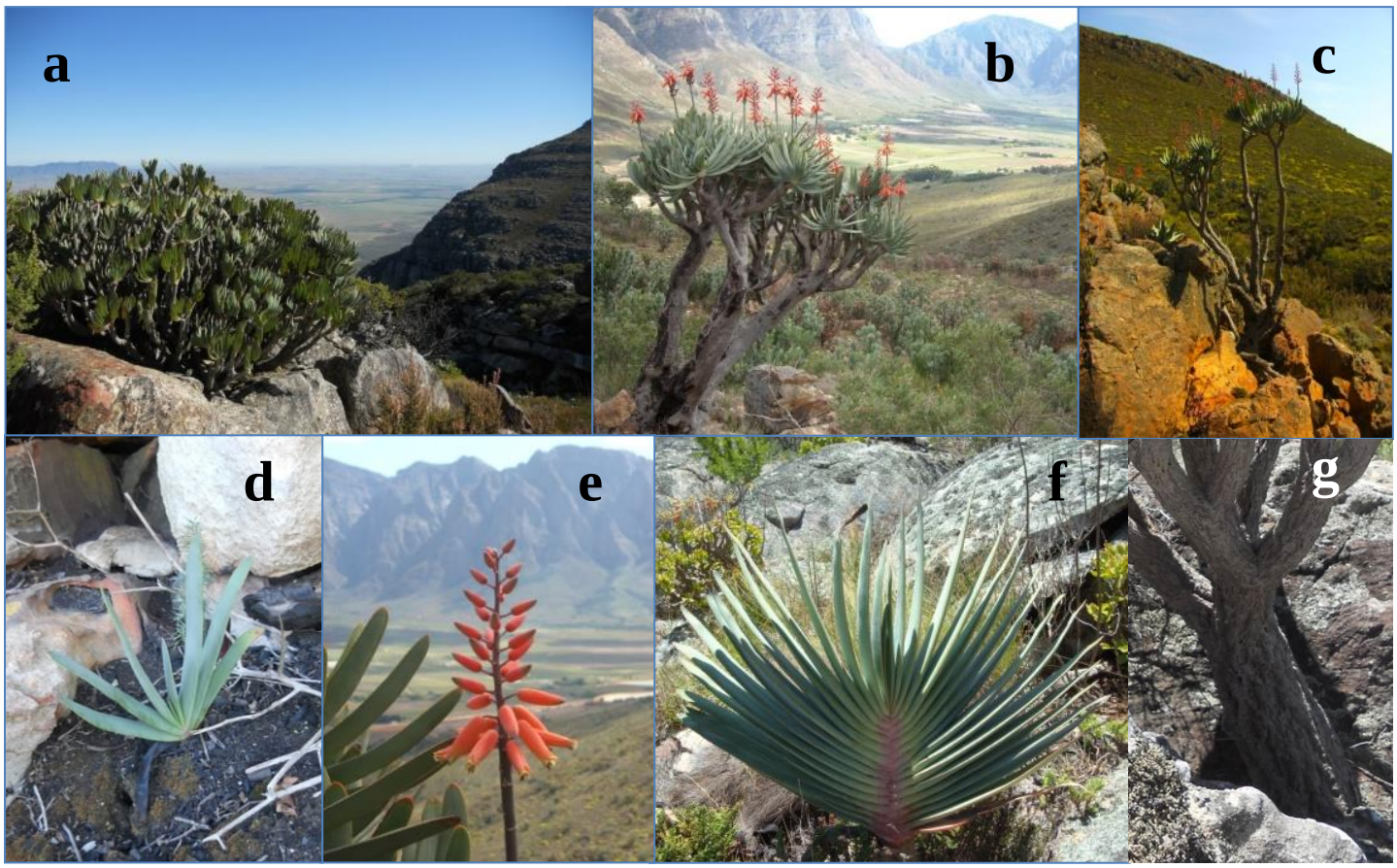


Fig. 1.2. (a) Large adult *Aloe plicatilis* individual on Saronskop near Tulbagh, showing a compact, shrubby growth form. This plant occurred on an exposed rocky slope where strong, persistent and gusty summer winds likely result in height limitations. (b) Large adult *A. plicatilis* plant growing in a site shielded from strong winds (large boulders were situated behind) at Goudini Badsberg near Rawsonville. (c) Tall, slender reproductive individual at Voorsorg near Rawsonville. A harsh microclimate at the site (high summer average annual temperatures and low average annual rainfall compared to other populations) has resulted in sparsely-branched plants with small leaf clusters. (d) Juvenile *A. plicatilis* individual on Saronskop. (e) Mature *A. plicatilis* inflorescence. (f) Juvenile A. plicatilis plant on Paarl Mountain illustrating the distichous leaf arrangement that is characteristic of the species. (g) Stem morphology of a mature *A. plicatilis* individual showing the species' thick, corky, fissured bark.

1.5. Taxonomic designation

Chase et al. (2009) proposed that the family Asphodelaceae (which includes two subfamilies, viz. Asphodeloideae and Alooideae, with the genus *Aloe* incorporated into the latter) be placed within the Xanthorrhoeaceae, with *Aloe* allocated to the subfamily Asphodeloideae. However, in the present study, the designation Asphodelaceae subfam. Alooideae is retained in line with the view adopted by PRE (South African National Herbarium, Pretoria), that the Asphodelaceae and Xanthorrhoeaceae (which includes grass trees from Australia) are morphologically distinct and should not be combined.

In a very recent reclassification of the traditionally broadly defined genus *Aloe*, Grace et al. (2013) proposed a narrower generic concept for *Aloe sensu stricto*, which included the recognition of segregate genera to reflect accumulating evidence for monophyletic groups. In this taxonomic revision, the genus *Kumara* Medikus (1786: 69) was reinstated, with *Kumara disticha* Medik. (=*Aloe plicatilis*) as the only species in the genus. This reclassification reflects the segregation of *A. plicatilis* from true aloes and other tree-like aloes in the tree topology presented in Treutlein et al. (2003) and the cladograms in Daru et al. (2013). Grace et al. (2013) also proposed the establishment of the new genus *Aloidendron*, which includes all six other tree-like aloes besides *A. plicatilis.* However, in an even more recent publication on generic concepts in the Alooideae, Rowley (2013) points out that Grace et al. (2013) mistakenly adopted the name *Kumara disticha* Medik., since *plicatilis* is the priority name at the rank of species. Hence, the taxon's newly adopted name is *Kumara plicatilis* (L.) G.D. Rowley n. comb.

Parts of this dissertation were published/in press, and the vast majority already written, prior to the name change from *Aloe plicatilis* to *Kumara plicatilis* in 2013; hence, in order to maintain the validity of comparisons with other *Aloe* species throughout the text, the species' former name, *Aloe plicatilis* (L.) Mill. (Grace et al., 2011) has been retained.

1.6. Study area

Aloe plicatilis is endemic to the Cape fynbos in mountainous parts of the Cape Winelands (also known as the "Boland") within the Cape Floristic Region (CFR), south-western Cape, South Africa (Van Wyk and Smith, 2008). The CFR is characterized by a Mediterranean climate with hot, dry, windy summers (average midsummer temperatures = 15–25°C) and cool, wet winters (average midwinter temperatures = 7–15°C) (Manning, 2007; Keeley et al., 2012). Fynbos vegetation is fire-dependent, and fire plays a crucial role in shaping major vegetation patterns in the region (Manning, 2007; Keeley et al., 2012).

Fynbos has a crown fire regime and is extremely flammable when dry, with fires occurring primarily during summer, at intervals of 10–30 years depending on the vegetation type (Keeley et al., 2012).

Aloe plicatilis has a restricted geographical distribution that extends from the Franschhoek Mountains near Vyeboom northwards to the Elandskloof and Grootwinterhoek Mountains near Tulbagh (Van Wyk and Smith, 2008). East to west, it occurs from the Du Toit's Kloof Mountains near Rawsonville/Worcester to the Paardeberg between Malmesbury and Wellington. *Aloe plicatilis* occurs mainly in Hawequas and Kogelberg Sandstone fynbos, but some populations are also found in Granitic vegetation types (Mucina and Rutherford, 2006). The major mountain ranges within its distribution are dominated by Table Mountain sandstone, which is acidic and poor in nutrients (particularly nitrogen and phosphorus), with outcrops of Cape granite to the west and southwest (Witkowski and Mitchell, 1987; Manning, 2007). Most *A. plicatilis* populations are found in mountain catchment and conservation areas, but some also occur on privately-owned land.

1.7. Conservation status and threats to *Aloe plicatilis*

Aloe plicatilis is classified as Least Concern (LC) on the 2009 IUCN Red List (Raimondo et al., 2009); however, although it is not threatened, it should be protected owing to its limited natural distribution (Van Wyk and Smith, 2008). In a Detailed Species Report compiled for the South African National Biodiversity Institute (SANBI) Threatened Species Program (TSP), Agenbag and Helm (2008) noted that *A. plicatilis* would benefit from both a survey of the global population and population monitoring as it could possibly qualify under the "C" criterion on the IUCN Red List (i.e. small population size and decline) if any declines could be detected. The highly specific habitat requirements of *A. plicatilis* – well-drained acidic soil on steep rocky mountain slopes – have safeguarded it to a degree from the farmlands and forestry plantations that often extend around the localities where it occurs (Agenbag and Helm, 2008). Two potential threats to the persistence of *A. plicatilis* in the wild are illegal harvesting of wild plants for the horticultural trade (M.F. Pfab, pers. comm.) and the encroachment of invasive alien species such as pines and Australian *Acacia* and *Hakea* species (Agenbag and Helm, 2008). However, the impacts of invasive alien plant species on *A. plicatilis* are relatively minimal at present (personnel observations), as they are either being actively managed or, in the case of the invading pine seedlings, burned by fires before they grow large enough to pose any serious threat (Agenbag and Helm, 2008).

1.8. Aim and objectives

The primary aim of this study was to investigate three key elements of the ecology of *Aloe plicatilis*, namely (1) demographic trends across the species' distribution, (2) its reproductive ecology, and (3) fire ecology.

The objectives were to:

i) Provide a broad review of the ecology of African *Aloe* species to contextualize the ecology of *A. plicatilis* (Chapter two).

ii) Determine the habitat profile of *A. plicatilis* (including geology, aspect, altitudinal range, vegetation type, rainfall and temperature) (Chapter three).

iii) Determine the geographical distribution and number of populations of *A. plicatilis* and estimate the size of each population and globally (Chapter three).

iv) Determine the population size structure and density of a large proportion of *A. plicatilis* populations (Chapter three).

v) Investigate the reproductive biology of *A. plicatilis* (including flowering, pollination, fruit and seed production, seed dispersal and germination) (Chapter four).

vi) Investigate the fire ecology and resprouting response of *A. plicatilis*, including habitat suitability and plant traits that confer fire survival, the impacts of a natural fire on population structure, and post-fire sprouting and resprouting after stem removal (Chapter five).

vii) Provide a synthesis of all studied aspects of the ecology of *A. plicatilis* highlighting and extrapolating the findings and the implications these have for other *Aloe* species and other long-lived, slow-growing plant taxa. (Include, in addition, management and population monitoring recommendations, and directions for future research.) (Chapter six).

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DISSERTATION STRUCTURE

Chapter one comprises a general introduction that contextualizes the study, and a statement of the project rationale, aims and objectives. The introduction begins with an outline of the different fields of study within the discipline of Plant Ecology, and highlights the position of the current study within the discipline. The chapter then provides background information on the study area and the study species (*Aloe plicatilis*), its taxonomic designation, and its conservation status. Chapters two to five have been written as stand-alone scientific papers, all of which have one or more co-authors. Chapters two and four were published in Journal of Arid Environments and South African Journal of Botany respectively. The third chapter has also been submitted to South African Journal of Botany, while chapter five is planned for submission to Austral Ecology. Consequently, there is a degree of repetition between chapters, but this is limited primarily to the methods sections.

Chapter two provides a broad review of the ecology of African *Aloe* species. Although it is a stand-alone chapter and published review paper, it forms part of the introduction to the succeeding chapters that deal with the ecology of *A. plicatilis* specifically. The first author was responsible for collecting and reading all the relevant literature, for synthesizing the information and writing the manuscript, and for producing the tables and figures. The second author provided comments and suggestions on drafts of the paper with regard to its content, formatting, style and grammar, both before submission to the journal and during its revision.

The third chapter investigates the trends in the population structure and density of a subset of *A. plicatilis* populations across the species' distribution. Chapter four deals with the reproductive ecology of *A. plicatilis*, focusing primarily on its pollination and seed ecology. The fifth chapter covers the fire ecology of *A. plicatilis* and includes an assessment of the demographic impacts of a natural fire on population structure and an investigation of the roles that habitat occupation and plant traits play in fire survival. For chapters three to five, the principal author was responsible for the experimental design, data collection (field work and/or laboratory work), data analysis, production of tables and figures, and write-up. As with chapter two, the co-authors commented on components of the manuscripts at various stages of their development. The only exception was Chapter four, where the fourth co-author did not review the manuscript, but conducted the germination experiments under nursery conditions at the Karoo Desert National Botanical Garden in Worcester.

The final chapter provides a synthesis of the preceding chapters and includes management and population monitoring recommendations for *A. plicatilis*, as well as directions for future research. A popular article on the study entitled "Fanfare in the fynbos: *Aloe plicatilis*, a unique Western Cape tree aloe", published in Veld and Flora, appears in Appendix I.

CHAPTER TWO

African aloe ecology: A review

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2.1. Abstract

Aloe L., is the largest genus in the Asphodelaceae, a family of succulent-leaved, petaloid monocots, geographically restricted to the Old World. Aloes exhibit remarkable morphological variability and range in size from dwarf species only a few centimetres tall to tree aloes reaching heights of 20m. Aloes form a striking and important component of many arid and semi-arid African landscapes. Most aloe species occur in arid savanna, which is widespread over subtropical southern and eastern Africa. In southern Africa, aloes receive considerable interest from both scientists and succulent plant enthusiasts. World-renowned for their medicinal properties, aloes are used in numerous natural products traded in the health and cosmetic industries. There is a wealth of popular literature on aloes, as well as various scientific publications, although these have tended to focus on aloe pollination biology and medicinal use. Knowledge on aloe ecology is vital for the management and conservation of wild populations as well as the arid and semi-arid lands in which they occur. Sound ecological understanding of the genus is also important for making decisions regarding sustainable utilization, as well as predictions relating to possible threats posed by climate change, and the utility of the genus in practical applications such as ecosystem restoration. Hence, this review provides a synthesis of a wide range of available information on several aspects of aloe ecology, and highlights opportunities for future research. The key aspects covered include aloe distribution, ecophysiology, functional role in the ecosystem, population dynamics, fire tolerance, resprouting, pollination ecology, seed biology, economic botany and conservation.

Key words: conservation, economic botany, ecophysiology, fire, pollination, population structure, resprouting, seeds

2.2. Introduction

Aloes are among the most familiar of the world's succulent plants, and form a conspicuous element of the African landscape, occupying a wide range of habitats and assuming various growth forms (see Appendix) (Holland, 1978; Van Jaarsveld, 1987; Van Wyk and Smith, 2008; Smith and Van Wyk, 2009). Aloes are well-represented in southern Africa and especially South Africa, where they form an important component of the local flora from taxonomic, ethnomedicinal, chemical/chemotaxonomic, ecotouristic and horticultural perspectives (Smith et al., 2000). Hence, this unique group of succulent plants provokes wide-ranging interest among both scientists and plant collectors (Smith et al., 2000; Smith and Van Wyk, 2009). Medicinal use of aloe leaves dates back thousands of years, and today aloes are world-renowned as a source of natural products derived from the leaf exudate and mesophyll (Dagne et al., 2000; Grace et al., 2009). The genus name *Aloe* is derived from the Arabic word *alloeh*, which translates to 'a shiny bitter substance' in reference to the exudate (Dagne et al., 2000). Trade in wild and cultivated aloes for health products is central to the livelihoods of many people in arid and semi-arid lands where the cultivation of conventional crops is unfeasible. Aloes also have the ability to act as nurse plants in degraded ecosystems and have therefore shown significant potential for use in ecosystem restoration (King, 2008; King and Stanton, 2008).

Their unique aesthetic appeal, relative ease of cultivation, and marked ability to hybridize has endowed aloes with considerable popularity amongst gardeners and succulent enthusiasts (Van Wyk and Smith, 2008). Consequently, aloes are well-entrenched in the popular literature and numerous publications document the various taxa and their means of cultivation (Holland, 1978). Numerous scientific studies have been conducted on aloe pollination biology, medicinal use, population dynamics, and to a lesser extent, other ecological aspects such as fire survival. However, a comprehensive synthesis of these studies, highlighting opportunities for further research is lacking. Hence, the primary aim of this paper is to assemble and integrate information on the general ecology of African aloes from a wide range of sources, and make recommendations regarding future studies to address areas where ecological understanding is limited.

2.3. Distribution

The genus *Aloe* Linneus, (Asphodelaceae: Alooideae) comprises a total of 548 accepted species (Grace et al., 2009), the majority of which (±350) are found in Africa and concentrated in southern and eastern Africa as well as Madagascar (Fig.1) (Knapp, 2006; Klopper and Smith, 2007; Crouch et al., 2009). The centre of highest diversity lies south of the Kunene, Okavango and Limpopo Rivers in southern Africa (Smith and Van Wyk, 1991). With approximately 140 aloe taxa, South Africa has the largest number of aloes of any African country (Klopper and Smith, 2007; Crouch et al., 2009; Klopper et al., 2009). Other centres of diversity include parts of West Africa, the East-Afro Arc of tropical southern Africa (Fig. 1), Saudi Arabia and Yemen (Smith et al., 2000). Aloes are also found on several Indian Oceanic islands such as the Mascarene Islands (Mauritius and Réunion), Comoros, Seychelles, Pemba and Socotra (Fig. 1) (Smith and Van Wyk, 2009). The cosmopolitan *A. vera*, which is thought to have originated in Saudi Arabia, has been traded for leaf exudate since the fourth century BC, resulting in the species' movement along trade routes from the Arabian Peninsula to the Mediterranean, Indian subcontinent, the Americas and the Caribbean, where it has become naturalised (Grace, 2011). Apart from *A. vera*, there do not appear to be many *Aloe* species that have become alien invaders outside their natural distributions.

Aloes are generally associated with dry habitats, however, they are also well-represented in subtropical summer rainfall and winter rainfall regions (Van Jaarsveld, 1989). The majority of species occur in arid savanna, which is widespread over subtropical southern and eastern Africa (Van Jaarsveld, 1989). Aloes occupy a wide array of habitats, from closed-canopy forests to desert shrublands, and occur from sea level to altitudes of 2700m (West, 1974; Holland, 1978; Sachedina and Bodeker, 1999). Individual species, however, tend to be geographically restricted (West, 1974; Holland, 1978; Sachedina and Bodeker, 1999). The three primary factors influencing the distributions of *Aloe* species are fire tolerance, moisture (rainfall and soil moisture), and temperature (frost tolerance) (Jordan, 1996). It has also been suggested that their distributions are affected by the presence of specific pollinators and by seed morphology (Jordan, 1996). Some aloe seeds have large, efficient wings that aid dispersal, and may account for their widespread distributions (e.g. *A. excelsa*) (Kamstra, 1971; Jordan, 1996). Others produce wingless seeds, presumably limiting their dispersal, thus resulting in dense stands of plants in localised areas (e.g. *A. aculeata*) (Kamstra, 1971; Jordan, 1996).

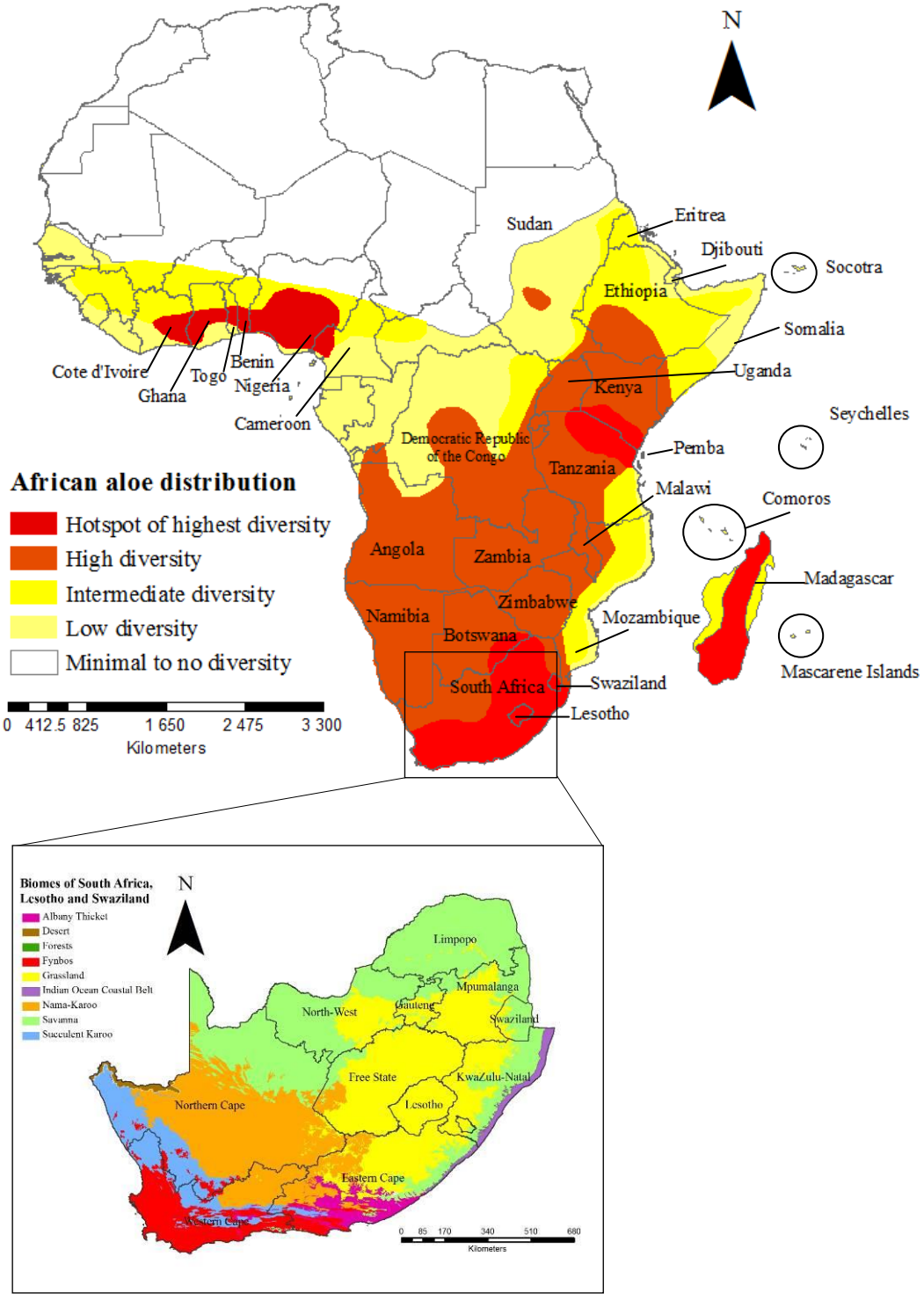


Fig. 1. Map showing the distribution of aloes on the African continent and several Indian Oceanic islands. Hotspots of high aloe diversity occur in Madagascar, East and West Africa, and especially southern Africa. Enlarged map of South Africa, Lesotho and Swaziland shows the provinces of South Africa and major vegetation biomes in the region. Aloes occur in all the biomes indicated. Note: the map of Africa was adapted from the aloe distribution maps in Smith and Van Wyk (2009) and Carter et al. (2011), neither of which included political boundaries. While the political boundaries in this map give an indication of the countries in which aloes occur, the distribution hotspot polygons were not constructed using exact point locality data. These hotspot ranges should therefore be seen as broad regions of aloe diversity rather than distinct distribution bands.

2.4. Anatomy and ecophysiology

2.4.1. Anatomy

All *Aloe* species are perennial, monoecious, shallow rooted, long-lived succulent plants (up to ca. 150 years in some species) (Smith and Van Wyk, 2009). Aloes flower primarily during winter and produce large quantities of small, air-borne seeds and many species also propagate asexually by forming suckers at their base (Holland, 1978; Smith and Van Wyk, 2009; Wabuyele and Kyalo, 2008). All aloes are characterised by fleshy, tapering, spiny-margined leaves that are boat-shaped in cross-section and arranged in rosettes or spirals (Morton, 1961; Van Jaarsveld, 1989; Smith and Van Wyk, 2009). Aloes produce a bitter-tasting exudate just below the surface of the leaves which provides a means of chemical defence against herbivores (Van Jaarsveld, 1989; Sity, 2009). Most aloes also possess spines along their leaf margins and occasionally throughout the leaf surface as mechanical defense (Van Jaarsveld, 1989; Sity, 2009). Other species lack an armature of spines, but are well camouflaged and therefore difficult for herbivores to detect (e.g. grass aloes) (Van Jaarsveld, 1989). Aloes usually produce racemose inflorescences that bear tubular flowers; however, other inflorescence types include many-flowered spikes and compound racemes or panicles (Van Jaarsveld, 1989; Smith and Van Wyk, 2009).

Aloes are closely related to the genera *Gasteria*, *Haworthia* and *Kniphofia*, which also have racemose inflorescences, tubular flowers and, usually, succulent leaves (West, 1974). The genus *Aloe* exhibits extensive morphological variability and various growth forms include single-stemmed, multi-stemmed, tree, creeping, rambling and stemless rosette types (Fig. 1) (Holland, 1978; Van Wyk and Smith, 2008; Klopper et al., 2010). Aloes range in size from dwarf species only a few centimetres high (e.g. *A. longistyla*), to giant 20m tall tree aloes (e.g. *A. barberae*) (Van Jaarsveld, 1989; Knapp, 2006; Crouch et al., 2009). (See Appendix 1 for photographs of representative species of the 10 aloe growth forms *sensu* Van Wyk and Smith (2008)). Grass aloes have leaves that closely resemble the blades of true grasses (Smith and Crouch, 2010), and some species (e.g. *A. bullockii*, A. *buettneri* and *A. kniphofioides*) possess underground bulbous stems consisting of fleshy leaf bases (Bornman and Hardy, 1971; Van der Riet, 1977; Van Jaarsveld, 1989). Morphologies often vary considerably with environmental conditions, and sometimes taxa appear to intergrade (Smith and Van Wyk, 1991).

2.4.2. Ecophysiology

2.4.2.1. Plant water relations

Water stored in fleshy leaves, stems, or occasionally fleshy, fusiform roots enable aloes to survive dry seasons or cyclical droughts (Van Jaarsveld, 1989; Newton, 2008). Many aloes use the CAM (Crassulacean Acid Metabolism) photosynthetic pathway that minimizes water loss that would otherwise occur with standard photosynthesis in hot climates (Denius and Homann, 1972; Sity, 2009). Aloes also possess waxy coated leaf surfaces that further prevent moisture loss by reflecting excess sunlight and minimizing evaporation from cells on the leaf surfaces (Van Jaarsveld, 1987; Sity, 2009). Adventitious root systems that grow only a few centimetres below the soil surface allow aloes to benefit from relatively low amounts of precipitation (Smith and Van Wyk, 2009; Jack, 2012). Some *Aloe* species are exceedingly drought-resistant, e.g. *A. globuligemma*, which has been reported to survive for twenty-three consecutive months with no measurable rainfall in Matabeleland, Zimbabwe (Ewbank, 1978). It is suggested that the dense accumulation of dead leaves around the base of stemless aloes such as *A. globuligemma* results in a lower soil surface temperature and the deposition of dew within reach of the shallow roots, thereby enabling the plants to survive long periods of drought (Ewbank, 1978).

Flach et al. (1995) studied the transpiration and water uptake of *A. jucunda* under variable environmental conditions. Findings showed that high water vapour saturation deficits coupled with increases in the ambient air temperature resulted in a rapid increase in transpiration, but only a minor change in water uptake (Flach et al., 1995). Water loss exceeding uptake was buffered by internal water reserves which refilled within a day after relief from heat and drought stress (Flach et al., 1995). While internal water reserves undoubtedly enable aloes to survive drought conditions, they do require periodic rainfall events to replenish depleted water reserves, and hence generally do not inhabit exceptionally dry areas such as the Sahara Desert.

2.4.2.2. Radiation requirements

Almost without exception, aloes require full sun, especially as mature plants. However, aloe seedlings are sensitive to harsh, direct sunlight while their leaves are soft and their roots poorly developed (Giddy, 1973; Smith and Van Wyk, 2009).They generally require dappled shade provided by nurse plants such as grasses, small shrubs or open-canopy trees (Giddy, 1973; Smith and Van Wyk, 2009). The leaves of many *Aloe* species are known to turn red, usually during the cold, dry winter season

when they experience considerable environmental stress (Smith and Van Wyk, 2009). High irradiance levels in winter contribute substantially to the colour change from green to red or reddish-brown, when chlorophyll breaks down revealing hidden red-coloured pigments such as anthocyanins. Anthocyanins are known to protect leaves from harmful light waves such as ultraviolet and green wavelengths, and they also offer protection against damage by free radicals, which can be particularly harmful during stressful periods (Smith and Van Wyk, 2009).

2.4.2.3. Temperature requirements

2.4.2.3.1. Heat tolerance

Many aloes can tolerate very high temperatures, e.g. *A. dichotoma, A. pillansii, A. ramosissima* and *A. pearsonii,* which all inhabit the climatically severe Richtersveld in South Africa and Namibia, where summer temperatures can exceed 50°C. A study by Jack (2012) on the differential sensitivity of *A. dichotoma* age classes to contemporary climatic variables (precipitation and solar radiation (as a proxy for temperature)) showed that both variables are important controls on juvenile abundance, especially at climatic extremes. The dependency of juveniles on regular moisture inputs for survival in arid ecosystems is well-documented (e.g. Noy-Meir, 1973). By contrast, adult *A. dichotoma* density was generally highest in areas in which climate is relatively harsh (more variable, and generally lower rainfall) (Jack, 2012). Elevated temperatures associated with high solar radiation, and consequently lower plant water balance, appeared to have little effect on adult plant health and abundance (Jack, 2012). Tolerance of greater environmental extremes in adult *A. dichotoma* plants is likely due to buffering provided by a larger water storage capacity and reduced surface-area-to-volume ratio, which results in less evapotranspirational water loss compared to juveniles (Jack, 2012).Water stress resulting from high temperatures is also intensified by the proximity of juvenile individuals to the soil surface, where maximum temperatures can be several degrees higher than 0.5m above the ground (Nobel, 1984). This phenomenon provides a likely explanation for why microhabitats provided by nurse plants and rock crevices are so crucial for juvenile survival directly after germination and during drought events not only in aloes, but also functionally similar genera in arid environments (Giddy, 1973; Smith and Van Wyk, 2009).

Succulent plants are generally fairly cold-tolerant, and some genera can withstand temperatures well below freezing point (Smith and Van Wyk, 2009). Nobel (1982) showed that 16 cactus species had an average minimum temperature tolerance of -10°C, while the 14 *Agave* species studied by Nobel and Smith (1983) tolerated an average minimum temperature of -11°C. Most *Aloe* species are reasonably cold-tolerant, although they seldom naturally occur in areas that experience severe frosts. While the

leaves of most aloes can withstand mild frost, more severe frost events often cause die-back from the leaf tips, although the plants usually recover quickly in spring (Smith and Van Wyk, 2009). The cold-tolerance threshold for most *Aloe* species appears to be -5°C to -7°C, below which, plants generally suffer serious damage or death (Smith and Van Wyk, 2009). The flowers of winter-flowering species are especially vulnerable to frost damage during cold snaps in winter e.g. *A. variegata* (Smith and Van Wyk, 2009) and *A. marlothii* (pers. obs.). Significantly, the few *Aloe* species that can survive temperatures lower than -7°C flower mostly in summer (or at least not in mid-winter), which is probably a phenological adaptation that prevents reproductive failure in these species.

2.4.2.3.2. Cold tolerance

The least cold-tolerant species are those found in subtropical and near-tropical regions, such as *A. thraskii*, which occurs along the humid subtropical KwaZulu-Natal coastline in South Africa (Smith and Van Wyk, 2009). Species that occur in high-lying parts of southern Africa, for example the Drakensberg of the Eastern Cape, Lesotho and Mpumalanga, as well as the Great Karoo, can withstand very low temperatures (Smith and Van Wyk, 2009). *Aloe polyphylla* (spiral aloe), for example, is particularly well-adapted to the sub-zero temperatures and snow commonly encountered in its Lesotho mountain habitat, approximately 2400m above sea level (Abrie and Van Staden, 2001; Smith and Van Wyk, 2009). Some members of genus *Aloe* are known to survive extreme cold by producing antifreeze compounds that protect cells against intracellular ice formation. These antifreeze compounds induce supercooling in the plant's tissues, thereby maintaining water within the plant in a liquid state below 0°C (Smith and Van Wyk, 2009).

2.5. Soil requirements

The soil requirements of *Aloe* species vary – some grow only in very alkaline soils, e.g. *A. arenicola, A. asperifolia, A. claviflora, A. hereroensis* and *A. littoralis*, while others prefer acidic soils e.g. *A. commixta, A. haemanthifolia, A. plicatilis,* and most grass aloe species (Giddy, 1973). In cultivation, grass aloes prefer well-aerated, friable soil, supplemented with liberal quantities of decomposed organic material (Smith and Van Wyk, 2009). The occurrence of some *Aloe* species appears to be restricted to very specific soil types. *Aloe ortholopha*, for example, grows in the highly mineralised soils of the Great Dyke in Zimbabwe, and is known to depend on the uptake of chrome, nickel and magnesium for its survival (Bullock, 1975; Wild, 1975; Kimberley, 1996). Other species such as *A. dewinteri, A. argenticauda* and *A. pachygaster* are restricted to limestone and dolomite soils (Jankowitz, 1975), while *A. ballii* occurs almost exclusively on quartzite (Ellert, 1998). Some aloes appear to respond to the mineral composition of the soil by producing different colour flower varieties

depending on the local soil chemistry. *Aloe ferox* usually produces orange-red to bright scarlet flowers, but some populations are known to produce much paler flowers ranging from lemon-yellow to almost pure white (Cloete and Plumstead, 2000). These unusual populations occur in hot, dry river valleys confined to soils associated with gabbroic intrusions, which are rich in nickel, copper and other heavy metals (Cloete and Plumstead, 2000).

Apart from the abovementioned species that have specific pH or mineral requirements, the large majority of aloes thrive in almost any soil in cultivation, requiring little or no fertilizer nor any special soil preparation before planting (Lloyd, 1898; Smith and Van Wyk, 2009). Notwithstanding, since aloes are succulent plants, they do not respond well to water-logged soil, and may rot if drainage is inadequate, hence their occurrence in well-drained sandy soil or rocky sites in habitat. While aloe seedlings often require nurse plants for their establishment, it has been shown that adult plants of some species e.g. *A. greatheadii* var. *davyana* and *A. secundiflora* can act as nurse plants themselves, colonising and ameliorating harsh conditions in sparsely vegetated or completely denuded landscapes (Smith and Correia, 1992; King, 2008). It is therefore reasonable to assume that the same would apply to other widely distributed, hardy *Aloe* species with relatively non-specific soil requirements.

2.6. The functional roles of aloes in their associated ecosystems

Aloes are an important component of many dryland ecosystems where they are often associated with species of *Acacia, Kleinia, Cissus* and *Euphorbia* (Wabuyele and Kyalo, 2008). Aloes produce copious amounts of nectar, a vital food source for an abundance of avian and insect species across southern Africa during the dry winter months when alternative food sources are scarce (Hoffmann, 1988; Nicolson and Nepi, 2005; Symes et al., 2008; Botes et al., 2009a, b; Forbes et al., 2009). The dilute nectar of species such as *A. greatheadii* var. *davyana* and *A. dichotoma* is also thought to be a source of moisture and carbohydrates for honeybees during winter (Tribe and Johannsmeier, 1996; Human and Nicolson, 2008). The dry inflorescences of aloes are used by a range of hymenopteran insects from four families (Anthophoridae, Chrysididae, Megachilidae and Sphecidae) as nest cavities (Parker and Bernard, 2009). Some mammals, particularly elephants, utilize aloe leaves as a food source. Elephants have a predilection for consuming aloes and will selectively feed on them if available (Parker and Bernard, 2008; 2009). Greater kudu are also known to browse aloe leaves; baboons feed on the leaves and flowers, while porcupine and black rhinoceros are known to uproot entire plants (Parker and Bernard, 2009).

Aloes can be important indicator species in particular vegetation types, such as *A. africana* and *A. ferox* in the Thicket Biome of the Eastern Cape (Parker and Bernard, 2009). When thicket vegetation becomes heavily browsed by livestock or elephants and/or other herbivores, aloes are exposed to further exploitation by herbivores, as well as physical factors such as strong winds that could increase their mortality (D.M. Parker, pers. comm.). *Aloe africana* and *A. ferox* therefore reflect the "health" of the vegetation, i.e. the degree to which the thicket is in an undisturbed, natural state without severe over-browsing by livestock or elephants and/or other herbivores (D.M. Parker, pers. comm.). In the arid Northern and Western Cape Karoo, *A. dichotoma* and *A. pillansii* are regarded as keystone species, where they provide food, nesting and shelter, as well as vantage points for raptors in an otherwise sparsely vegetated landscape (Midgley et al., 1997; Powell, 2005). Adult *A. dichotoma* and *A. pillansii* also contain large water reserves, which a number of species rely on during periods of extended drought (Powell, 2005; Duncan et al., 2006).

In certain ecosystems aloes are the primary colonisers and appear to act as nurse plants, modulating the harsh environment in which they occur, thus facilitating the later colonization of other less resilient species (Huenneke and Noble, 1996; Wabuyele and Kyalo, 2008). King (2008) showed that in degraded semi-arid Kenyan rangelands, areas within a two metre radius of *A. secundiflora* plants were positively associated with higher vegetation cover, species richness, litter cover, soil seed banks and soil water retention, compared with conditions surrounding *Maerua decumbens* shrubs and areas lacking vegetation cover. The aloes were therefore suggested to act as facilitators in the associated plant community, and this may be the case for other *Aloe* species as well (King, 2008). Planting aloes in degraded rangelands is also known to improve the effectiveness of grass reseeding for rangeland restoration (King and Stanton, 2008). Furthermore, their dense, spreading, mat-like root systems make aloes suitable for binding and stabilizing soil (Smith and Van Wyk, 2009). To this end they are often used on mine tailings and road cuttings to prevent soil erosion (Smith and Van Wyk, 2009). A prime example is *A. greatheadii* var. *davyana*, which grows in poor soils, multiplies vegetatively, and is therefore frequently used as a stabilizer of disturbed areas (Smith and Correia, 1992; Smith and Van Wyk, 2009). Hence, aloes have significant potential for use in ecosystem restoration and are both practically and economically beneficial since they are extremely hardy when transplanted, require no watering, and livestock are strongly deterred by their bitter sap (King and Stanton, 2008).

2.7. Population dynamics

2.7.1. Tree aloes in the Northern Cape, South Africa

The tree aloes *A. dichotoma* and *A. pillansii*, in the xeric Northern Cape, South Africa and Namibia, have received much attention in recent years due to significant changes in population structure and numbers (Midgley et al., 1996, 1997; Bolus et al., 2004; Duncan et al., 2005, 2006; Foden et al., 2007; Jack, 2012). In the decade prior to 2003, *A. pillansii* suffered a 50% reduction in population size (Powell et al., 2003) and there have also been numerous reports of widespread mortalities in *A. dichotoma*, apparently induced by drought (Foden et al., 2007). There has been much concern over *A. pillansii* in particular, since it is Critically Endangered (CR) (Duncan et al., 2005). Surveys of the population at Cornell's Kop in the Richtersveld, South Africa revealed that the number of adult *A. pillansii* individuals has halved between 1937 and 2004 (Duncan et al., 2006). Although there has been significant recruitment, there is an annual mortality of 1.4%, which includes a relatively high proportion of seedlings (Duncan et al., 2006). The reasons for the population declines in *A. pillansii* are still unclear, but likely causes include grazing by domestic livestock, theft by illegal plant collectors, damage by baboons and porcupines, off-road vehicle damage and possibly drought stress due to climate change (Midgley et al., 1996; Duncan et al., 2005; 2006).

An alternative hypothesis is natural death from old age (Duncan et al., 2006), which is supported by the large numbers of dead individuals in the largest size classes. Furthermore, none of the other plant species in the immediate vicinity of the aloe populations have shown any major changes in population structure over the same time period (Bolus et al., 2004; Duncan et al., 2006). A study of all known South African *A. pillansii* populations revealed a bimodal height class distribution with a gap in the 2-4m height class, suggesting poor recruitment 20 years earlier (Bolus et al., 2004). However, theft and herbivory may also explain this missing size class phenomenon (Bolus et al. 2004; Duncan et al., 2006). This is supported by anecdotal evidence that during the 1960s and 70s truckloads of succulent seedlings were removed from the Richtersveld by plant collectors (Duncan et al., 2006). The illegal removal of wild Quiver Trees (*Aloe dichotoma*, *A. pillansii* and *A. ramosissima*) from the Northern Cape is still a major threat (Powell, 2005; Duncan et al., 2005; 2006). *Aloe dichotoma* is highly sought after by landscapers and flora traders, and drought-stricken farmers are reported to collect it for sale in order to keep their farms running (Powell, 2005).

It has also been suggested that climate change is negatively impacting wild populations of *A. dichotoma* (Powell, 2005; Foden et al., 2007). Results from Foden et al. (2007) on the impacts of regional climate change on population die-back in *A. dichotoma* suggest that the species is experiencing

population declines at its equatorward limits in response to anthropogenic climate change trends. Indications are that the distribution of *A. dichotoma* in South Africa may undergo a 50% reduction by the year 2050 (Powell, 2005). A study by Jack (2012) revisited the suitability of *A. dichotoma* as an indicator of climate change in southern Africa. Results showed that proportional mortality was greatest within the Gariep River valley between 28 and 29° south, and *not* at the equatorward range limit as indicated by Foden et al. (2007). Findings suggest that current demographic patterns reflect longer-term climatic fluctuations rather than recent anthropogenically-driven climate change (Jack, 2012). The study also emphasises the importance of considering the way in which longer-term climatic and demographic processes may have contributed to the patterns currently observed within populations of *A. dichotoma*.

2.7.2. Stemless aloes

Scholes (1988) studied the changes in a population of the slow-growing, stemless *A. peglerae* in the Magaliesberg, South Africa, from 1976-1986. The size structure was relatively stable throughout the study period, with a high prevalence of aloes in the intermediate and large size classes (0.2 - >0.3m in diameter), and very few juveniles and seedlings. Flowering and seed production were both erratic (Scholes, 1988), which may account for the relatively low numbers of seedlings. A follow-up stochastic population modelling study on the same population of *A. peglerae* yielded an additional eight years of monitoring data (Pfab and Scholes, 2004). Results showed that *A. peglerae* is relatively long-lived; with an average adult lifespan of 60 years (Pfab and Scholes, 2004). Recruitment levels are low, and on average, seedlings grow to juveniles after four years and juveniles mature to adults within six years (Pfab and Scholes, 2004). Low densities of *A. peglerae* and population decline observed in areas with easy public access are probably the result of incidental removal of plants by hikers. The study showed that *A. peglerae* is extremely sensitive to harvesting of adult plants, and removal of only one plant annually from a population of 100 adults will cause a rapid decline to extinction (Pfab and Scholes, 2004). This is likely to be the case for other similar slow-growing aloe species that show low levels of recruitment.

Weisser and Deall (1989) showed that the size structure of a population of *A. petricola*, a stemless aloe in Mpumalanga, South Africa, was characterized by a preponderance of individuals in the intermediate height classes (0.2 - <0.5m), and very few seedlings and juveniles. This height distribution, which mirrors that of *E. peglerae* in Pfab and Scholes (2004), was suggested to be typical of aloes, since they generally reach flowering size relatively quickly (±5 years), and then continue growing slowly for many years before senescing (Weisser and Deall, 1989). Hence, seedlings that established in the years prior to the study may have reached maturity fast enough to have outstripped the smallest size class (0 -

<0.1m) before the next cohort of seedlings emerged. However, it is also suggested that the scarcity of seedlings and juveniles may have been due to fire damage, since larger aloes are generally more fire-resistant than smaller ones (Weisser and Deall, 1989).

2.7.3. Single-stemmed aloes

A study by Stokes and Yeaton (1995) showed that the population structure of *A. candelabrum* (=*A. ferox*) at Otto's Bluff in KwaZulu-Natal, South Africa, was characterized by large numbers of aloes in the smaller size classes (0.3-1.0m) occurring in open areas and taller individuals (1.6 - >3.0m) occurring predominantly in shaded areas associated with trees. No aloe recruitment was observed under tree canopies. The skewed height distribution of aloes associated with trees was thought to be indicative of tree invasion rather than aloes showing a positive growth response to shading (Stokes and Yeaton, 1995). Furthermore, height as an adaptation for evading canopy shading allows for the persistence of those aloes that established prior to the development of the tree canopy (Stokes and Yeaton, 1995). The population exhibited a distinct aggregated distribution, with the tallest and oldest plants at the nuclei of clumps. A large difference in height (and age) between individuals at the centre and those on the fringes of clumps suggests that spreading of clumps from nuclei is slow, and this may be attributed to the limited seed dispersal ability of *A. candelabrum* (Stokes and Yeaton, 1995).

Bredenkamp and Van Vuuren (1987) discussed the occurrence and distribution of *A. marlothii* on the Pietersberg Plateau, South Africa, with reference to its association with ruins of African Iron Age Ndebele settlements (A.D. 1650 – 1880). At these historic sites, *A. marlothii* often occur in extremely dense, impenetrable stands, the age of which is estimated to be 80 – 100 years (Bredenkamp and Van Vuuren, 1987). Many individual aloes are of the same age as the stands themselves, and the occurrence of juveniles is rare (Bredenkamp and Van Vuuren, 1987). Aerial photographs of the areas clearly reveal that *A. marlothii* tends to follow the stone walls of the old settlements. It is suggested that the aloes originated from an enormous seed bank that accumulated due to some action of the Ndebele and became established after the villages were abandoned (Bredenkamp and Van Vuuren, 1987; Smith et al., 2008). Careful observations of the sites suggest that a gradual invasion of the aloe as a pioneer plant in a successional series is improbable, as the sites are situated in open grassland where climatic conditions are unfavourable for the occurrence of *A. marlothii* populations. This observation is supported by the scanty presence and absence of *A. marlothii* at later Ndebele sites and other disturbed areas left by European settlers. Symes (2012) suggests that the establishment of the Ndebele villages would have resulted in a large accumulation of stones for building, protective rocky walls, and reduced fire frequency near dwellings. These safe sites would have been likely to promote the persistence of *A. marlothii*, whose population expansion may be limited (Symes, 2012). The arrival of seeds at these

sites may simply have been by wind dispersal, and not necessarily by the actions of humans (Symes, 2012).

The Thicket Biome of the Eastern Cape Province, South Africa has become synonymous with large aesthetically pleasing stands of *A. ferox*, reaching densities of >10 plants/km^2 (Parker and Bernard, 2008). Data from farms and reserves indicate that although *A. ferox* is common in survey plots outside elephant enclosures, it is rare or absent where elephants have access to it as a preferred food item (Parker and Bernard, 2008; 2009). It appears that elephants selectively feed on aloes of a particular height and kill these individuals, leaving behind only smaller/younger aloes (Parker and Bernard, 2008). Wiseman et al. (2004) monitored the composition and structure of the woody vegetation in a portion of the Ithala Game Reserve, Northern KwaZulu-Natal, from 1992-2000. Most large herbivores were extirpated from the region around the turn of the 20th century, releasing woodland areas from browsing. After establishing the fenced reserve in 1972, browsers were reintroduced (including elephants). Consequently, *A. marlothii* basal area dropped from 91.7 m^2/ha in 1992, to 0.19 m^2/ha in 2000 (Wiseman et al., 2004). Of the 35 woody species monitored, *A. marlothii* experienced the largest reduction in canopy area, predominantly due to browsing by Black rhino. Not only was there a dramatic decline in the number of mature individuals, but recruitment was low, and the aloes were therefore considered vulnerable to local extirpation (Wiseman et al., 2004).

Findings such as these have raised concerns regarding plant species loss through herbivore reintroduction, particularly in the Eastern Cape Thicket Biome (Parker and Bernard, 2008). Parker and Bernard (2008) contend that the large, relatively even-aged stands of aloes in parts of the Eastern Cape can be likened to the even-aged stands of tall trees in the riparian forests of Botswana, both being artefacts of the loss of large herbivores through disease (e.g. rinderpest) and hunting in the past (Parker and Bernard, 2008, 2009; Smith et al., 2008). Elephant (and other large mammals) browsing on aloes may therefore be the first step in the vegetation reverting to a situation similar to the one prior to excessive hunting and widespread disease in the region (Parker and Bernard, 2008).

2.8. Fire ecology

2.8.1. Fire tolerance

A major factor influencing the local distribution of aloes is their relative intolerance of fire (Jordan, 1996). However, *Aloe* species vary widely in their sensitivity to fire and are habitat-specific in relation to the occurrence of fires (West, 1974). Aloes are generally associated with dry, stony habitats largely due to fire intolerance, not because of their ability to survive limited water availability (Jordan, 1996). Succulents generally adopt one of two fire-survival strategies: survival due to fire avoidance in refugia,

or survival due to fire tolerance by vegetative recovery (Thomas and Goodson, 1992; Pfab and Witkowski, 1999). However, despite their adaptive strategies for surviving fire, all aloes, especially those that are medium-sized, can be detrimentally affected by fire (Smith and Van Wyk, 2009). If fires are too frequent (or in some cases too infrequent), flowering and seeding may be adversely affected, or if an exceedingly hot fire occurs during the flowering season, the inflorescences may be seared, resulting in poor seed set (Smith and Van Wyk, 2009). In southern Africa many *Aloe* species occur in habitats generally regarded as fire-free, such as parts of the Great Karoo, where fuel availability is insufficient and inter-plant distances too great for the development and spread of fires (Smith and Van Wyk, 2009). Aloes are also an important component of succulent thicket vegetation, especially in the Eastern Cape, where many plants with stout, moisture-filled leaves limit the ability of fires to take hold (Bond, 1983; Smith and Van Wyk, 2009).

Most Zimbabwean aloes are severely inhibited by burning (Bullock, 1975) and of the ~30 species, 14 are restricted to areas of relatively high rainfall and 19 are completely intolerant of fire (Jordan, 1996). By contrast, only nine species are fire tolerant, and two entirely dependent on fire for survival (Jordan, 1996). While many aloes appear to be fire-avoiders, some habitats in which aloes occur are subjected to regular and relatively predictable fires (Smith and Van Wyk, 2009). These fire-prone areas are generally colonised by fire-tolerant and fire-dependent aloes and include the grassland and savanna biomes, as well as the Cape Floristic Region (Jordan, 1996; Craib, 2005; Smith and Van Wyk, 2009). Fire-intolerant aloes are typically found in soil pockets within rock fissures, amongst boulders where grass cover is scant, in cracks, on ledges of cliff faces, or on bare ground (Bullock, 1975; Jordan, 1996). Some fire-intolerant aloes occur in fire-prone habitats, but avoid fire by occupying very rocky sites, such as *A. perfoliata* and *A. brevifolia*, which occur in lowland fynbos (Smith and Van Wyk, 2009).

2.8.2. Grass aloes

Grass aloes are inseparably linked to the occurrence of grass fires (Table 1), which are associated with all aspects of their annual growth and dormancy cycles (Craib, 2005). For some grass aloes, fire regulates the conditions under which they grow and flower, while for others, fire is a direct stimulant of flowering (Craib, 2005). Extensive grass fires followed by substantial early summer rainfall stimulates widespread flowering in the larger grass aloe species (Craib, 2005), and the flowering of some species, such as *A. chortolirioides* is entirely dependent on the occurrence of fire (Craib, 2005; Smith and Van Wyk, 2009). Grass fires burn the surrounding moribund vegetation thus releasing nutrients through ash production, which enriches the soil, enhances seed germination, and stimulates the production of new leaves in early spring (Craib, 2007; Smith and Van Wyk, 2009). Furthermore, by clearing the landscape

of moribund plant material, the fires afford grass aloe seeds the opportunity to germinate in areas where grass cover would otherwise be too dense (Smith and Craib, 2005). In *A. neilcrouchii*, a robust grass aloe from KwaZulu-Natal, South Africa, fire appears to promote the branching of young stems, and possibly offshoots in older stems (Klopper and Smith, 2010). Many grass aloes survive fires by resprouting from rootstocks, and some possess specialised physical adaptations such as fleshy bulbous bases, e.g. *A. inconspicua* and *A. kniphofioides* (Van Jaarsveld, 1989; Craib, 2005). Furthermore, grass aloes are usually deciduous, and their dead foliage becomes dry and combustible during the winter months (Craib, 2005). Although fire encourages flowering and seeding, successive annual fires over a long period may cause a decline in recruitment, since seedlings seldom survive fires (Craib, 2005). Fire is therefore central to the management of grass aloe populations, especially those occurring between forest plantations in South Africa, where the annual burning of fire breaks or long-term fire suppression can have equally detrimental effects on survival (Craib, 2005).

2.8.3. Single-stemmed and tree aloes

Many single-stemmed aloes such as *A. ferox* and *A. marlothii* are protected from fire by persistent skirts of withered leaves around their stems (Bond, 1983) (Table 1). These leaf skirts may form compact insulators, of which usually only the outer leaves are scorched during fire (Bond, 1983; Van Jaarsveld, 1989). Bond (1983) showed that fire tolerance of southern African tree aloes is strongly related to the degree to which stems are protected by dry leaf skirts. (The definition of 'tree aloes' in Bond (1983) includes single-stemmed species such as *A. ferox* as well as true tree aloes *sensu* Van Wyk and Smith (2008) such as *A. barberae*). Results suggest that bare-stemmed *Aloe* species (e.g. *A. barberae*) are likely to occur in fire-free environments, or where fires are rare or of low intensity, whereas species with stems fully clothed (e.g. *A. ferox*) occur in both fire-prone and fire-free habitats (Bond, 1983) (Table 1). The stems of *A. marlothii* are usually fully-covered, and this species generally occurs in fire-prone habitats (Bond, 1983). However, large populations often occur on rocky north-facing slopes and mountainous areas, where some populations appear to be confined to fire-protected islands (Bredenkamp and Van Vuuren, 1987). Hence, *A. marlothii* appears to be fire-adapted, but prefers fire-free sites within its fire-prone habitat. *Aloe thraskii* is unusual in that it occurs exclusively in fire-free thicket; despite its fully-covered stems (Bond, 1983). *Aloe plicatilis*, a bare-stemmed tree aloe, and the only aloe that has corky bark, is restricted to rocky outcrops in the Cape fynbos (Van Jaarsveld, 1989; Van Wyk and Smith, 2008). After a fire has passed through an *A. plicatilis* population, the plants appear dead; however, they often recover by resprouting from their growing points (Van Jaarsveld, 1989). Their thick, insulating bark protects against fire, but large, hot fires in old, dense fynbos stands can engulf and destroy whole aloes.

2.8.4. Multi-stemmed, stemless, speckled and spotted aloes

Most multi-stemmed, stemless, speckled and spotted (or maculate) aloes occur predominantly in the grassland and savanna biomes (Smith and Van Wyk, 2009) and appear to be relatively fire-tolerant (Table 1). However, they often occur in rocky sites within fire-prone vegetation (e.g. *A. reitzii*), and occasionally on cliff faces where fires cannot reach (e.g. *A. petrophila*). Large plants of the stemless *A. petricola* are reasonably fire-tolerant, and only their outer leaves are scorched during fires (Weisser and Deall, 1989). The most severely damaged *A. petricola* individuals in the population studied by Weisser and Deall (1989) were generally those in the smallest size classes. It appears that in years between grass fires, seedlings of stemless, speckled and spotted aloes may germinate and reach a size at which they are tolerant of intermittent fires by virtue of their tough outer leaves. These older, protective leaves may be scorched, but prevent the flames from reaching the plant's sensitive growing point (R.R. Klopper, pers. comm.). However, if fires are extremely intense or too frequent, aloes of these growth forms may be severely damaged or even die, especially those occurring in more exposed areas. The stemless *A. haemanthifolia*, which grows in the fire-prone fynbos, is an exception, since it survives fire by resprouting from its strong underground rootstock (Smith and Van Wyk, 2009). Although the above-ground biomass may be completely destroyed, the plants are rarely killed (Smith and Van Wyk, 2009).

2.8.5. Dwarf, creeping and rambling aloes

The diminutive appearance of dwarf aloes suggests they may easily be damaged or killed by fire. Most dwarf species appear to avoid fire by occupying rocky sites (e.g. *A. brevifolia*) or very arid areas where grass cover is scant (e.g. *A. variegata*) (Table 1). Nevertheless, all members of the group produce suckers and hence form clumps. If a clump is large enough, the outer suckers may be damaged or killed by fire, while the more protected inner plants would probably survive (R.R. Klopper, pers. comm.). Creeping aloes appear to be mostly fire-avoiders, occupying protected rocky sites within fire-prone regions (e.g. *A. perfoliata*), cliff-faces (e.g. *A. meyeri*), or very arid areas where fires are unlikely (e.g. *A. arenicola*) (Van Wyk and Smith, 2008) (Table 1).

However, fire-tolerance is likely to vary according to species, habitat type, and disturbance regime. Of the six South African rambling aloes, *A. commixta, A. juddii* and *A. gracilis* var. *decumbens* are endemic to the Cape fynbos, and all three are fire-tolerant (McDonald, 1994; Van Jaarsveld and Struck, 1996; Van Jaarsveld and Deacon, 2010). The remaining rambling aloes are found predominantly in the Thicket Biome of the Eastern Cape where fires are infrequent (Van Wyk and Smith, 2008; Smith and Van Wyk, 2009); hence their fire tolerance is likely to be lower than that of the fynbos species.

However, due to the generally vigorous resprouting ability of the group as a whole (Van Jaarsveld, 1989), most, if not all, rambling aloes would be expected to recover after fire by basal resprouting (Table 1).

2.9. Resprouting

2.9.1. Multi-stemmed and tree aloes

While aloes are generally known to respond to damage to plant organs by increasing growth and suckering (Wabuyele and Kyalo, 2008), this does not appear to be the case for all species. It appears that resprouting aloes are typically, but not exclusively, species that are subjected to fire on a regular basis (R.R. Klopper, pers. comm.). Furthermore, since resprouting plants tend to be multi-stemmed (Kruger et al., 1997), it is likely that aloes that exhibit branching (e.g. tree, multi-stemmed, and rambling aloes) have the ability to resprout, while aloes with single stems or no stems do not. *Aloe barberae,* a large South African tree aloe, exhibits vigorous resprouting after the removal of branches, and in some cases, large individuals are grown purely for the purpose of continually removing branches for propagation by cuttings (L. Hayes, pers. comm.). The closely related *A. tongaensis* is also probably a vigorous resprouter. However, the other South African tree aloes (*A. dichotoma, A. pillansii, A. plicatilis and A. ramosissima*) appear to be poor resprouters due to an absence of dormant bud-banks along their stems (E. Van Jaarsveld, pers. comm.). The multi-stemmed *Aloe arborescens* is known to resprout vigorously after stem damage or stem removal (R.G. Csernus, pers. comm.), and other multi-stemmed aloes also probably resprout provided they possess bud-banks along their stems. *Aloe pembana* from the island of Pemba off the coast of Tanzania, is known to produce side shoots on the uppermost parts of its main stem, which grow roots and then supposedly fall to the ground and act as bulbils, forming new separate plants (Newton, 1998).

2.9.2. Single-stemmed aloes

Most tall single-stemmed species such *as A. ferox* and *A. africana* do not habitually form plantlets along their stems, the significance of which is that once their growing tips are severely damaged or destroyed, they tend to be unable, or very reluctant to resprout (Smith et al., 2008). Studies on the impact of elephant browsing on tall single-stemmed aloes have shown that there is generally a higher proportion of dead aloes at sites where elephants are present than control sites where they are absent (Penzhorn et al., 1974; Parker and Bernard, 2008; 2009). Elephants either break off the aloe's crown, or push the whole plant over to access the succulent apical meristem, both of which usually result in plant

death (Parker and Bernard, 2009). Furthermore, Breebart et al. (2002) showed that goat browsing has a similar impact on *A. ferox*, with only 2% of individuals surviving after utilization by Boer goats. In contrast, Shackleton and Gambiza (2007) report that several *A. ferox* plants damaged by wild animals and cattle at two sites near Grahamstown, South Africa, showed coppicing and produced multiple rosettes where their stems had been damaged.

2.9.3. Stemless, rambling and grass aloes

Since stemless aloes have little or no stem tissue from which to resprout, it is likely that they are generally non-resprouters, suffering death after severe crown damage or crown removal (Table 1) (R.R. Klopper, pers. comm.). However, suckering species may recover from mechanical injury by producing basal suckers (R.R. Klopper, pers. comm.). *Aloe haemanthifolia* has a strong root system from which it resprouts if the above-ground parts are destroyed by fire (Smith and Van Wyk, 2009). In *A. peglerae*, if the growing tip is damaged, the plant may produce several heads at the apex (Smith and Van Wyk, 2009). Creeping, spotted and speckled aloes probably respond to mechanical injury in a similar way to stemless aloes. The South African rambling aloes (*A. ciliaris, A. commixta, A. gracilis, A. juddii, A. striatula* and *A. tenuior)* are generally fast-growing and most appear to be resprouters (Van Jaarsveld, 1989) (Table 1). *Aloe commixta, A. juddii* and A. *gracilis* var. *decumbens* readily resprout after fire damage, and this adaptation is key to their survival in the fire-prone Cape fynbos (McDonald, 1994; Van Jaarsveld and Struck, 1996; Smith and Van Wyk, 2009; Van Jaarsveld and Deacon, 2010). Grass aloes are generally well-adapted to resprouting after grass fires (Craib, 2005). Some species such as *A. kniphofioides* and *A. inconspicua* possess bulbous bases from which they resprout annually (Van Jaarsveld, 1989; Craib, 2005). Grass aloes are also likely to resprout during the growing season if their above-ground parts are damaged by mechanical injury (R.R. Klopper, pers. comm.).

It appears that both growth form and habitat play a major role in determining an aloe's resprouting ability. Species that exhibit branched growth forms with dormant bud banks along their stems, and those occurring in fire-prone habitats appear to be the most likely to resprout after disturbance. Further research on the resprouting response of the genus as a whole would contribute to a broadened understanding of this important aspect of aloe ecology. Knowledge on the resprouting of important commercial species harvested for cosmetics and medicine, as well as popular ornamental species in the horticultural trade, would be valuable for determining sustainable harvesting quotas and implementing appropriate management practises.

Table 1. Trends in the fire ecology and resprouting response of the ten growth forms (*sensu* Van Wyk and Smith (2008)) of South African aloes.

Growth form	Fire tolerance	Resprouting behaviour (after mechanical damage)
Tree	Poor due to lack of insulating skirts of dead leaves (Bond, 1983). Habitats generally preclude fires except for *A. plicatilis* in the fire-prone fynbos; this species has corky bark that protects against fire	Dichotomous branching species*: A. dichotoma, A pillansii, A. plicatilis* and *A. ramosissima* generally do not resprout (E. Van Jaarsveld, pers. comm.). *A. barberae* resprouts vigorously
Single-stemmed	Species with skirts of persistent dead leaves are generally fire-tolerant (Bond, 1983)	Generally poor (Smith et al., 2008)
Multi-stemmed	Fire tolerance varies depending on species, habitat and disturbance regime	Resprouting ability probably varies according to species, habitat and disturbance regime. Resprouting possible in taxa that possess dormant bud banks along their stems
Rambling	Fynbos species are fire-tolerant (Smith and Van Wyk, 2009; Van Jaarsveld and Deacon, 2010). Eastern Cape Thicket species probably less fire-tolerant	Generally vigorous resprouters (Van Jaarsveld, 1989)
Creeping	Most appear to be fire-avoiders (Van Wyk and Smith, 2008).	Resprouting ability unknown, but possibly varies among species, habitat type and disturbance regime
Stemless	Generally tolerant of mild to warm fires, but plants may be killed by very hot and frequent fires, especially small and/or exposed individuals (e.g. *A. petricola* in Weisser and Deall (1989))	Generally poor resprouters (except for *A. haemanthifolia*), but sometimes multiple heads are produced at the apex (Smith and Van Wyk, 2009). Suckering species may resprout by producing basal suckers (R.R. Klopper, pers. comm.)
Speckled and Spotted	Generally tolerant of mild to warm fires, but plants may be killed by very hot or frequent fires, especially small and/or exposed individuals (R.R. Klopper, pers. comm.)	Generally poor resprouters, except for suckering species (R.R. Klopper, pers. comm.)
Dwarf	Most appear to be fire-avoiders, occupying rocky sites, or arid, sandy areas. Outer suckers may be damaged but provide protection to inner rosettes that may survive (R.R. Klopper, pers. comm)	Minimal resprouting response, except for suckering species (R.R. Klopper, pers. comm.)
Grass	Highly tolerant of fire; some species fire-dependent (Craib, 2005; Smith and Van Wyk, 2009)	Deciduous, therefore resprout from subterranean rootstocks in spring (Craib, 2005), but probably also resprout due to mechanical injury during the growing season (R.R Klopper, pers comm.)

2.10. Pollination ecology

2.10.1. Bird pollinators

Studies on *Aloe* pollination ecology encompass a range of different growth forms, with grass aloes and single-stemmed species being the mostly frequently studied (Table 2). Aloes are generally self-incompatible and are therefore dependent on animal floral visitors for pollination and seed set (Hoffman, 1988; Botes et al., 2009a). Many *Aloe* species attract insect and bird pollinators by providing abundant nectar primarily during winter, when alternative sources, such as insects, fruits and other nectars are limited (Beyleveld, 1973; Nicolson and Nepi, 2005; Botes et al., 2008). Few aloes produce fragrant flowers, and *A. modesta* is the only scented aloe on the African continent; all other scented aloes occur in Madagascar (Van der Riet, 1977). The primary pollinators of *A. modesta* appear to be bees, and the scent emitted probably attracts bees and aids them in alighting on the flowers (Van der Riet, 1977).

Direct observations and experiments on several *Aloe* species have confirmed the existence of extensive bird pollination systems (Wilson et al., 2009), and the majority of South African *Aloe* species have floral traits consistent with bird pollination (Botes et al., 2009a; Symes et al., 2009) (Table 2). These traits include red-orange tubular perianths, strongly exserted anthers and stamens, and copious supplies of dilute nectar at the base of the flowers (Botes et al., 2009a; Symes et al., 2009). Furthermore, the flowers of many *Aloe* species have a constriction in the corolla which prevents most insects from reaching the nectar, thus excluding them as potential pollinators (Tribe and Johannsmeier, 1996). *Aloe ferox* and *A. marlothii* often grow in dense stands and produce large inflorescences of brightly coloured flowers, known to attract diverse communities of nectar-foraging birds (Oatley, 1964; Hoffmann, 1988; Symes et al., 2009). However, the coexistence of *Aloe* species in certain habitats has been difficult to explain, since aloes hybridize easily, often co-flower *en masse* and share a floral syndrome consistent with bird pollination (Botes et al., 2008). A study by Botes et al. (2008) showed that co-flowering ornithophilous aloes partition the bird pollinator community through differences in floral morphology and nectar characteristics, while species that share bird pollinators tend to flower sequentially or deposit pollen on different pollen placement sites on the same birds. Thus, given the scarcity of genetic barriers to hybridization in aloes, it is likely that these differences enable a larger number of *Aloe* species to coexist than would otherwise be possible (Botes et al., 2008).

Botes et al. (2008) also showed that two distinct bird pollination systems occur in ornithophilous *Aloe* species. Aloes that produce long-tubed flowers with small volumes of relatively concentrated nectar are associated with specialist long-billed sunbirds as pollinators (Botes et al., 2008). On the other hand, aloes that produce short-tubed flowers with large quantities of relatively dilute nectar are generally pollinated by short-billed occasional nectarivores (Botes et al., 2008; Human and Nicolson, 2008). Nonetheless, most *Aloe* species appear to be adapted for sunbird pollination (Human and Nicolson, 2008). Aloes that produce dark, bitter-tasting nectar, such as *A. vryheidensis* do not attract sunbirds or honeybees, but are frequented by insectivorous and frugivorous birds that are seemingly unaffected by the nectar's bitter taste (Johnson et al., 2006). It has therefore been suggested that the dark phenolic component of the nectar of *A. vryheidensis* acts as a floral filter by attracting some animals visually and deterring others by its taste (Johnson et al., 2006).

2.10.2. Insect pollinators

In addition to birds, most, if not all, *Aloe* species are visited by a range of insects, most commonly nectar- and/or pollen-collecting bees (Hoffman, 1988; Hargreaves et al., 2008; Botes et al., 2009a) (Table 2). However, aloes appear to show extensive variation among species in the contribution that bees make to their pollination (Wilson et al., 2009). Jordan (1996) notes that eight Zimbabwean *Aloe* species exhibit floral characteristics suggestive of insect pollination such as bell-shaped flowers (e.g. *A. ballii*), insect landing strips (e.g. *A. suffulta*), and flowers with stamens and style exserted far from the perianth (e.g. *A. sessiliflora*). Some small grass aloe species that produce short-tubed, white or cream-coloured flowers such as *A. inconspicua*, *A. minima* and *A. linearifolia* are exclusively insect (bee) pollinated (Hargreaves et al., 2008; Botes et al., 2009b). However, bees appear to make relatively small contributions to seed production in other 'ornithophilous' (predominantly bird-pollinated) aloes e.g. *A. marlothii* (Botes et al., 2009a; C.T. Symes, pers. comm.). Furthermore, bees also have the potential to clog stigmas with self-pollen, which would prevent further cross-pollination and therefore diminish reproductive output in the generally self-incompatible genus *Aloe* (Wilson et al., 2009). Overall, there appear to be three roles played by bees in aloe pollination ecology. They may be the exclusive pollinators (e.g. *A. inconspicua*), they may co-pollinate with birds (e.g. *A. greatheadii* var. *davyana*), or act as resource robbers and contribute very little towards pollination (e.g. *A. marlothii*). However, there is still a lack of clarity regarding the general importance of bees in aloe pollination ecology, and further studies are required to elucidate this subject further (Wilson et al., 2009).

Table 2. Pollinators and visitors of selected African *Aloe* species, with reference to their distribution, growth form, inflorescence type and flowering time. Pollinators/visitors marked with an asterisk (*) are the primary pollinators based on exclusion experiments. (South African Provinces: Eastern Cape = EC, Free State = FS, Gauteng = GP, KwaZulu-Natal = KZN, Limpopo = LP, Mpumalanga = MP, North-West = NW, Northern Cape = NC, Western Cape = WC).

Aloe species	Distribution[a]	Inflorescence description[b]	Flowering time[c]	Pollinators and visitors	Reference
Tree aloes					
A. barberae	South Africa: EC, MP, KZN; Swaziland; Mozambique	Branched panicle 40-60cm long; densely-flowered racemes 20-30cm long. Inflorescences often hidden amongst the leaves; flowers salmon-pink to orange	May-August	Short-billed generalist nectarivores (e.g. Weavers, White-eyes & Starlings)	Van Jaarsveld (2010)
A. dichotoma	South Africa: NC; Namibia	Short, erect, branched inflorescences, bearing 3-5 racemes of bright yellow flowers	June - August	Short-billed generalist nectarivores (Weavers, White-eyes & Starlings); Sunbird spp. & honeybees (*Apis mellifera)*	Tribe and Johannsmeier (1996); Van Jaarsveld (2010)
A. eminens	Somalia	Branched 50-60cm long candelabriform panicle; racemes 16cm long & subdensely flowered; flowers glossy red[e]	March (southern hemisphere)	Sunbird spp.	Van Jaarsveld (2010)
A. pillansii	South Africa: NC; Namibia	Branched inflorescence arising from lowest leaves of the rosettes, each with numerous racemes bearing yellow flowers that are swollen in the middle	October	Short-billed generalist nectarivores (Weavers, White-eyes & Starlings); Sunbird spp. & honeybees (*Apis mellifera)*	Tribe and Johannsmeier (1996)
A. plicatilis	South Africa: WC	Single laxly-flowered racemes with up to 30 tubular, scarlet flowers	August - October	Malachite Sunbirds & bees	S.R. Cousins (unpublished data)
A. ramosissima[i]	South Africa: NC southern Namibia	Short inflorescence with comparatively large, swollen yellow flowers	June - August	Short-billed generalist nectarivores (Weavers, White-eyes & Starlings); Sunbirds & honeybees (*Apis mellifera)*	Tribe and Johannsmeier (1996)
A. tongaensis	South Africa: KZN; southern Mozambique	Cylindric, 47-50cm long; distinctly inward-curved; outer segments fused in lower half; flowers yellowish orange, vertically presented[f]	April & May	Sunbird spp.	Van Jaarsveld (2010)

Single-stemmed aloes					
A. africana	South Africa: EC	Inflorescence comprises 1-4 strongly tapering racemes bearing bright yellow-orange flowers that curve upwards when open	July - September	Pollen-collecting bees, Nectar-collecting bees, Cape honeybees (*Apis mellifera capensis*) & Short-billed Weavers (destructive foragers)	Botes et al. (2009a)
A. ferox [=*A. candelabrum*]	South Africa: KZN, south-eastern FS, WC & EC; South-western Lesotho	Inflorescence branched into 5-12 erect racemes with bright orange-red (occasionally yellow or white) flowers	May - August; (September - November in colder northern parts of distribution)	Red-winged starling, Black Sunbird, Lesser Double-collared Sunbird, Cape Weaver, Streaky-headed Canary, African honeybee (*Apis mellifera*), Sweat bee spp., Formicine ants, Chaleid wasps & Hover flies	Hoffman (1988)
				Bees & (Sunbirds & other bird spp.)*	Stokes and Yeaton (1995)
				Pollen-collecting bees, Nectar-collecting bees & Cape honeybees (*Apis mellifera capensis*)	Botes et al. (2009a);
				Birds[g]: Primarily Malachite Sunbirds, Streaky-headed Seedeaters, Weavers, Karoo Prinia & Red-faced Mousebirds, Insects: Cape honeybees (*Apis mellifera capensis*) & Solitary bees (primarily *Lasioglossum* sp.)	Forbes et al. (2009)
A. lineata var. *muirii*	South Africa: EC & WC	Up to four simple racemes produced consecutively on a single rosette; flowers light pink to bright red	June - November	Pollen-collecting bees, Nectar-collecting bees, Cape honeybees (*Apis mellifera capensis*), solitary bees (Primarily Lasioglossum sp.) & unidentified bird spp.	Botes et al. (2009a)
A. marlothii	South Africa: LP, MP, NW, GP & KZN; Botswana; Zimbabwe; Mozambique & Swaziland	Inflorescences branched into 20-30 horizontal racemes, bearing bright orange-red flowers (racemes in the southern form from KwaZulu-Natal are slanted to almost erect)	May - September	Primarily African Red-eye Bulbul, Cape Weaver, Cape White-eye, Red-faced Mousebird, Southern Masked Weaver, Fiscal Flycatcher & Streaky-headed Seedeater[h]	Symes et al. (2008)

A. pluridens	South Africa: EC & KZN	Branched inflorescence held well above the rosette, with 4-5 long, conical racemes bearing orange, pinkish-red or occasionally yellow flowers	May - July	Pollen-collecting bees, Nectar-collecting bees, Cape honeybees (*Apis mellifera capensis*) & unidentified bird species	Botes et al. (2009a)
A. vryheidensis	South Africa: northern KZN, MP, LP & NW	Up to five single, erect, narrowly-cylindrical, densely multi-flowered racemes per plant; flowers orange-yellow; racemes have a bottlebrush appearance due to the densely crowded bell-shaped flowers with exserted stamens	July & August	Dark-capped Bulbuls, Cape White-eyes, Streaky-headed Canaries, Buff-streaked Chats, Cape Rockthrushes, Greater Double-collared Sunbirds[j], honeybees (*Apis mellifera)*& Halictid bees	Johnson et al. (2006)
Multi-stemmed aloes					
A. divaricata	Madagascar	Laxly flowered, much-branched, pyramidal panicle up to 1m tall; flowers reddish-scarlet[d]	April[e]	Sunbirds* (*Nectarinia souimanga*; & stingless bees (*Trigona* sp.)	Ratsirarson (1995)
Stemless aloes					
A. peglerae	South Africa: GP & NW	Short, usually simple inflorescences bearing racemes of broadly tubular flowers that are bright red as buds, opening pale greenish-yellow	July & August	Dark-capped bulbuls & Cape Rock Thrushes and Streaky-headed Seed-eaters	Arena et al. (submitted)
Spotted aloes					
A. greatheadii var. *davyana*	South Africa: LP, MP, NW, GP, KZN & FS	Up to four inflorescences reaching heights of 1,5m with up to six branches bearing pale pink to red flowers	June & July	Honeybees (*Apis mellifera)** & Sunbirds	Symes et al. (2009); H. Human, (unpubl. data)
A. pruinosa	South Africa: KZN	Single much-branched inflorescence reaching 2m, bearing dark pinkish flowers with a constriction in the middle, and a basal swelling	February & March	Amethyst Sunbirds, honeybees (*Apis mellifera*) & membrane bees (Colletidae)	Wilson et al. (2009)
Grass aloes					
A. inconspicua	South Africa: KZN	Simple, cylindrical, densely-flowered raceme bearing erect, more or less stalkless, green & white flowers	November	Primarily Solitary bees (mainly female *Amegilla fallax*)*& an unidentified *Pseudapis* sp. (Halictidae)	Hargreaves et al. (2008)
A. linearifolia	South Africa:	Single head-shaped raceme with short	February &	Primarily Solitary and Sub-social bees*	Botes et al.

	southern & central KZN	greenish-yellow to pure yellow tubular flowers	March	& *Megachile* bees (refer to Table 2 in Botes et al. (2009) for full list of species)	(2009b)
A. minima	South Africa: KZN & MP; Swaziland	Simple inflorescences bearing small dull pink flowers with petals slightly spreading	February & March	Primarily solitary & sub-social bees* (refer to Table 2 in Botes et al. (2009) for full list of species)	Botes et al. (2009b)
A. modesta	South Africa: MP & the MP-KZN border	Simple densely-flowered inflorescences; flowers greenish-yellow, fragrant, tubular and virtually stalkless	January & February	Bee spp.	Van der Riet (1977)

[a,b,c]Van Wyk and Smith (2008).
[d]Reynolds (1966).
[e,f]Van Jaarsveld (2010)
[g]Only the five most commonly observed bird species for *A. ferox* are reported in this table. Karoo Prinias (*Prinia maculosa*) and Red-faced Mousebirds (*Urocolius indicus*) had equal counts. For the full list of 40 bird species refer to Forbes et al. (2009).
[h]A total of 83 bird species were observed, 38 of which were recorded. Refer to Appendix Table 2 in Symes et al. (2008) for the full list of species.
[i]In a recent taxonomic revision, *A. ramosissima* was reduced to a variety of *A. dichotoma* (Van Wyk and Smith, 2008); however, it is still listed as a separate species on the PRECIS database and is recognised as such at the National Herbarium in Pretoria, South Africa (R.R. Klopper, pers. comm.).
[j]Only one Greater Double-collared Sunbird was observed feeding at an *A. vryheidensis* individual in this study (Johnson et al., 2006)

2.11. Seed biology

2.11.1. Seed production and dispersal

Aloe fruits are typically three-angled oblong capsules which dry and dehisce when ripe (Kamstra, 1971; Jordan, 1996). The capsules generally house a number of two-winged, wind-dispersed seeds (Kamstra, 1971; Van Jaarsveld, 1989; Jordan, 1996). The form and size of aloe seeds vary considerably among species (Kamstra, 1971), and variations include a third wing, which may increase travelling distances of individual seeds; and the absence of wings, which is likely to result in poor dispersal, and hence the establishment of dense seedling stands in close proximity to the parent plant (Jordan, 1996). Despite aloes having the ability to produce an abundance of seeds, establishment of recruits is occasional, and is dependent on the availability of rainfall, which is frequently scant and erratic throughout much of the range of the genus (Wabuyele and Kyalo, 2008). The quantities and duration of seed production may vary widely, even among species in a particular aloe group (Craib, 2005). Some grass aloes, for example, produce vast quantities of seed over a limited period, while others are shy seed bearers, but their clump-forming habit and extended flowering period ensure that seed is released over several months (Craib, 2005). *Aloe vera* appears to be the only species in the genus that exhibits seedlessness. A study by Gupta and Sharma (2011) suggests that both environmental and genetic factors are responsible for the anomalous chromosomal behaviour that results in seedlessness in the species.

Few *Aloe* species have very broad distributions, and species tend towards niche specialization, which may be linked to limited seed dispersal ability (Holland, 1978; Stokes and Yeaton, 1995). Stokes and Yeaton (1995) suggest that selection for limited seed dispersal occurs in *A. candelabrum* (=*A. ferox*), a direct consequence of which is that the spatial distributions of young populations are usually clumped. These clumps act as nuclei from which plants spread slowly over time, with mature individuals forming the centre of the densest stands (Stokes and Yeaton, 1995). *Aloe droseroides* from Madagascar produces wingless seeds that are inordinately large relative to the size of the plant (Lavranos and McCoy, 2003). This unusual seed morphology suggests that the seeds are not wind-dispersed, and may account for the highly restricted distribution of the species (Lavranos and McCoy, 2003). By contrast, the seeds of *A. arborescens* are virtually wingless, yet this species has an extensive range. These conflicting findings suggest that further investigation is required to clarify the links between aloe seed morphology, dispersal efficiency and distribution patterns.

2.11.2. Germination

Aloe seeds typically germinate within three weeks of dispersal, and their viability is often considerably reduced a year after dispersal (Van Jaarsveld, 1989). Giddy (1973) conducted experiments with the same batch of aloe seed sown at fortnightly intervals under identical controlled conditions, and showed a marked decline in percentage germination over time. While grass aloe seeds lose their viability by the second growing season after dispersal, the seeds of aloes from drier regions, such as *A. dichotoma* and *A. asperifolia* remain viable for up to three years after dispersal (Giddy, 1973). This prolonged viability period is probably an adaptation to the occurrence of erratic rainfall in these arid regions, whereby seeds released in dry years can stay dormant until more favourable conditions arrive. *In vitro* germination tests conducted by Bairu et al. (2009) on *A. ferox* seeds showed that germination was very erratic, with the first seeds germinating after 10 days, and the remaining seeds continuing to germinate for over a month. Germination trials using soil samples collected from a population of *A. marlothii* one year after flowering showed that no seeds germinated, suggesting that the persistence of seeds in the seed bank is unlikely to extend beyond the following flowering season (Symes, 2012). However, Smith and Correia (1992) report that *A. greatheadii* var. *davyana* seedlings continued to emerge in beds where seed had been sown the previous season, indicating that the seeds may remain viable for up to two growing seasons.

The germination and establishment of some (if not most) *Aloe* species is dependent on the protection of 'nurse' or companion plants that protect seedlings from excessive heat, radiation, desiccation, frost and herbivores (Smith and Van Wyk, 2009). Shade is especially important for the first three to four months following germination, as aloe seedlings are very sensitive to strong, direct sunlight, but not necessarily to high shade temperatures (Giddy, 1973). Tests on the effect of temperature on *A. ferox* seed germination showed that maximum percentage germination (76%) was achieved at 30°C, while the best germination overall (78%) was achieved at 25°C under constant dark conditions (Bairu et al., 2009). This result appears to be consistent with the findings of Giddy (1973) in terms of the shade and temperature requirements of aloe seedlings. Smoke-water treatment was also shown to significantly improve germination and appears to elicit a similar response to that of plant growth regulators (Bairu et al., 2009).

Mukonyi et al. (2011) studied the germination and growth performance of two commercially important Kenyan *Aloe* species: *A. turkanensis* and *A. secundiflora* using various growth media. Under

greenhouse conditions, germination of both species commenced on the ninth day after sowing, and maximum germination occurred between the second and third weeks (Mukonyi et al., 2011). On the whole, *A. turkanensis* showed better germination than *A. secundiflora* in most growth media. Sawdust and/or vermiculite blended with either forest humus or soil collected from habitat gave the best germination results. Five months after germination, poor growth performance was observed in media containing sawdust and/or vermiculite, while seedlings in substrates containing soil from habitat enriched with manure performed very well (Mukonyi et al., 2011). Findings suggest that growth media that favour optimal germination may not necessarily facilitate subsequent growth and establishment, while media conducive to growth subsequent to germination do not necessarily improve germination success. Similar germination and propagation studies on other commercially important *Aloe* species that are currently predominantly wild-harvested would be beneficial for establishing protocols for large-scale propagation to satisfy consumer demand and reduce harvesting pressure on wild populations.

2.12. Economic botany

2.12.1. Aloes as medicinal plants

Aloe leaves are renowned for their medicinal properties, and have been important medicinal plants for centuries (Hodge, 1953; Klein and Penneys, 1988; Smith, 1993; Low et al., 2006; Van Wyk and Smith, 2008). The laxative property of the bitter resinous juice in the leaves of the renowned Socotra aloe, *A. perryi*, was exploited by the Greeks at least as early as the fourth century B.C. (Hodge, 1953; Simione-Senelle, 1994). Aristotle, tutor of Alexander The Great, recognised the commercial potential of the Socotra aloe, and advised his student to establish a Greek colony on Socotra off the coast of Yemen, and cultivate the aloe for export to Greece, Syria and Egypt (Simione-Senelle, 1994). Surprisingly, of all the *Aloe* species and hybrids thereof, very few have been important to pharmacology, notably the Socotra aloe (*A. perryi*), *A. vera* and *A. ferox* (Haller, 1990). Nowadays, the key commercial medicinal species *A. ferox* and *A. vera* are traded in vast quantities to supply the global market for health and skincare products (Sachedina and Bodeker, 1999; Van Wyk and Smith, 2008). *Aloe vera* is primarily sourced from plantations in Mexico, the United States and parts of South America and is generally used in semi-processed products manufactured in the same regions (Grace, 2011). By contrast, *A. ferox* and *A. secundiflora*, are mainly wild-harvested in South Africa and Kenya respectively, and supply largely unprocessed natural products to domestic and commercial export markets in Europe and Asia

(Shackleton and Gambiza, 2007; Grace et al., 2008, 2009; Grace, 2011). Other species wild-harvested and/or cultivated in East Africa include *A. marsabitensis, A. ngongensis, A. rabaiensis* and *A. scabrifolia* (Grace, 2011). Income generated from indigenous aloe tapping in Kenyan drylands (and elsewhere in Africa) contributes significantly to peoples' livelihood strategies and standards of living (Mukonyi et al., 2011).

Aloe leaves yield two medicinal products - a gel obtained from the mucilaginous cells in the central zone of the leaf, and a bitter exudate known as "bitter aloes" or "drug aloes" which is derived from the pericyclic cells beneath the epidermis (Klein and Penneys, 1988; Dagne et al., 2000). The gel possesses moisturizing and emollient properties and is used in a range of cosmetic products, shampoos and skincare creams (Klein and Penneys, 1988; Dagne et al., 2000; Grace, 2011) The bitter exudates contain the anthraquinones aloin and aloe-emodin and are used as strong stimulant-laxatives and sometimes as bittering agents in certain beverages (Klein and Penneys, 1988; Dagne et al., 2000; Grace, 2011). The chemical composition of aloes varies according to species, climate and growing conditions (Klein and Penneys, 1988), and reasons for the limited number of *Aloe* species entering the international trade may include selection of species with the most desirable medicinal qualities, local abundance, and the proximity of aloe populations to major transport nodes (Grace, 2011).

While the most frequently reported medicinal use of aloes is for the treatment of infections and parasites (Grace et al., 2009), they are also used during pregnancy, labour and post-natal care, as well as for treating, *inter alia*, digestive ailments, skin conditions, inflammation, arthritis, pain, and poisoning (Low et al., 2006; Grace et al., 2008; 2009). In the Mascarene Islands, aloe leaves are widely used to treat cutaneous bacterial infections and boils, and they are also taken as an antispasmodic during menstruation (Ranghoo-Sanmukhiya et al., 2010). Aloes are also used for traditional medicine to treat sexually-transmitted diseases such as HIV/AIDS despite a lack of scientific evidence to support their efficacy (Nyika, 2007; Campbell-Barker, 2009). Other uses include the consumption of aloe flowers as a food source, the planting of aloes around graves and as living fences for animal enclosures, the extraction of dyes and inks, and use as an ingredient in dips for pest control (Watt and Breyer-Brandwijk, 1962; Lane, 2004; McCoy, 2007; Grace et al., 2009; Smith and Van Wyk, 2009). Aloes also have several social uses, especially for magical and ritual purposes, such as fertility and initiation ceremonies, charms for good fortune, protection against lightning, safety at funerals and protection for the home (Watt and Breyer-Brandwijk, 1962; Grace et al., 2009). Some aloes such as *A. greatheadii* var. *davyana* are important bee plants in South Africa, and beekeepers are known to move their

beehives to aloe fields in winter to make use of the highly nutritious aloe pollen and copious nectar, which contribute substantially to the honey crop (Nepi et al., 2006; Human and Nicolson, 2008).

2.12.2. Aloes in African traditional medicine

Aloes are also harvested and utilized for traditional medicine in numerous African countries (Hutchings, 1996; Neuwinger, 1996; Von Koenen, 2001; Williams et al., 2001; Von Ahlefeldt et al., 2003), and approximately 60 species are used in southern Africa alone (Grace, 2011). Rock paintings by San Bushmen suggest that aloes were being used traditionally long before European settlers arrived in Africa (Sachedina and Bodeker, 1999). In South Africa, a number of *Aloe* species are traded in traditional medicine markets and shops. Species such as *A. aristata* and *A. maculata* have been observed in traditional medicine shops in Gauteng (Williams et al., 2001) and in markets on South Africa's eastern seaboard (Von Ahlefeldt et al., 2003). *Aloe arborescens* and *A. tenuior* have been recorded in trade on the western boundary of the Kruger National Park (Botha et al., 2001). Besides these studies, references to local and small-scale trade in aloes for traditional medicine are scant, which suggests mainly opportunistic use of local species and poor market demands (Grace, 2011). The paucity of data on the informal trade in *Aloe* species for traditional medicine calls for a detailed study to determine the species and quantities traded, as well as the key harvesting areas targeted by plant gatherers. In terms of sustainable harvesting of aloes for traditional medicine, in the past, harvesting was conservative, as only a few leaves were sufficient for occasional household use. However, with the booming trade in *A. vera,* for cosmetics and health products, the demand for aloes has increased, and it appears that nowadays harvesting often involves whole plant removal as opposed to leaf collection only (Maundu et al., 2006). Many herbalists are reportedly collecting wild aloes and planting them in their own herbal gardens, and hence these actions are threatening the persistence of wild populations (Maundu et al., 2006).

2.12.3. The horticultural trade in aloes

Aloes long been the subject of intense horticultural interest, and there are numerous publications on aloe natural history, distribution, cultivation, and morphology of garden hybrids (Holland, 1978). Through the efforts of Reynolds (1950, 1966, and 1969) and Jeppe (1969), aloes became exceedingly popular in domestic and amenity horticulture, particularly in South Africa, thus contributing to the '*Aloe* craze' of the 1970s (Smith et al., 2000). The most sought-after aloes among succulent plant

collectors include rare endemics (e.g. *A. polyphylla*), morphologically distinctive taxa (e.g. *A. plicatilis*) and difficult-to-grow species (e.g. *A. haemanthifolia*) (Grace, 2011). The desirability of these taxa is reflected in their high retail prices in the horticultural trade (Grace, 2011). The illegal collection of sought-after species such as *A. polyphylla and A. peglerae* has depleted wild populations, and their persistence in the wild is still in jeopardy due to illicit harvesting (Beverly, 1978; Pfab and Scholes, 2004; Gildenhuys, 2005; Mofokeng and Jiwen, 2009). An insatiable demand for the charismatic Quiver Tree *A. dichotoma* in the Northern Cape ostensibly results in the illegal collection of an estimated 41 plants per month, and is threatening the long-term survival of this species in the wild (Powell, 2005). Permits are required for collecting, research and commercial harvesting in most countries in which *Aloe* species naturally occur (Grace, 2011). Nevertheless, the permitting system does not appear to have precluded the illicit aloe trade, and while the trade is reasonably well characterised, especially in South Africa, it is almost impossible to quantify, and necessitates tighter measures of trade control (Newton and Chan, 1998; Grace, 2011).

2.12.4. Sustainable use of aloes

Sound and effective policy implemented by well-structured and well-equipped conservation agencies backed by government, is pivotal for supporting conservation and optimising the sustainable use of any natural resource (Child, 2003; Grace, 2011). Realistic and objective compromises should be made based on how costs, benefits and accountability are best shared between stakeholders (Child, 2003). In the case of aloes, sustainable exploitation hinges largely on the actions of stakeholders in the horticultural and natural products industries, and the aloe trade in Kenya is a case in point (Grace, 2011). Following a presidential decree against the exploitation of wild Kenyan aloes in 1986, the Kenya Wildlife Service has maintained a ban on the commercial exploitation of wild *Aloe* species (Wabuyele et al., 2006; Wabuyele and Kyalo, 2008). Subsequently, the National Strategy for Conservation and Management of Commercial *Aloe* species was formulated and lunched in 2008 to promote *in situ* and *ex situ* aloe conservation through, amongst other things, sustainable harvesting controlled by Aloe Management Units and the establishment of *ex situ* collections in botanical gardens (Wabuyele and Kyalo, 2008).

The Kenya Aloe Working Group was also initiated to promote the cultivation of key species used for leaf exudate and mesophyll (Wabuyele and Kyalo, 2008; Grace, 2011). The working group encourages the establishment of aloe plantations in areas of low and erratic rainfall, where cultivation of

conventional food crops is insecure, thereby enhancing the livelihood security of local communities (Grace, 2011).The working group also facilitates the linking of stakeholders throughout the supply chain, and uses export markets as incentives for nurserymen, farmers and manufacturers to use propagated aloe stocks as a profitable alternative to illicitly-harvested wild material (Grace, 2011). However, these conservation initiatives have not been entirely problem-free, as in 2006, wild harvesting of *A. secundiflora*, *A. turkanensis* and *A. scabrifolia* was still taking place, largely due to law enforcement difficulties (Maundu et al., 2006). Nevertheless, Kenya's integrated approach to sustainable utilization and aloe conservation is exemplary, and similar strategies would be highly relevant to other emerging aloe-based industries elsewhere in Africa.

2.13. Aloe conservation

2.13.1. Legislation, CITES and Red list status

Aloes present an archetypal conservation challenge, requiring protection of taxa that are rare, endemic and/or exploited, and effective management to ensure their sustainable use as natural resources important for livelihood security (Grace, 2011). Aloes are protected by law, and all *Aloe* species appear on CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendices, with the exception of *Aloe vera* L. (Klopper et al., 2009). This means that trade in wild-collected aloes is regulated to prevent utilization that would be incompatible with their survival in the wild (Klopper et al., 2009). Twenty-one *Aloe* species appear on CITES Appendix I and the remaining taxa are listed under Appendix II (CITES 2010). The genus is represented in several biodiversity hotspots including the Horn of Africa, Madagascar and Mascarene Islands, the Maputaland-Pondoland-Albany region, the Cape Floristic Region and the Succulent Karoo (Myers et al., 2000; Grace, 2011). Forty-six of South Africa's ~140 *Aloe* taxa are listed as threatened, 11% of which are Critically Endangered (CR) and 9% are Endangered (EN) (Raimondo et al., 2009). Redlisting of aloes elsewhere in Africa is vital for identifying important conservation hotspots, implementing conservation action plans for rare and threatened taxa, and initiating long-term monitoring projects.

2.13.2. Threats to wild aloe populations

The threats to *Aloe* species are multifaceted, but plant use especially is playing an increasingly important role in determining their survival in the wild (Smith et al., 2000). Major threats include habitat loss and extensive collection from the wild for horticulture and natural products (Smith et al., 2000; Grace et al., 2009). However, ill-advised farming practises, trampling by farm animals, afforestation, mining and urbanization have also contributed to the decline of many species (Jankowitz, 1975; Newton and Vaughan, 1996). A large number of aloes have significant ornamental value, and several of these species are threatened due to intense harvesting pressure from succulent collectors, e.g. *A. peglerae* and *A. polyphylla* (Abrie and Van Staden, 2001; Van Wyk and Smith, 2008; Pfab and Scholes 2004; Mofokeng and Jiwen, 2009). Furthermore, the threats faced by many taxa are exacerbated by their naturally restricted distributions (Holland, 1978; Newton and Vaughan, 1996), which not only makes them highly sought-after collector's items, but also amplifies the effects of other threats due to small populations (Raimondo and Donaldson, 2003).

2.13.3. Conservation and research of aloes in understudied regions

There is a large gap in knowledge on the ecology of many threatened aloes in Madagascar and countries at the Horn of Africa (e.g. Eritrea, Djibouti and Somalia). The *Aloe* species in these regions are primarily threatened by habitat destruction for agricultural development (Medhanie and Dioli, 2006; Kew Royal Botanic Gardens (KRBG), Madagascar Aloe Conservation Project (MACP), 2012). There are 121 *Aloe* species (147 taxa) indigenous to Madagascar, all of which are endemics, and most have highly restricted distributions and small populations (KRBG, MACP, 2012). Spiny Forest vegetation in semi-arid South and South-West Madagascar is a succulent plant hotspot, and >85% of the Spiny Forest plant species are endemics, many of which have important local medicinal uses (KRBG, Succulents of Madagascar, 2012).

Madagascan Spiny Forest is currently under major threat due to excessive bushfires, demands for wood for fencing and charcoal production, and plant removal by succulent collectors for the horticultural trade (KRBG, Succulents of Madagascar, 2012; J.-B. Castillon, pers. comm.). Currently there are two Madagascan *Aloe* species on the IUCN Red Data List, namely *A. suzannae* and *A. helenae*, both of which are assessed as Critically Endangered. This number is likely to change, as the Kew Royal Botanic Gardens has launched a collaborative initiative, the Madagascar Aloe Conservation Project

(MACP), which aims to assess the conservation status of all Madagascan *Aloe* taxa, develop an identification key for fieldworkers, and implement an effective conservation action strategy (KRBG, MACP, 2012). Not only is this project expected to contribute significantly to *Aloe* conservation in Madagascar, but aloes may also be good indicator species for plant endemism hotspots in the country, and it is hoped that findings will help target important biodiversity hotspots as priorities for conservation.

2.14. Concluding remarks

While a considerable volume of information on aloes is available in both the scientific and popular literature, data on certain ecological and conservation aspects are lacking. Knowledge on resprouting behaviour in the genus *Aloe* is valuable for establishing sustainable harvesting quotas for commercially important species and for informing appropriate management decisions. The studies conducted on aloe population structure have mostly focused on the Northern Cape tree aloes (*A. dichotoma* and *A. pillansii*). Population monitoring of other endangered aloes, especially those targeted by harvesters and plant collectors would be valuable for their conservation and management. Other opportunities for further research include the fire ecology of certain aloe groups, such as grass aloes, especially in areas where commercial forestry and agricultural development have resulted in habitat fragmentation and associated increases and/or suppression of fires. Additional germination and long-term seed storage studies on Critically Endangered aloe taxa would also be beneficial for enhancing their conservation. The use of aloes for ecosystem restoration in degraded areas is also largely understudied. It is therefore recommended that further research and experimentation be undertaken in this field, especially considering the significant potential aloes have in combating problems such as erosion and desertification associated with global climate change.

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Appendix



Fig. 1. Representatives of the ten growth forms of South African aloes (*sensu* Van Wyk and Smith (2008)). (a) Tree aloe: *A. dichotoma*, (b) Single-stemmed aloe: *A. marlothii,* (c) Multi-stemmed aloe: *A. succotrina*, (d) Rambling aloe: *A. ciliaris*, (e) Creeping aloe: *A. perfoliata*, (f) Stemless aloe: *A. peglerae*, (g) Speckled aloe: *A. zebrina*, (h) Spotted aloe: *A. microstigma*, (i) Dwarf aloe: *A. longistyla*, and (j) Grass aloe: *A. hlangapies*.Photographs courtesy of: (a) G.W. Reynolds, (b) C.T. Symes, (c) A.W. Klopper, (d) E. J. Van Jaarsveld (e) S.R. Cousins, (f) C.T. Symes, (g) R.R. Klopper, (h) A.W. Klopper, (i) A.W. Klopper, (j) W. Chin.

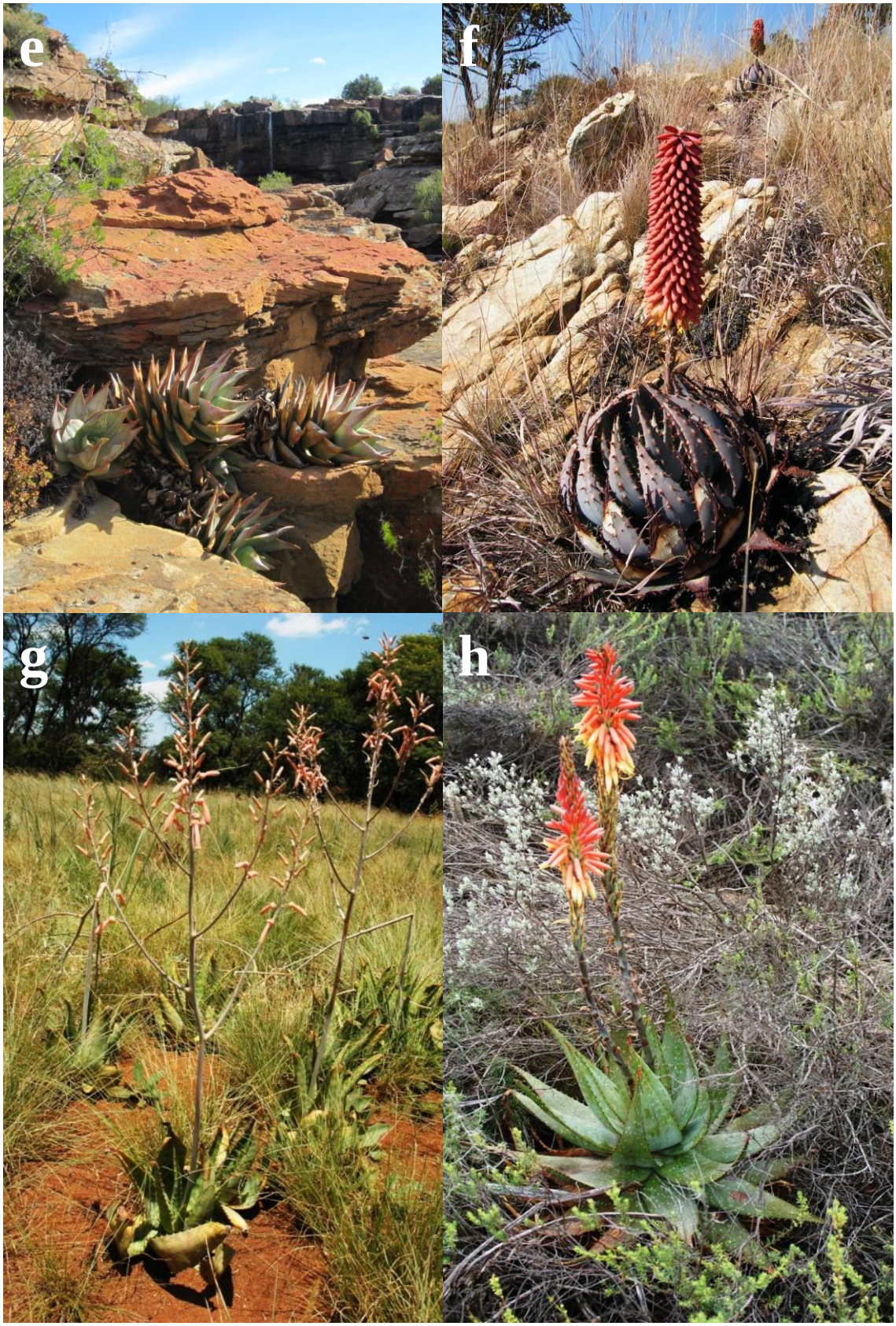


Fig. 1. (continued)



Fig. 1 (continued)

CHAPTER THREE

Elucidating patterns in the population size structure and density of *Aloe plicatilis*, a tree aloe endemic to the Cape fynbos, South Africa

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3.1. Abstract

Studies on plant population size structure provide baseline information for monitoring and conservation. Traditionally, inverse-J-shaped size class distributions (SCD) were considered indicative of 'healthy', stable plant populations; however, this may not hold true for slow-growing, long-lived species. This study assessed the population size structure of 19 populations of *Aloe plicatilis*, a Cape fynbos endemic tree aloe, and quantified population size and density. A strong positive linear relationship between stem diameter (SDr) and height was used to align SDr and height SCD widths, and to harmonize stage and size classes. Onset of reproduction in *A. plicatilis* occurs at ~15 cm SDr and ~0.8 m in height. *Aloe plicatilis* displays the 'bonsai effect' whereby the growth of individuals in very rocky sites may be suppressed. Stunted plants may be non-reproductive 'suppressed juveniles' or 'reproductive dwarfs'. Population size, extent and density ranged from 31 to >110000 individuals, 0.05 – 103 ha and 75–3000 plants/ha respectively. *Aloe plicatilis* shows little support for the 'abundant centre hypothesis', which holds that populations at the centre of a species' distribution tend to be larger and/or denser than those at the edges. SDr and height SCDs for all 19 populations combined were bell-shaped. Bell-shaped SCDs were the most common (50% of populations). Seven populations displayed irregular SCDs, but were similar in structure to the bell-shaped SCDs, both of which were attributed to an adult-persistence population survival strategy. This study challenges the suitability of the inverse-J as the only SCD indicative of healthy, stable populations for long-lived, slow-growing species. The

study provides baseline demographic data on *A. plicatilis* across its distribution for long-term monitoring, and provides insights useful for examining trends in the demographics of other long-lived, slow-growing species.

Key words: Bell-shaped size class distributions; Bonsai; Height; Long-lived; Slow-growing; Stem diameter

3.2. Introduction

Population ecologists endeavour to understand the numerical impact of the interactions between species and their environment by studying population size, distribution and size structure, and how and why these change or stay constant over time (Silvertown, 1987; Rockwood, 2006). All biological populations have age, size, spatial and genetic structures, and understanding the dynamics of these structures provides insight into the functioning of populations (Hara, 1988). The present size structure of a plant population is determined by temporal variation in several biotic and abiotic factors that have acted on both past and current individuals in the population (Bullock, 1996; Hutchings, 1997). These factors may be either intrinsic or extrinsic. Intrinsic factors include genetic variation, age differences, heterogeneity of resources, competition, and recruitment patterns, which are determined by seed production, the presence of soil seed banks, germination rates and seedling survival (Silvertown, 1987; Bullock, 1996; Hutchings, 1997). Factors that are extrinsic to the population encompass weather patterns and mortality risks to which seeds and recruits have been exposed, such as seed predation, disease, harvesting and herbivory (Silvertown, 1987; Bullock, 1996; Hutchings, 1997).

The spatial structure of plant populations is also a legacy of the spatial arrangement of parent plants, and the historical interactions between them (Hutchings, 1997). However, inferences made from population size structure may be not only of past, but also future demographic events (Bullock et al., 1996). Huston and DeAngelis (1987) proposed that changes in size class distributions (SCDs) result from, *inter alia*, (a) the size and time dependence of each individual's growth rate, which results from interaction between its life history pattern with the environment, and (b) mortality that may affect size classes in different ways. Interactions between the factors that shape population structure, may, however result in considerable complexity (Huston and DeAngelis, 1987); hence, inferring mechanisms from known SCDs can be challenging, and necessitates a holistic, integrated approach, with maximal use of available data.

Long-term population monitoring data provide a substantial depth of knowledge about plant population dynamics and their implications for conservation and management. Recent studies on the impact of climate change on plant populations demonstrate the importance of longer-term climatic and demographic processes in shaping the patterns currently observed in plant populations (e.g. Foden et al., 2007; Jack, 2012). However, long-term studies are costly, and in conservation biology it is often unadvisable to wait until long-term data sets have accumulated before making management decisions, especially for rapidly declining species (Wiegand et al., 2000). A more feasible way to investigate population dynamics is to use snapshot population assessments distributed over space instead of time. Pérez Farrera and Vovides (2004) emphasise that it is important not to make demographic characterisations of a species based on one population only, especially if a snapshot study is used. Demographic studies should be carried out at a metapopulation level to understand the variation and behaviour of the species within and between populations in the range of habitats in which it occurs (Pérez Farrera and Vovides, 2004).

In addition to knowledge of a species' population size structure, information on the distribution of its abundance in both time and space helps elucidate the relationships between the species and its environment (Brown et al., 1995). Furthermore, studies on population size and density add extra weight to baseline population data, which are important for testing hypotheses relevant to conservation and management, as well as species' responses to climate change (Sagarin et al., 2006). For example, an appraisal can be conducted on the species' adherence to the 'abundant centre hypothesis' which suggests that large populations of a species occur at the centre of its distribution, while smaller ones occur at the fringes (see Sagarin and Gaines, 2002). Knowledge of population sizes and densities also helps pinpoint populations that are important for conservation and monitoring (e.g. small populations at the range edge may be the first to show signs of decline as the climate changes). Hence, characterisation and interpretation of population size structure, and population size and density over space provides useful data that are readily available for management (Botha et al., 2002; Mwavu and Witkowski, 2009) and for planning long-term monitoring (e.g. Knowles and Witkowski, 2000).

To gain the utmost insight into a population's demographics using snapshot data, it is important to extract the maximum amount of information available therein (Wiegand et al., 2000). Several recent short-term studies on plant population structure quantified differences in structural patterns across populations using size class distribution (SCD) slopes (*sensu* Condit et al., 1998) combined with

indices such as Simpsons index of dominance, Permutation index, evenness, and quotients (e.g. Wiegand et al., 2000; Botha et al., 2002; Mwavu and Witkowski, 2009; Venter and Witkowski, 2010; Helm and Witkowski, 2012). These indices condense large volumes of data contained in SCDs (Wiegand et al., 2000) and facilitate analyses of the patterns within and between populations. The next step is to attempt to understand and explain the mechanisms responsible for the patterns that have been revealed using these indices. These mechanisms may be numerous and inter-related, and may operate in concert, for example disturbances such as fire and herbivory (e.g. Helm and Witkowski, 2012), climatic effects such as rainfall, temperature gradients, and frost (e.g. Whitecross et al., 2012), and exploitation e.g. harvesting for traditional medicine (e.g. Botha et al., 2002; Williams et al., 2007) or the horticultural trade (e.g. Donaldson and Bösenberg, 1999).

Both height and stem diameter (SDr) are important when examining SCDs, especially in high disturbance environments (Helm and Witkowski, 2012). Basal diameter is usually more useful than height as a measure of tree size as it is not modified by damage from herbivory or fire; however, analysing height and SDr in tandem provides deeper insight into patterns in population structure (Helm and Witkowski, 2012). For the sake of simplicity and practicality, most studies use only SDr or height. Nevertheless, for a given genus or species, it might prove useful to investigate whether there are major differences in SDr and height SCDs within populations, and whether one or the other provides a better reflection of population size structure. Such knowledge may be useful for follow-up studies, where eliminating either SDr or height measurements may reduce the time spent and costs incurred.

When interpreting SCDs it is vital that individuals are placed in appropriately delimited size classes and that these size classes correspond with stage classes that are biologically meaningful for the species in question (e.g. Helm and Witkowski, 2012). Dividing a population into groups that differ in their probabilities of survival and abilities to reproduce is important for predicting the dynamics of the entire population (Łomnicki, 1988). Traditionally, most plant populations have been thought to have a ‘size hierarchy’, i.e. a frequency distribution of plant sizes in which relatively few individuals constitute most of the population’s biomass and most individuals are fairly small (Weiner and Solbrig, 1984). In this context, relative proportions of seedlings, juveniles, sub-adults and adults theoretically provide a population health index and offer clues about past and future demographic events (Łomnicki, 1988). Abundant seedlings and juveniles relative to adults results in a classic inverse J-shaped SCD, which is generally interpreted as indicative of a healthy, ‘stable’ and potentially growing population (Condit et al., 1998). Conversely, a scarcity of seedlings and juveniles (represented by a J-shaped curve) may

indicate a declining population (Condit et al., 1998). Thus, deviation from an inverse-J SCD (for example by a bell- or J-shaped distribution) may be cause for concern. However, Venter and Witkowski (2010) caution that for slow-growing, long-lived species this may not hold true, since abundant mature individuals can sustain populations despite low or episodic recruitment. Indeed, bell- or J-shaped SCDs have been observed in a number of long-lived, slow-growing species, and were not always considered indicative of unstable or declining populations (see Scholes 1988; Witkowski and Liston, 1997; Pfab and Witkowski, 1999; Raimondo and Donaldson, 2003; Méndez et al., 2004).

Previous studies on aloe population structure have focused primarily on the Northern Cape tree aloes *Aloe dichotoma* Masson and *Aloe pillansii* L. Guthrie (Midgley et al., 1997; Bolus et al., 2004; Duncan et al., 2006; Foden et al., 2007; Jack, 2012). However, no detailed population studies have been conducted on any Cape fynbos *Aloe* species. *Aloe plicatilis* (L.) Miller (Asphodelaceae) is the only tree aloe found in the Cape fynbos, and one of only eight *Aloe* species in the region. Concerns surrounding sustainable use of this charismatic species for the horticultural trade, and a lack of knowledge regarding its ecology and conservation status prompted research to better understand dynamics and patterns across its distribution. The primary aim of this study was therefore to examine patterns in the population size structure and density of *A. plicatilis* across its distribution and attempt to understand possible factors responsible for these patterns. Five key questions were asked: (a) At what size does the onset of reproduction occur in *A. plicatilis*, and what factors might influence this threshold size? (b) How do population size and density vary across populations and does *A. plicatilis* conform to the 'abundance centre hypothesis'? (c) What are the salient patterns in the SCDs of a sample of 19 populations across the range of *A. plicatilis*? (d) Do SDr and height SCDs differ significantly within populations? (e) Is the inverse-J-shaped SCD indicative of a 'healthy' stable population of *A. plicatilis*?

3.3. Methods

3.3.1. Study area

Aloe plicatilis is endemic to the Cape fynbos in mountainous areas in the Cape Winelands (also known as the "Boland") within the Cape Floristic Region (CFR), Western Cape Province, South Africa. Covering approximately 90 000km^2, with ~9 000 indigenous vascular plant species, 69% of which are endemic, the CFR is one of the richest regions in the world in terms of botanical diversity (Goldblatt and Manning, 2000). The Cape fynbos has a Mediterranean-type climate, with hot, dry, windy summers

and cool wet winters (Keeley et al., 2012). Fynbos vegetation is fire-dependent, and fires are more common in the fynbos than any other Mediterranean-type climate region (Manning, 2007). Fires play a key role in determining major vegetation patterns within the region and occur at various frequencies depending on the vegetation type (Keeley et al., 2012). Fynbos has a crown fire regime and is extremely flammable when dry, with most fires occurring during summer, at intervals of 10–30 years (Keeley et al., 2012).

Aloe plicatilis has a restricted distribution that extends from the Franschhoek Mountains near Vyeboom in the south, to the Elandskloof and Grootwinterhoek Mountains near Tulbagh in the north (Fig. 1) (Van Wyk and Smith, 2008). East to west, it occurs from the Du Toit's Kloof Mountains near Rawsonville to the Paardeberg mountain between Malmesbury and Wellington (Fig. 1). Populations occur at altitudes of between 190 and 850 m in areas that receive an average annual rainfall of 400–2000 mm (Table 1). *Aloe plicatilis* occurs mainly in Hawequas and Kogelberg Sandstone Fynbos, but some populations also occur in Granitic vegetation types (Table 1) (Mucina and Rutherford, 2006). The major mountain ranges are dominated by Table Mountain sandstone, which is acidic and poor in nutrients (especially nitrogen and phosphorus), with outcrops of Cape granite to the west and southwest (Witkowski and Mitchell, 1987; Manning, 2007). Most *A. plicatilis* populations occur in mountain catchment and conservation areas, but some are also found on privately-owned land (Table 1).

3.3.2. Study species

Aloe plicatilis is one of six South African tree aloe species, and the only tree aloe that occurs in the Cape fynbos (Van Wyk and Smith, 2008). It is a relatively slow-growing, well-branched shrub to small tree, with dichotomously branching stems, each of which ends in a set of 12–16 alternate, fleshy leaves in a fan-like arrangement (Carter et al., 2011). Adult plants average 1.5–2 m in height (≥50–70 years old, based on measurements of the growth rates of plants in cultivation), but exceptionally large individuals may reach 4–5 m (≥130–160 years old). *Aloe plicatilis* flowers from August to October and the fruiting season starts in early November, with fruit capsules dehiscing from December – January (Van Wyk and Smith, 2008). The relatively small, winged seeds are wind-dispersed. The species grows in well-drained, acidic soils on steep rocky slopes and rocky outcrops in areas of high winter rainfall (Van Wyk and Smith, 2008; Carter et al., 2011). Although it occupies predominantly rocky sites that afford it some protection from fires, *A. plicatilis* is fairly fire-tolerant and burned individuals usually recover by resprouting from apical meristems (Van Jaarsveld, 1989; Thomas, 1991; Thomas and

Goodson, 1992). It is also the only aloe known to have thick, corky bark, which provides further protection against fire damage (Van Jaarsveld, 1989).

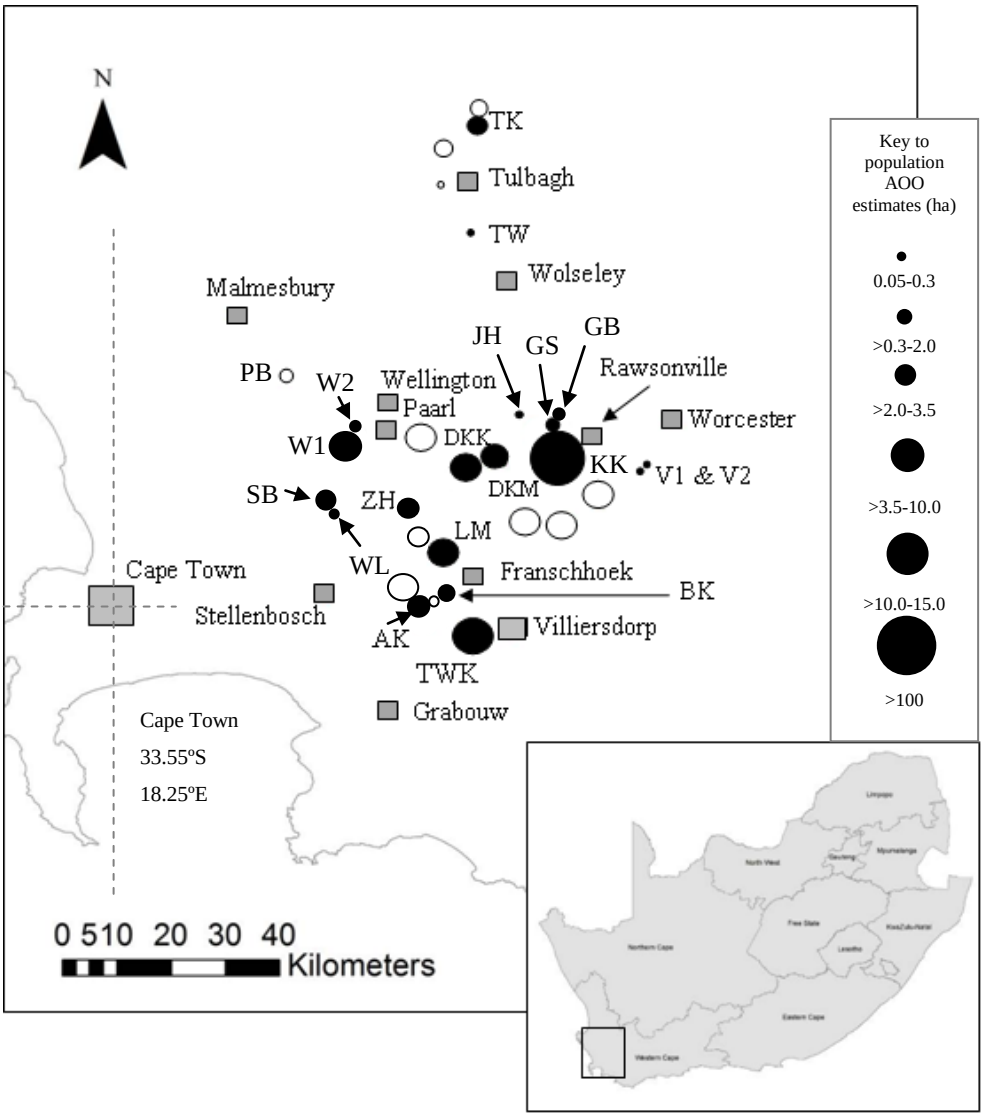


Fig. 1. Distribution of the 30 known populations of *Aloe plicatilis* in the Cape Floristic Region, Western Cape, South Africa. Shaded circles represent the 19 populations that were surveyed for population size structure and density, and open circles represent non-surveyed populations. Grey squares denote major towns or cities. The sizes of the circles correspond with estimated population size (calculated estimates for surveyed populations (see Table 2) and visual estimates for non-surveyed populations). Population names, abbreviations and localities: AK (Assegaaibooskloof; Berg River, Groot-Drakenstein Mountains, near Franschhoek), BK (Bosjemanskloof, Berg River, near Franschhoek), DKK (Du Toit's Kloof Krom River; Du Toit's Kloof, between Paarl/ Wellington & Rawsonville), DKM (Du Toit's Kloof Molenaars River; Du Toit's Kloof, between Paarl/ Wellington & Rawsonville), GB (Goudini Badsberg; near Rawsonville), GS (Goudini Spa; near Rawsonville), JH (Jason's Hill; Slanghoek Valley, near Rawsonville), KK (Kliphoutkloof; near Rawsonville), LM (La Motte; bordering Haweqwa Nature Reserve, Franschhoek), PB (Paardeberg; between Wellington & Malmesbury), SB (Skurweberg; Wiesenhof Wildpark, near Stellenbosch), TK (Tulbagh Kleinpoort; Groot-Winterhoek Nature Reserve, near Tulbagh), TW (Tulbagh Waterfall; Waterval Nature Reserve, near Tulbagh), TWK (Theewaterskloof; Theewaterskloof dam, near Vyeboom), V1 (Voorsorg 1; Watervalskloof, near Rawsonville), V2 (Voorsorg 2; Grootkloof, near Rawsonville), WL (Wiesenhof Lookout; Wiesenhof Wildpark, near Stellenbosch), W1 (Windmeul 1; Bordering Paarl Mountain Nature Reserve, Windmeul), W2 (Windmeul 2; Rhebokskloof, Windmeul) and ZH (Zachariashoek; Klein-Drakenstein Mountains, Haweqwa Nature Reserve, between Paarl and Franschhoek).

3.3.3. Locating the populations

Initially, a thorough literature survey, consultations with five South African herbaria and exploration of web-based species databases yielded nine known *A. plicatilis* populations, most of which were relatively accessible. There were, however, reports of other lesser-known, more inaccessible populations, and possibly others yet to be discovered, none of which were documented. Extensive networking with researchers, nature conservation officials and landowners was undertaken to locate these undocumented populations. Furthermore, an article on the study was published in *Veld & Flora* (Cousins, 2010), which included a request to the public to provide information on any lesser-known populations (Appendix I). A total of 21 additional populations were identified through these sources, bringing the total number currently known to 30 (Fig. 1). Triplicate voucher specimens were collected from most newly documented populations and lodged in the National (PRE), Compton (NBG), and C.E. Moss (J) herbaria.

3.3.4. Sampling and measurement

3.3.4.1. Delineating populations

Before commencing the population surveys, it was important to decide what exactly constituted a population of *A. plicatilis* (Rockwood, 2006). Some populations e.g. W1 and W2 (Fig. 1) had clear boundaries, consisted of fairly continuous aggregations of plants and could be circumnavigated in their entirety. Others, e.g. KK and LM were spread out over broad areas and showed dense aggregations of plants in some areas, with more widely scattered plants elsewhere. Due to challenging manoeuvrability in the very steep, mountainous terrain, it was sometimes not feasible to attempt to delineate the boundaries of these very large, widely scattered populations. Discrete populations were delineated by taking GPS coordinates of the periphery of the entire population, whereas with very large, more loosely defined populations, only the most accessible and/or most distinct aggregation of individuals that constituted the core of the population was delineated. Attempts were then made to determine the area covered by the rest of these populations using photographs, visual observations with binoculars and topographical maps. Of the 30 known populations, 19 were surveyed (Fig. 1; Table 1). The surveyed populations provided a representative sample over the entire geographical range of the species and a fair representation of high- and low-lying populations, which avoided bias towards easily accessible populations. The eleven unsurveyed populations were discovered subsequent to the major data

collection period and hence could not be sampled, but the approximate centres of these populations were recorded by GPS (Fig. 1).

3.3.4.2. Plant-based measurements

Basal SDr 10cm above the basal swelling was measured using tree callipers and height of the tallest stem was measured with a tape measure (where the leaf cluster emerges from the stem). Two methods were used to estimate plant density and the total number of individuals: (a) Point centred quarter method (PCQ) and (b) Nearest neighbour method (NN) (Cottam and Curtis, 1956; Marom, 2006). The individuals measured using NN were those closest to the individual measured in each quadrant for the PCQ. A minimum of 40 and a maximum of 90 individuals were sampled for populations with >50 individuals, while every plant was measured in populations with ≤50 individuals. For very inaccessible populations, (e.g. TK), sample sizes were sometimes <40 due to severe time constraints caused by long travelling distances and/or inclement weather conditions. For large populations (>50 plants), transects were laid across the population at lengths and distances apart that were appropriate to the spatial extent of the population, with PCQ points spaced at 15–20m intervals along each transect. Placement of transects in some populations proved challenging due to steep slopes, sheer rock faces, large boulders and dense bush clumps. When laying out the transects, attempts were made to encompass as much topographical variation within each population as possible, so as to avoid any bias towards the gentlest slopes. In order to investigate the relationship between plant size and degree of surrounding rock cover, the rock cover within a 1m radius of each *A. plicatilis* individual was visually estimated. These estimates were then regressed against plant size (SDr and height) to test for significant relationships.

3.3.5. Data and statistical analyses

3.3.5.1. Delimitation of size and stage class widths

Size class widths were delimited to accommodate more individuals with increasing size, as advised by Condit et al. (1998). This method balances the samples across the size classes, since the number of individuals in successive classes generally declines with increasing size (Condit et al., 1998). Furthermore, stage classes (juveniles, sub-adults and adults) were also taken into account in order to make the size classes biologically meaningful (Helm and Witkowski, 2011). Most studies on the population structure of trees provide little detail on how SDr or height classes relate to stage class.

McLaren et al. (2005) and Helm and Witkowski (2011) harmonized stage classes with size classes, but the delineation of boundaries between stage classes was not explicitly defined. Few studies have used a combination of SDr and height to assess population structure, and in this study an attempt was made to match SDr classes with height classes in order to facilitate easy comparisons between SDr and height SCDs. To this end, a linear regression between height and SDr for individuals from all 19 populations was performed to ascertain the numerical relationship between the two (Fig. 2). This relationship was then used to synchronise SDr and height classes.

To determine the SDr and height classes that correspond with the appropriate stage classes, it was necessary to define the approximate size at which juveniles become sub-adults, and sub-adults become adults. The onset of reproduction provides a relatively clear distinction between juveniles and adults (Donovan and Ehleringer, 1991), however, there is little consensus regarding the point at which a seedling becomes a juvenile (Hanley et al., 2004). For this reason, seedlings were not classified as separate from the juvenile stage class. Juveniles were defined as non-reproductive individuals; sub-adults as plants occupying size classes where the proportion of non-reproductive individuals outweighed, equalled, or was slightly less than the proportion of reproductive plants (threshold of 40%), and adults were defined as individuals occupying size classes where the large majority of plants were reproductive. In order to do this, a SCD was constructed for reproductive versus non-reproductive individuals using five populations (n=221 plants) for which flowering data were available (Fig. 3). The stage classes were then defined as: juveniles (SDr ≤4 cm; height≤ 0.2 m), sub-adults (4 cm< SDr ≤15 cm; 0.2 m< height ≤0.8 m) and adults (SDr >15 cm; height >0.8 m). Following delimitation of size and stage class widths, individuals were assigned to size classes and SCDs were constructed for SDr and height.

3.3.5.2. Estimates of density and population size

For populations of >50 individuals, both PCQ and NN were used to estimate plant density (except for WL where only NN could be used), while for small populations (<50 individuals) only NN was used. For PCQ, density (plants/m^2) = $1/q^2$, where 'q' is the mean distance from each PCQ point to the centre of the nearest *A. plicatilis* individual.

For NN, $D = \frac{0.3556}{(\sum_{i=1}^{n}(\frac{r}{p}))^2}$

Where 'D' = density, '*n*' is the number of individual plants sampled, '*r*' is the distance from each sampled individual per quadrant to its nearest neighbour, and '*P*' is the total number of random points sampled. For both PCQ and NN: Number of individuals in the population = density × population area. Population area (ha) was calculated using ArcMap, whereby GPS points of the periphery of each population were used to create area of occupancy polygons. For populations with ≤50 individuals, density was calculated as the total number of individuals divided by the population area.

3.3.5.3. Patterns in population size structure

SDr and height SCDs were constructed for all populations combined (Fig. 4) and for each individual population (Fig. 5). The following measures were then used to investigate patterns in population structure within and between populations: (a) Permutation index (P), (b) Simpson's index of dominance (λ), (c) Evenness (E) and (d) Sørensen similarity index (Sør) (=Bray-Curtis). The diversity indices λ, E and Sør were calculated using the software *EstimateS.* P was calculated using the formula in Wiegand et al. (2000) and measures the degree of deviation of a SCD from a monotonic decline (i.e. a distribution with a smooth inverse-J shape). A monotonically declining population will have P=0 and a population with a discontinuous SCD will have a P>0 (Wiegand et al., 2000). The higher the P, the greater the deviation from a monotonic decline (Wiegand et al., 2000).

The index λ is based on the assertion that diversity is related to the probability that any two individuals selected from a sample of the population at random are of the same size class, by measuring the occurrence of dominant (more frequent) size classes (Maurer and McGill, 2011). The closer λ is to 1, the higher the probability that two individuals drawn at random belong to the same size class. λ values close to 0 indicate that individuals are more evenly distributed among the size classes. Evenness quantifies the unequal representation of size classes against a hypothetical population in which all size classes are occupied equally (Maurer and McGill, 2011). The Sørensen index expresses the degree to which occupation of the size classes between populations is alike, with high values associated with large numbers of shared size classes (Maurer and McGill, 2011).

SDr and height SCD slopes were calculated using the methods in Condit et al. (1998). A regression was performed using corrected abundance per size class (N_i+1) as the dependent variable and the size class midpoint (d_i) as the independent variable. The corrected abundance was calculated by dividing the number of individuals in each size class by the width of the size class (see Helm and Witkowski, 2012). Following Everard et al. (1995), negative slopes indicate ongoing recruitment (or growth suppression), with more individuals in smaller size classes than larger ones (steep negative slopes indicate better recruitment than gentle ones). Flat slopes indicate equal numbers of plants in small and large size classes, suggesting either limited recruitment or relatively high numbers of large plants, possibly from earlier recruitment events. Positive slopes imply limited recent recruitment, but possibly prior episodic recruitment (or perhaps accelerated growth across intermediate size classes). Comparisons between SDr and height SCDs within populations were conducted using Kolmogorov-Smirnov tests in STATPAK. Significant differences between SDr and height SCDs within populations would suggest that SDr and height give different reflections of population structure.

The four indices and SCD slopes were then used to place the SCDs of each population into one of three groups depending on the patterns they displayed. Group 1 consisted of inverse-J-shaped SCDs, Group 2 comprised J-shaped SCDs and Group 3 included both bell-shaped and irregular (or 'flattened' bell-shaped) SCDs. A regression relationship between the mean similarity (Sør) between the size structure of each population and all the others combined, in terms of SDr and height, provided a visual representation of the degree of similarity between the structure of individual populations and that of all the other populations. Populations similar in structure clustered together on the Sør plot and were therefore placed in the same group.

3.3.6. Environmental and climatic factors associated with the distribution of *Aloe plicatilis*

Climate data for each population (median annual rainfall and mean monthly temperature) were extracted in ArcMap for each population from the Schulze Climate Database (Schulze, 1997) using the area of occupancy polygons mapped in the field. The year of the most recent fire within each population was obtained from nature conservation officials, local landowners and from Fire Products (MODIS fire locations) from the Wide Area Monitoring Information System (WAMIS), MODIS EVI time series data for southern Africa (CSIR-Meraka, http://afis.meraka.org.za/wamis/products/long-term-time-serie). The vegetation type in which each population occurred was determined using Mucina and Rutherford (2006).

Table 1 Environmental and climatic conditions associated with the 19 surveyed *Aloe plicatilis* populations in the south-western Cape, South Africa.

Population[a]	Land ownership[b]	Vegetation type	Long term average annual rainfall[c] (mm)	Long term average monthly temperature[c] (°C)	Altitudinal range (m)	Topographic position	Predominant Aspect	Most recent burn
AK	C	Kogelberg Sandstone Fynbos	1940	14	387-474	Lower mountain slopes	NE	December 2005
BK	C	Kogelberg Sandstone Fynbos	1526	15	288-386	Mid to lower slopes mountain slopes	W	February 2010
DKK	C	Hawequas Sandstone Fynbos	932	15	462-632	Hilltops, mid and lower mountain slopes	NW, SE	2009
DKM	C	Hawequas Sandstone Fynbos	1062	15	372-501	Lower mountain slopes	S	October 2007
GB	P	Hawequas Sandstone Fynbos	562	17	481-521	Mid to upper mountain slopes	E	2009
GS	P	Hawequas Sandstone Fynbos	607	17	236-396	Lower mountain slopes	E	2010
JH	P	Hawequas Sandstone Fynbos	608	16	337-373	Lower mountain slopes	NE	2005
KK	C/P	Hawequas Sandstone Fynbos	652	15	213-340	Mid to lower mountain slopes	E	January 2011
LM	C/P	Hawequas Sandstone Fynbos	771	16	248-445	Mid to lower mountain slopes	W	2003
SB	C	Boland Granite Fynbos	788	15	414-565	Crests and upper slopes of two ridges	NE, SW	2000
TK	C	Winterhoek Sandstone Fynbos	921	14	867-944	Mid to lower slopes in high-lying valley	NW	±10 years
TW	C	Hawequas Sandstone Fynbos	465	18	192-226	Single rocky outcrop on hillside	Various	±7 years
TWK	C	Kogelberg Sandstone Fynbos	1076	16	334-393	Rocky outcrops on lower mountain slopes	Various	2009
V1	P	Hawequas Sandstone Fynbos	422	15	443-485	Rocky outcrop on lower mountain slopes	N	January 2011
V2	P	Hawequas Sandstone Fynbos	426	15	458-542	Mid slopes	N	January 2011
WL	C	Boland Granite Fynbos	788	16	203-392	Hilltop	Various	2000
W1	C/P	Boland Granite Fynbos	580	16	285-338	Mid to lower mountain slopes	NE	≥10 years
W2	C	Swartland Granite Renosterveld	580	15	579-634	Hilltop and upper slopes	NW	≥10 years
ZH	C	Hawequas Sandstone Fynbos	1013	14	608-830	Rocky outcrops on high-lying plateau	Various	1999 & 2007[e]

[a]Key to population abbreviations appears in Fig. 1.
[b]C = Conservation area; P = Privately owned land; C/P = Parts of the population in a conservation area and others on privately owned land
[c]Mucina and Rutherford (2006).
[d]Schulze Climate Database (Schulze, 1997b).
[e]Some parts of the population last burned in 1999 and others in 2007.

3.4. Results

3.4.1. Relationship between stem diameter and height

The linear regression between SDr and height indicates a strong, significant relationship (r^2=0.75; p<0.0001) (Fig. 2), which justified its use for harmonizing SDr and height class widths. The exponential relationship in Fig. 2, however, also shows a strong, significant relationship (r^2=0.79; p<0.0001) indicating that *A. plicatilis* fits the model of elastic similarity for trees proposed by McMahon (1973), whereby SDr is predicted to vary in proportion to the 1.5 power of height according to the equation: SDr = f (height$^{1.5}$), where f is a constant. The equation for *A. plicatilis* is SDr = 0.02(Height)$^{1.33}$ (Fig. 2), only a minor departure from the generic equation.

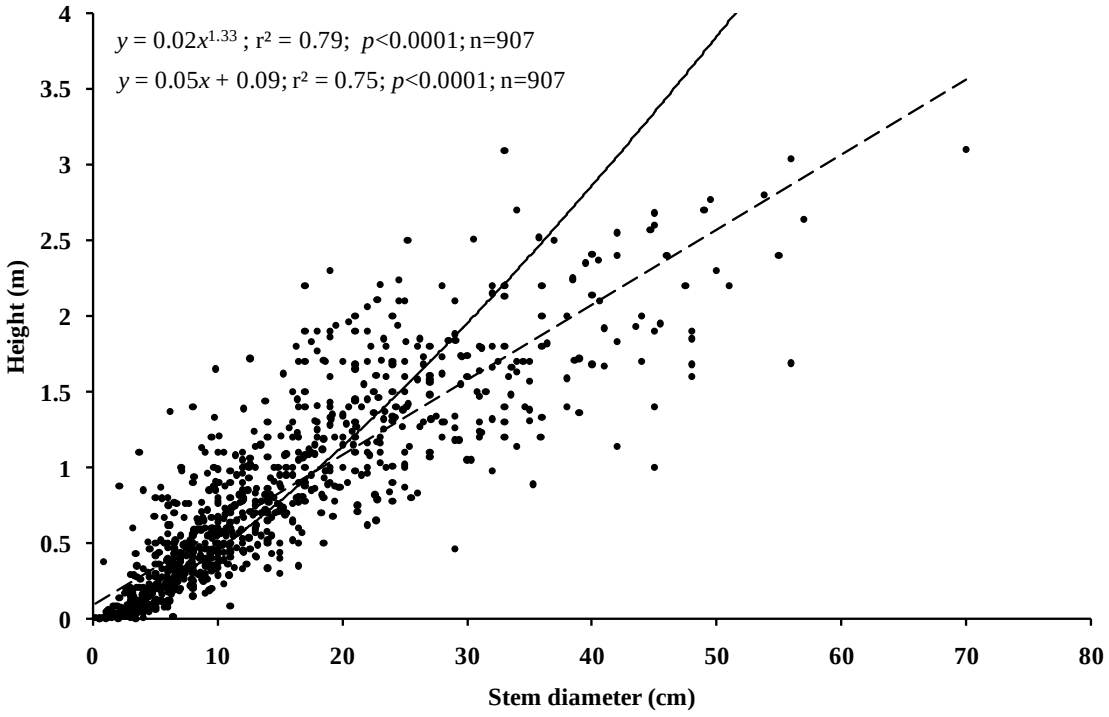


Fig. 2. Regression relationship between stem diameter and height for all plants in the 19 *Aloe plicatilis* populations surveyed. The linear fit (dotted line) was used to synchronise stem diameter size class distributions with height size class distributions. The exponential fit (solid line) was used to test for adherence to the model of elastic similarity for trees (McMahon, 1973).

3.4.2. Stage classes and size at reproductive maturity

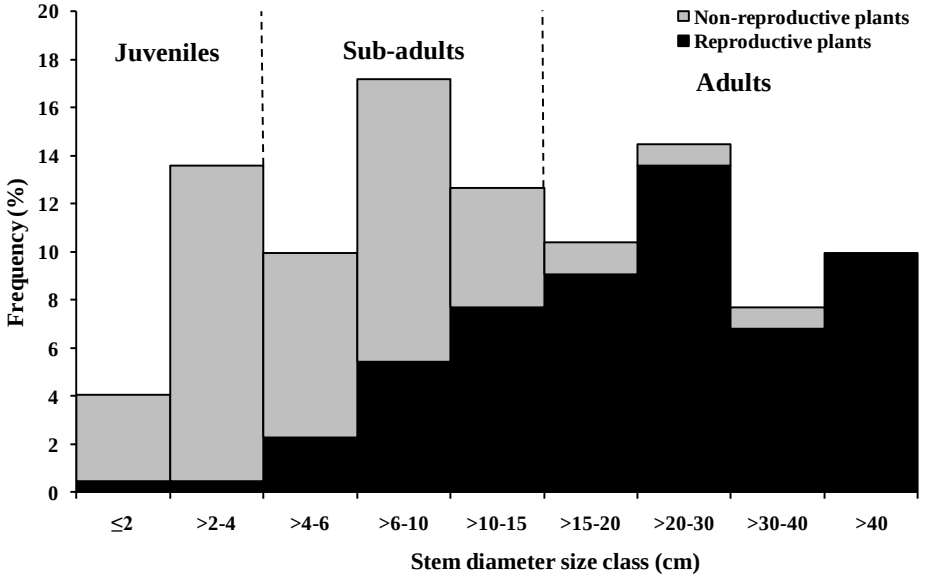
Aloe plicatilis individuals generally reach reproductive maturity at SDrs >4 cm and heights >0.2 m (sub-adult phase), but adults *sensu stricto* are usually individuals of approximately >15 cm SDr and >0.8 m in height (Fig. 3; Fig. 6a). Notwithstanding, reproductively mature individuals were found in even the smallest SDr size classes, but such plants were rare. There were weak, but significant negative relationships between percentage rock cover surrounding *A. plicatilis* individuals and plant size (SDr and height) (Fig. 7a, b), which suggests that individuals growing in very rocky areas tend to stay small, while those growing in less-rocky sites attain greater size.

Aloe plicatilis exhibits what shall be termed the 'bonsai effect' henceforth, whereby plants growing in small soil pockets in rock fissures with limited rooting space generally stay smaller than similarly-aged individuals that colonise less rocky sites. These 'mountain bonsais' may remain as non-reproductive 'suppressed juveniles' (Fig. 6c) for many years during which the onset of flowering is delayed due to growth restrictions and resource limitation, which is considered a key factor in determining the time of first flowering in plants (Lacey, 1986). Upon accumulation of sufficient resources for reproduction, they become 'reproductive dwarfs' (Fig. 6b). Hence, at any given time, an *A. plicatilis* population may consist of a mixture of true juveniles, suppressed juveniles, true adults and reproductive dwarfs (Fig. 6a-c).

3.4.3. Variations in population size and density

Population size varied widely over five orders of magnitude from 31 (JH) to >110 000 individuals (KK) (Table 2). There did not appear to be any relationship between a population's size and its position within the species' distribution, although many of the larger populations tended to be in the core (Fig. 1). Densities were comparable between populations, with only a few being markedly high or low (Table 2; Fig. 6d, e). The PCQ and NN methods often yielded somewhat different density estimates, with PCQ density usually higher than NN. These differences reflected accordingly in the estimated number of individuals per population. There was no relationship between population size and density (linear regression analyses yielded r^2 values of 0.02 and 0.01 (p>0.05) for PCQ and NN respectively). The population with the highest density (WL) showed high recent recruitment, with large numbers of individuals in the smallest size classes (Group 1, Fig. 5), while the least dense population (JH) showed no recent recruitment (Group 2, Fig. 5)

(a)



(b)

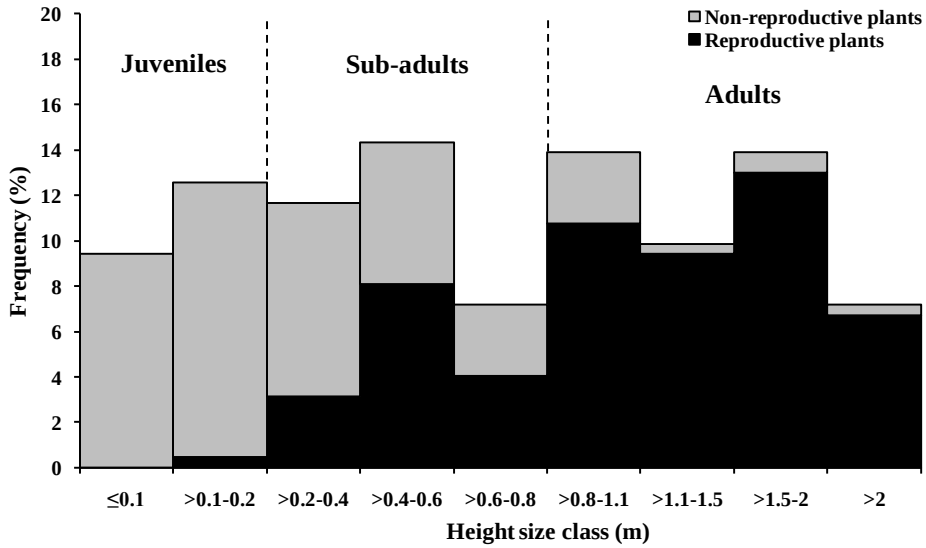


Fig. 3. (a) Stem diameter (SDr) and (b**)** height size class distributions for plants surveyed in five *Aloe plicatilis* populations for which flowering data were available (DKK, DKM, GB, GS & V1). The percentage of reproductive and non-reproductive individuals in each size class was used to delineate the boundaries between stage classes (juveniles, sub-adults and adults). Stage class boundaries are indicated by dashed lines.

3.4.4. Patterns in population structure

The SDr and height SCDs for all populations combined were bell-shaped (Fig. 4a,b). Of the individual populations, one displayed an inverse-J-shaped SCD (WL), two were J-shaped (DKM and JH), nine were clearly bell-shaped (AK, KK, LM, SB, TW, V2, W1, W2 and ZH) and seven were irregular or tended towards a 'flatter' shape (BK, DKK, GB, GS, TK TWK and V1). While the irregular SCDs were visibly different from the bell-shaped SCDs, the two types of SCDs were placed together in Group 3, since the Sør plot indicated a high degree of similarity between them (see Q2, Fig. 8).

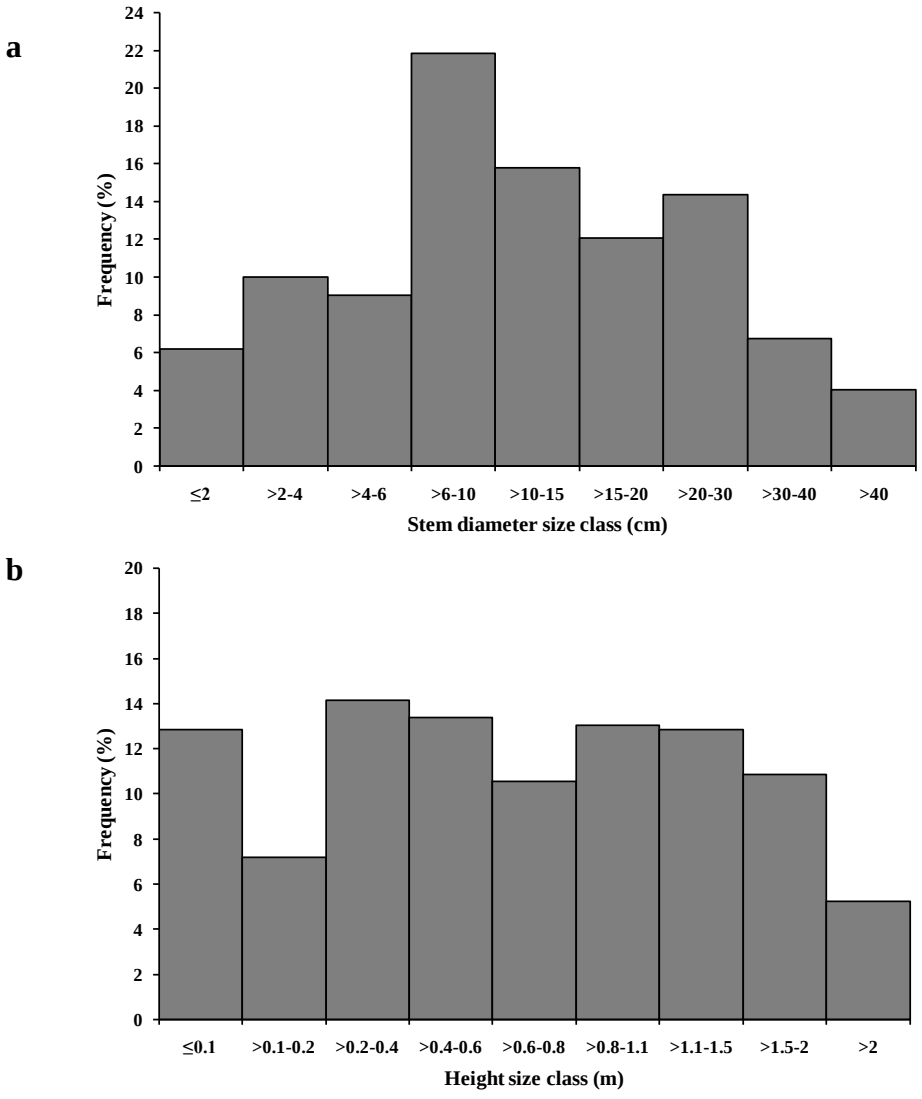


Fig. 4. (a) Stem diameter and (b) height size class distributions for *Aloe plicatilis* individuals from all 19 populations combined. (n=920 individuals for both (a) and (b).)

Group 1: Inverse-J-shaped distributions

High levels of recent recruitment were evident in WL, with large numbers of juveniles and few large adults – a pattern that was reflected in its low P (Table 3) and steep negative SCD slope for SDr (Table 4). Evenness was lower for height than SDr due to many individuals ≤0.01 m tall (Fig. 5). The SDr and height SCDs exhibited by WL were highly dissimilar to the SCDs of the other populations, and therefore WL grouped on its own in Q3 in the Sør plot (Fig. 8).

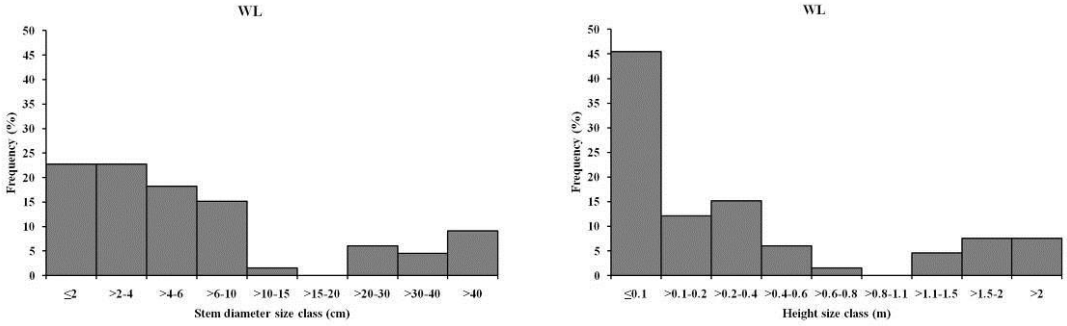
Group 2: J-shaped distributions

The J-shaped SCDs obtained for DKM and JH reflected a preponderance of large adults and few or no juveniles (Fig. 5). Approximately 60% of the individuals at both populations had SDrs ≥20 cm. Sixty-eight percent of the plants at DKM and 80% at JH had heights >1.1 m. The J-shaped SCDs were mirrored in the high P obtained for both populations (Table 3). The SCD of JH had a medium-high λ (Table 3), reflecting the dominance of larger plants. Both populations were highly dissimilar to all the other populations, and hence cluster together in Q4 in the Sør plot (Fig. 8).

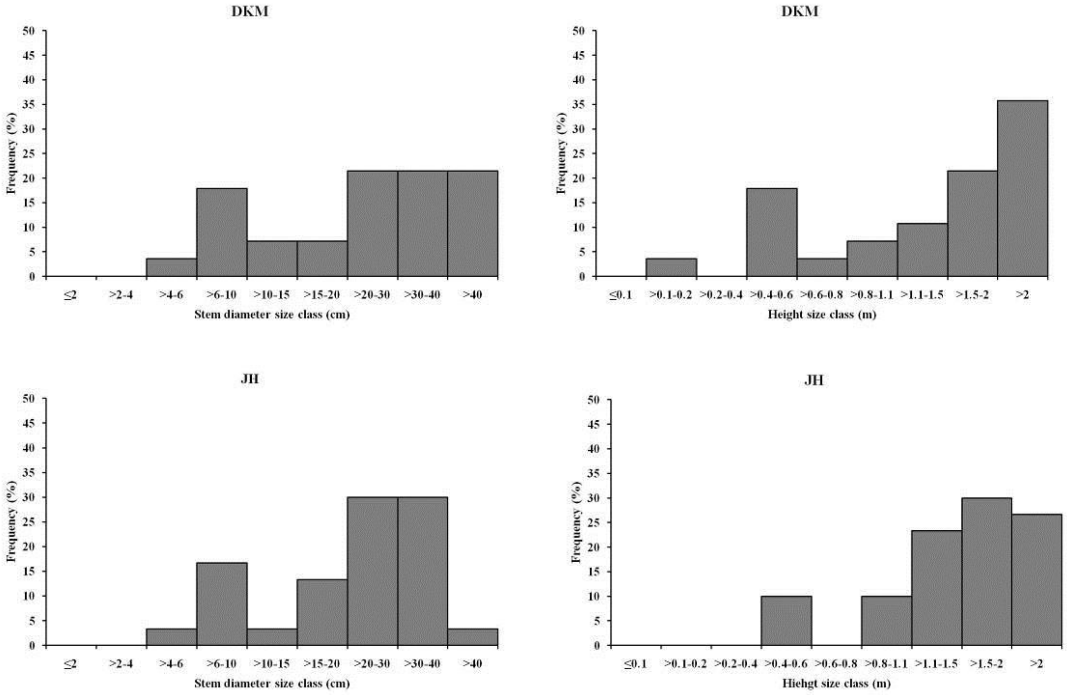
Group 3: Bell-shaped and irregular distributions

Approximately half the populations had clear bell-shaped SCDs, which were characterised by a dominance of intermediate-sized plants, with few juveniles and few very large adults. However, the bell shape was sometimes more obvious in the SDr SCDs than height (Fig. 5). The P for bell-shaped SCDs tended to be low-intermediate, with the SCDs of only two populations having medium-high values (W1 and SB) and only two with low values for both SDr and height (Table 5), which suggests an intermediate deviation from a monotonic decline for the majority of the populations. This trend is reaffirmed in the SCD slopes, 80% of which were gentle negative (Table 4), which usually corresponded with very gentle bell curves. Evenness measures for bell-shaped SCDs were mostly intermediate-high (due to gentle bell-shapes evident in six populations), while SCDs with a pronounced spike at the peak of their bells (KK, LM and ZH) had low evenness. All the populations clustered together in Q2 of the Sør plot (Fig. 8), indicating high similarity between them.

Group 1: Inverse J-shaped distributions (Q3 in Fig. 8)



Group 2: J-shaped distributions (Q4 in Fig. 8)



Group 3: Bell-shaped and irregular distributions (Q2 in Fig. 8)

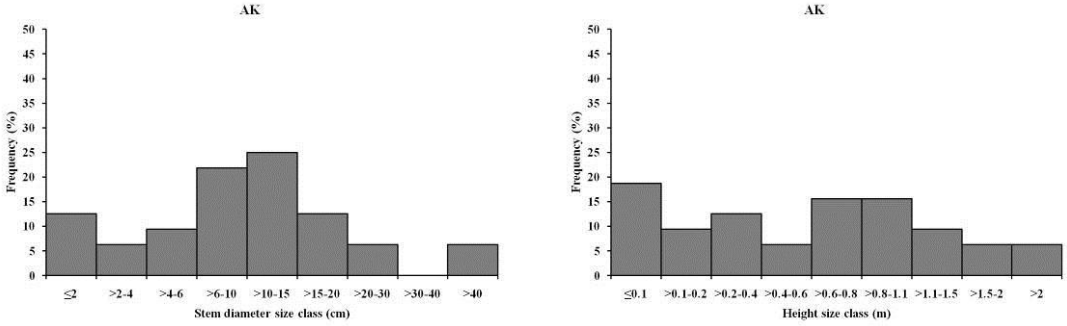


Fig. 5. Stem diameter (SDr) and height size class distributions (SCDs) for 19 surveyed *Aloe plicatilis* populations in the south-western Cape, South Africa. Key to population name abbreviations in Fig. 1.

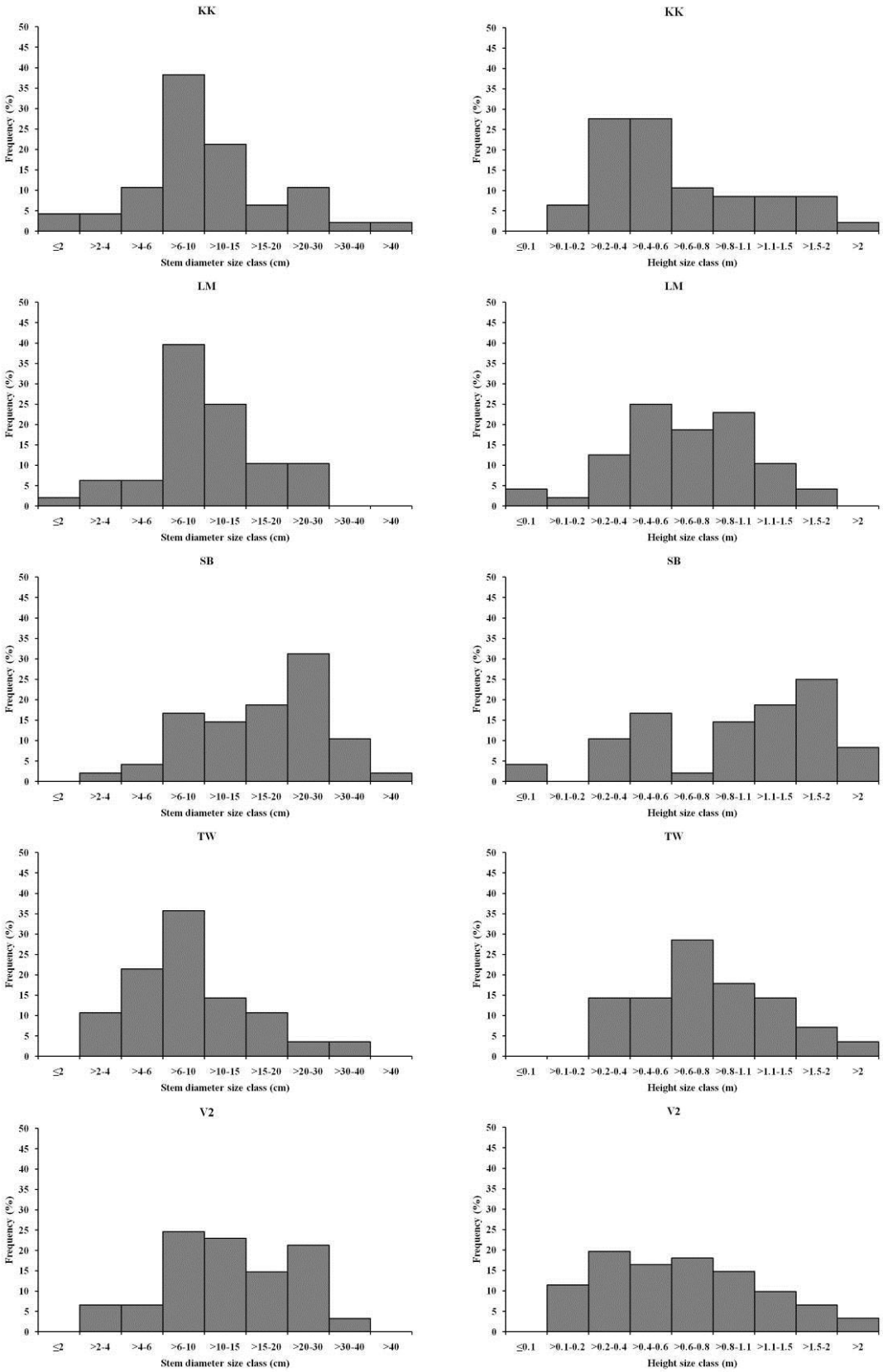


Fig. 5 (continued)

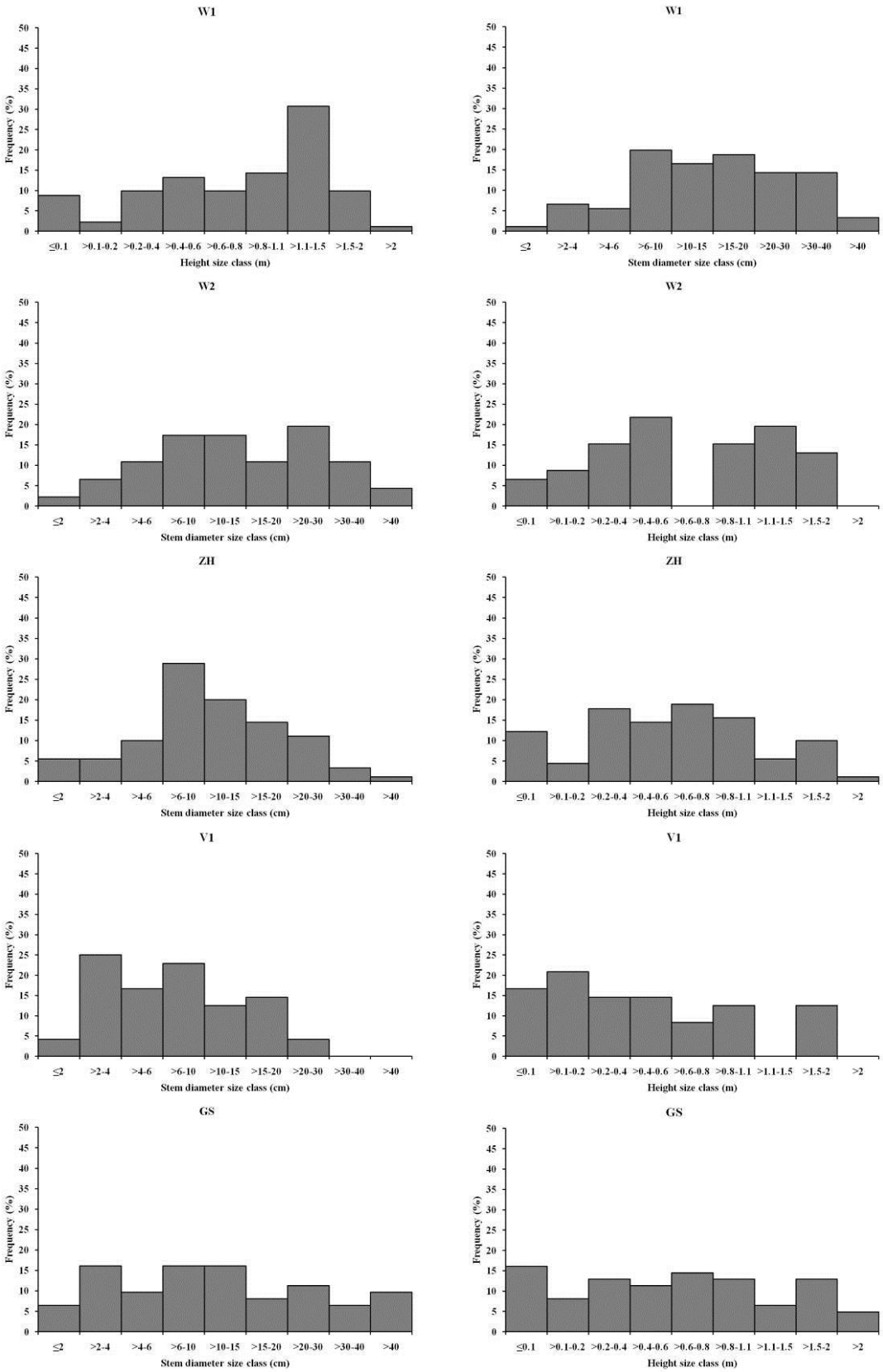


Fig. 5 (continued)

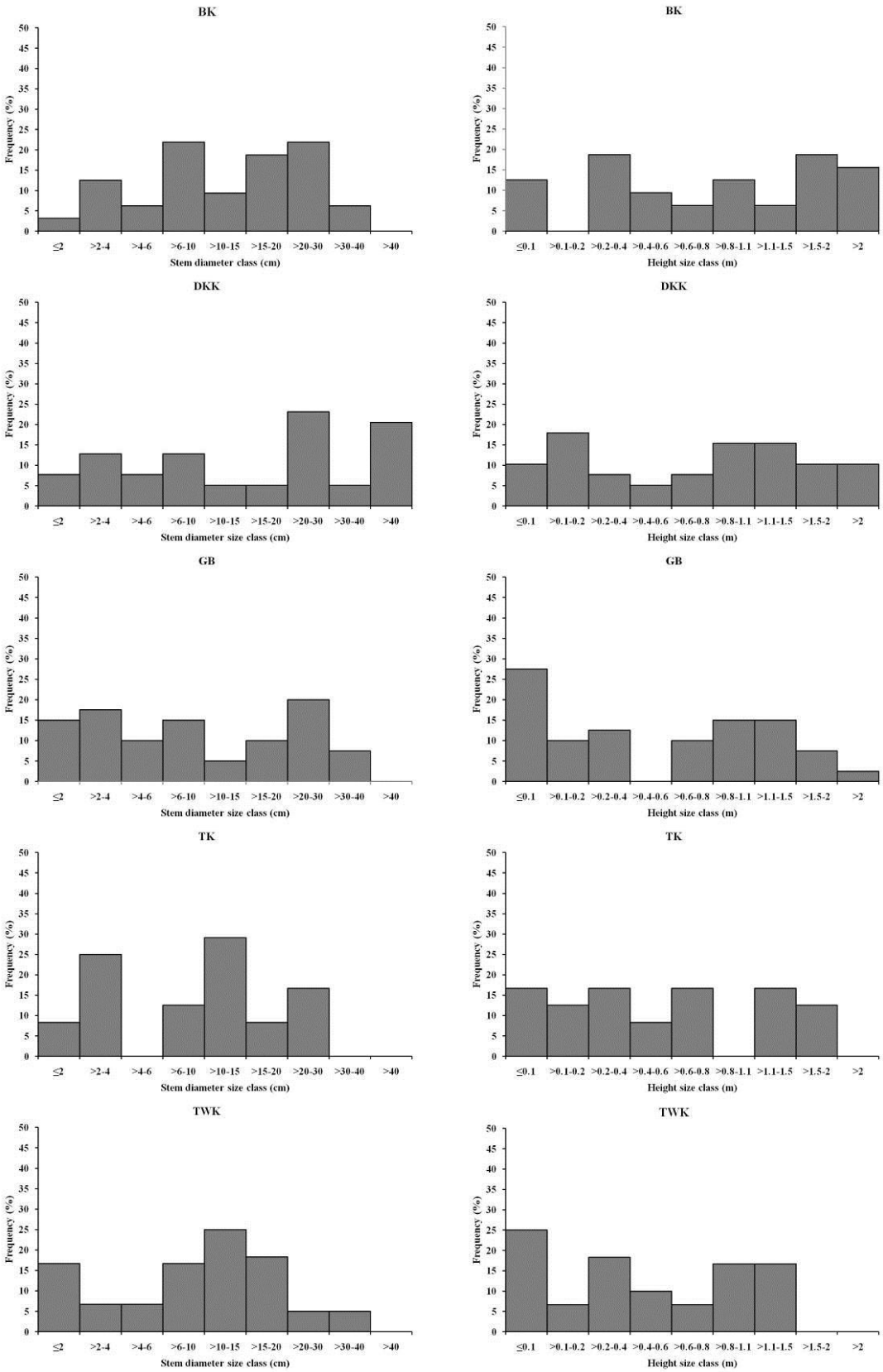


Fig. 5 (continued)

The shapes of the seven populations with irregular SCDs often appeared different from one another and differences were also visible between SDr and height SCDs within populations; however, the Kolmogorov-Smirnov tests revealed that these within-population differences were only significant for BK and TWK (Table 2). P was medium-low across the group, λ was generally low for at least the SDr SCD or the height SCD for all, and E was medium-high (Table 3). The high Sør values within the group were very similar to those of the bell-shaped SCDs, except for TK and GS (Fig. 8).

3.4.5. Comparisons between stem diameter and height size class distributions within populations

Only five out of the 19 populations showed significant differences between SDr and height SCDs (BK, SB, TW, TWK and WL) (Table 3). The SDr and height SCD of all five populations shared similar P scores except for TW, but for λ and E there was mostly little agreement between SDr and height SCDs across all five. Four of the five were in group 3 (bell-shaped or irregular SCDs) and one (WL) was in group 1 (inverse-J SCD). The SDr and height SCDs of all 19 populations combined were not significantly different (D=0.089; p>0.05).

3.5. Discussion

3.5.1. Onset of reproduction and the bonsai effect

Aloe plicatilis typically occurs in very rocky sites, which act as fire refugia in the fire-prone ecosystem inhabited by the species (Cousins et al., in prep; Chapter five). However, there appears to be a trade-off between degree of protection from fire and plant size, whereby individuals growing in extremely rocky sites are well-protected, but often stunted (bonsai plants), while plants in less-rocky sites can attain greater sizes, but are less protected from fires. There is a considerable body of literature on the effects of root restriction on plants, focusing primarily on the growth of plants in small pots (e.g. Tschaplinski and Blake, 1985; Boland et al., 1994). In most of these experiments, plants grown in small pots showed reduced aboveground biomass, belowground biomass and growth rate, thus demonstrating the relationship between root and shoot growth. Some *A. plicatilis* individuals were even observed growing in shallow hollows in rock sheets, and often attained heights of only 0.2m or less. A seedling that establishes in such a site may experience severe size restrictions and may take many more years to flower than a plant of equal age but in a less-rocky site where more rooting space is available. If a

stunted bonsai plant did eventually flower it would then become a 'reproductive dwarf' (a plant that flowers at a much smaller height and SDr than is typical for the species) or it may never flower at all, in which case it would remain a non-reproductive 'suppressed juvenile' despite its age.

3.5.2. Variations in population size and density

The two methods used to estimate density (PCQ and NN) often yielded somewhat different results (Table 3). In 10 out of 14 populations, PCQ yielded larger density estimates than NN. Cottam and Curtis (1956) showed that these methods gave very similar density estimates when applied to four different tree populations in fairly homogenous forests. In contrast, *A. plicatilis* is found in heterogeneous environments, and its occurrence on rocky outcrops in a patchwork of rocky and less-rocky sites means that plants are often clumped. This spatial arrangement of plants may explain the differences in density estimates between the two methods. PCQ density estimates ranged from 224–1356 plants/ha compared with NN estimates of 206–1331 plants/ha for the same populations, and thus overall they are quite comparable (Table 3). In a study of the population biology of *Delosperma* N.E.Br. emend. Lavis spp., a succulent plant genus that also inhabits heterogeneous rocky sites, Marom (2006) also obtained contrasting density estimates using PCQ and NN, which, similar to *A. plicatilis*, may have been due to patchy distributions. The *A. plicatilis* densities were similar to those obtained for five populations of the succulent shrub *Euphorbia barnardii* White, Dyer and Sloane in the Limpopo Province, South Africa (range = 163–1720 plants/ha) (Knowles and Witkowski2000) and that of *Portulacaria afra* Jacq. (588 plants/ha) in a botanical reserve in the Eastern Cape thicket, where elephants and goats were excluded (Stuart-Hill, 1992).

Population size varied from 31 to 6407 plants in the directly observed sampling areas, but increased to >110000 plants for one population (KK) when inaccessible parts of the population were incorporated (Table 2), thus resulting in almost five orders of magnitude variation. Although *A. plicatilis* is a restricted range endemic, it occurs across comparatively wide rainfall and altitude gradients, but variation in temperature is more limited (Table 1). The sizes of the populations at the longitudinal extremes of the distribution (V1 & V2 in the east and PB (Paardeberg – not surveyed) to the west), were very small, especially V1 and V2, while populations at the latitudinal extremes of the distribution (TK and TWK) were much larger. Rainfall and temperature may be a limiting factor on the easternmost extreme of the species' distribution, as average annual rainfall diminishes and temperatures increase towards the Little Karroo east of Worcester.

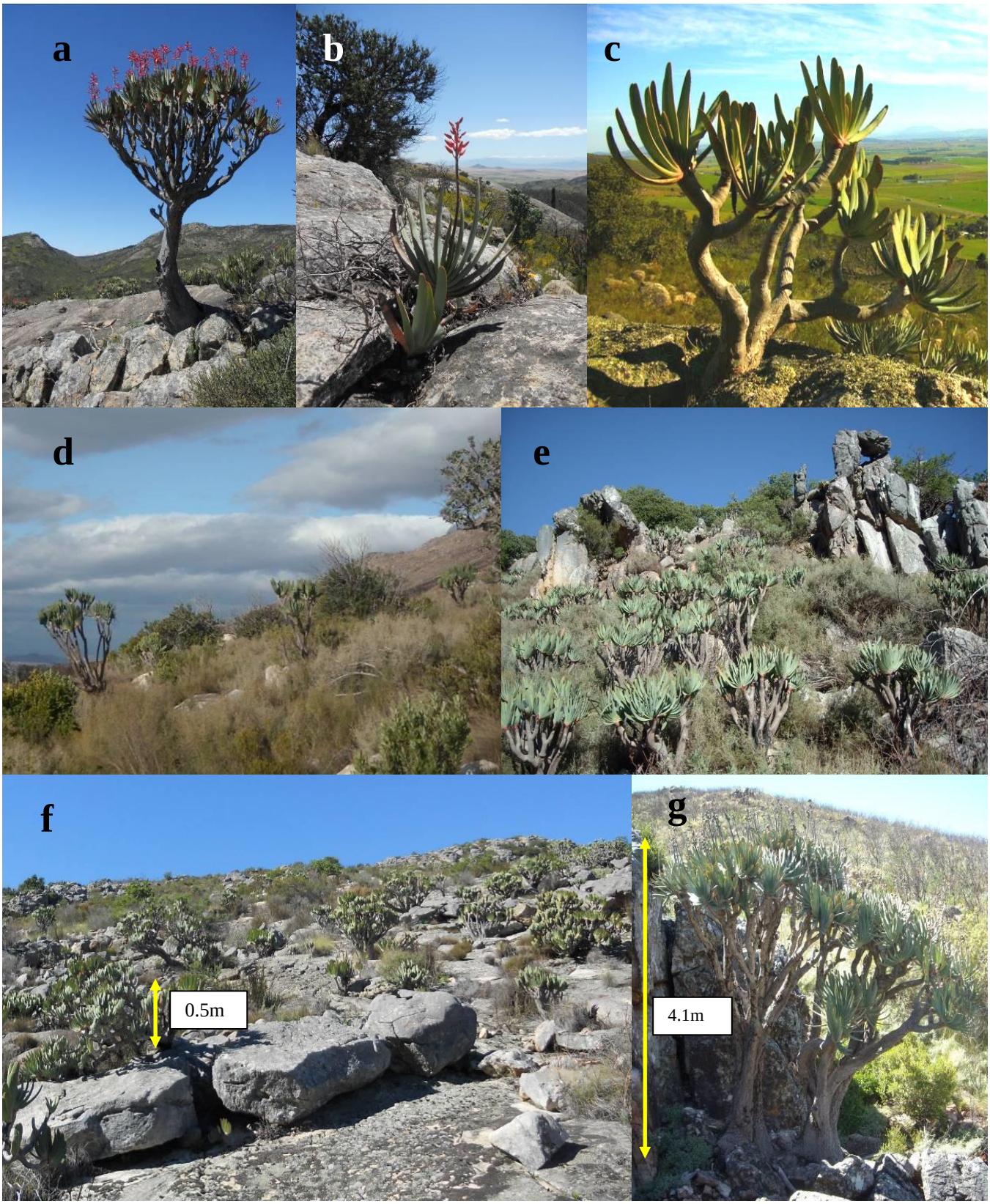


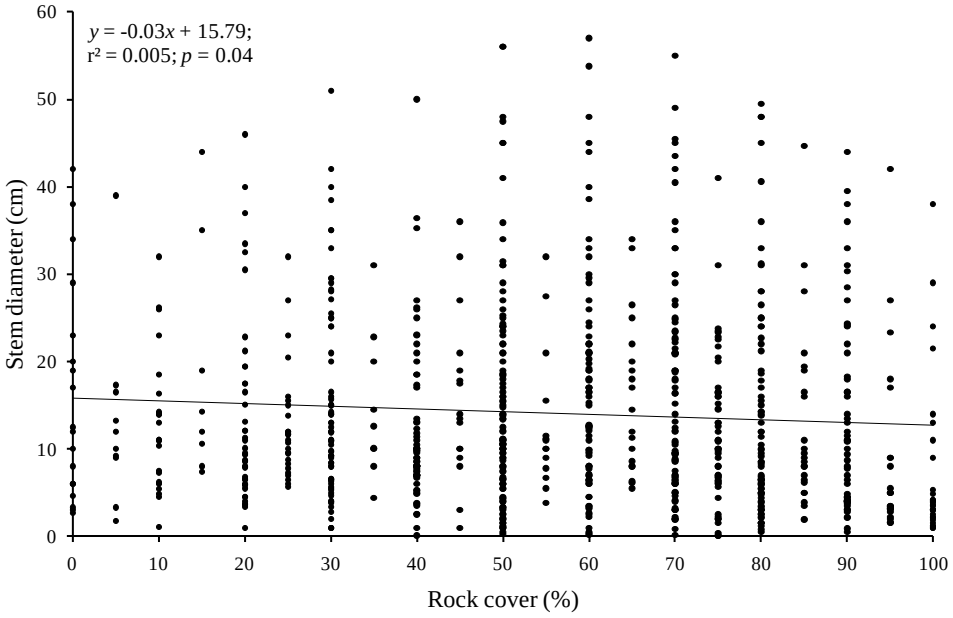
Fig. 6. (a) Reproductive adult *Aloe plicatilis* individual ~2 m high with numerous inflorescences. (b) Background: 'dwarf adult', which appears to be a juvenile due to its short height (~0.4 m) and small stem diameter, but the inflorescence indicates reproductive maturity; foreground: true juvenile. (c) 'Suppressed juvenile' (~0.4 m) that has likely remained in the juvenile state for many years, yet is of

the age where it could potentially reproduce, The plants in both (b) and (c) are displaying the 'bonsai effect'. (d) *Aloe plicatilis* at Jason's Hill (JH) showing a very sparse distribution of mostly large adults. (e) A stand of *A. plicatilis* at La Motte (LM) showing a very dense aggregation of similar-sized plants. (f) Part of an *A. plicatilis* population on Saronskop near Tulbagh consisting largely of short, compact individuals (~0.5 m) on an exposed, rocky hillside, where persistent strong summer winds possibly limit plant height. (g) The two largest large *A. plicatilis* individuals observed out of all 19 populations. These plants were growing at Du Toit's Kloof Krom River (DKK) in a rocky alcove that provided shelter from strong winds, thus reducing mechanical stress on the plants and allowing them to attain considerable height

The same scenario probably applies to its northern-most limit in the Tulbagh region, where rainfall decreases northwards towards the Northern Cape. *Aloe plicatilis* does not appear to conform to the 'abundant centre hypothesis', which states that populations at the centre of a species' distribution are larger than those at the range edge (see citations in Sagarin and Gaines, 2002). Five of the ten largest populations (KK, LM, DKK, ZH and GS) are close to the centre of the distribution, but the other five (TWK, W1, WL, SB and TK) are nearer the fringes. Notably, the population with the second largest number of individuals, and largest area of occupancy (TWK), occurs at the southernmost extreme of the distribution. Two populations at the northernmost extreme (TK and another unsurveyed population) are also fairly large. Population density also showed little support for the abundant centre hypothesis, with the 10 densest populations scattered throughout the distribution.

Sagarin and Gaines (2002) reviewed 145 studies that assessed species abundance at various populations, and 61% concurred with the results for *A. plicatilis* in that no support for the formerly widely-accepted abundant centre hypothesis was found. In a review of more recent studies on abundance distributions, Sagarin et al. (2006) report that an increasing number of studies show a non-abundant centre population pattern. Ranges are said to be determined by "alignment of different contributory mechanisms", so that range boundaries and population densities can be set by multiple factors that interact in complex ways across ranges over time (Sagarin et al., 2006). Physiological responses to climate are likely to be important drivers of population-abundance patterns, yet a clear model linking physiology, climate and macroecology is still lacking (Sagarin et al., 2006).

a



b

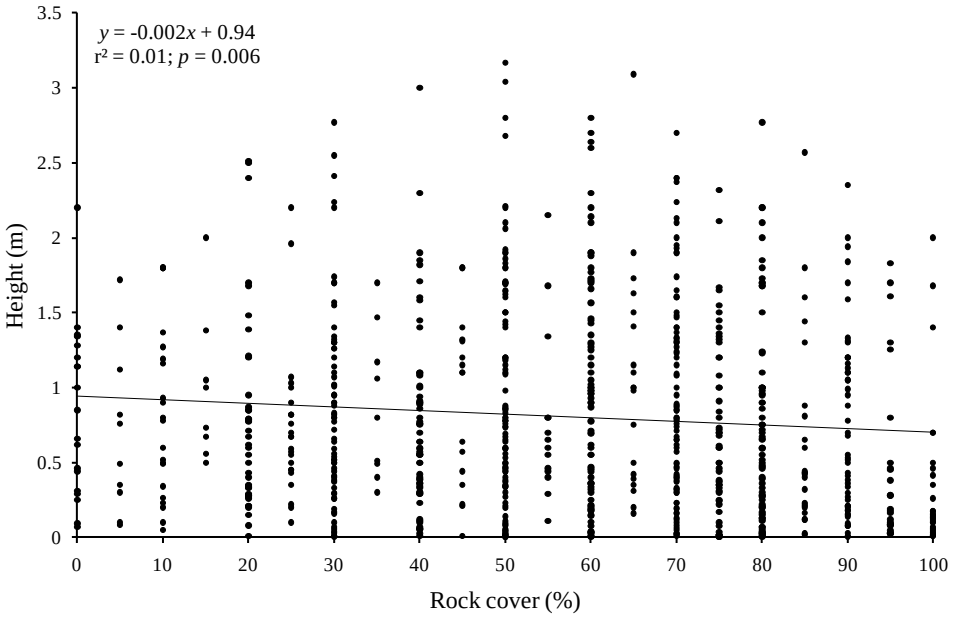


Fig. 7. Regression relationships between percentage rock cover around *A. plicatilis* individuals at all 19 populations combined and (a) stem diameter and (b) height.

3.5.3. Trends in population size structure

3.5.3.1. Bell-shaped distributions

A cursory scan of most *A. plicatilis* populations may suggest that the species is a multi-stemmed aloe rather than a tree aloe (see classifications in Van Wyk and Smith, 2008), since many individuals appear compact and shrub-like, averaging 1–2 m in height. This generally ubiquitous, visually obvious pattern is reflected in the dominance of individuals in intermediate size classes and the bell-shaped SCDs. Some studies suggest bell-shaped SCDs may be due to episodic recruitment (e.g. Witkowski and Liston, 1997; Venter and Witkowski, 2010; Helm and Witkowski, 2012), possibly during high rainfall years or after fire, when seedlings take advantage of increased light, nutrients and space.

In most Mediterranean-type regions, and especially the Cape fynbos, fire plays a crucial role in determining major vegetation patterns, and induces mass recruitment events in many genera such as *Protea* L. and *Leucadendron* R.Br. (Keeley et al., 2012). Such pulsed post-fire recruitment typically results from the stimulation of post-fire flowering, seed release from serotinous species, breaking of physical seed dormancy, and smoke-induced germination (Bradshaw et al., 2011).

Wabuyele and Kyalo (2008) suggest that in the case of aloes, despite producing large quantities of seeds, seedling establishment is occasional, and is dependent on the availability of rainfall, which is often scant and erratic throughout much of the range of the genus. Most *Aloe* species do not appear to exhibit mass recruitment after disturbances such as fire; rather, small numbers of seedlings establish in a 'drib-drab' fashion over long periods of time (E. Van Jaarsveld, pers. comm.). Furthermore, a mass episodic recruitment event would also require the presence of a large seed bank of long-lived seeds, but the seeds of most *Aloe* spp. are known to have limited longevities (1-2 years) (Giddy, 1973; Van Jaarsveld, 1989), and are therefore likely to form only transient seed banks. This hypothesis is supported by what appears to be an absence of large, persistent seed banks in studied populations of both *Aloe marlothii* A.Berger (Symes, 2012) and *A. plicatilis* (Cousins et al., 2013; Chapter four).

However, the Quiver tree *A. dichotoma*, a tree aloe that occurs in the arid Northern Cape, South Africa and Namibia, appears to exhibit both drib-drab and mass recruitment (S.L. Jack, pers. comm.). Mass recruitment in *A. dichotoma* appears to be more common in summer rainfall areas, especially in populations that experience exceptionally hot and dry conditions (S.L. Jack, unpublished data). By

contrast, in cooler winter rainfall areas, all indications are that a strong drib-drab strategy applies and hence, where cooler, moister conditions allow, seedlings will recruit almost every year (S.L. Jack, unpublished data). The comparatively longer viability period of *A. dichotoma* seeds (up to three years) would allow for mass episodic recruitment (at least at some populations), which is probably an adaptation to erratic rainfall, whereby seeds released in dry years can remain dormant until wetter conditions arrive (Giddy, 1973). Further support is given for episodic recruitment in Quiver trees by population studies on *A. pillansii*, a tree aloe very similar to *A. dichotoma* (Midgley et al., 1997; Bolus et al., 2004; Duncan et al., 2006). The bell-shaped, J-shaped and bimodal SCDs observed for many *A. pillansii* populations were ascribed to episodic recruitment linked to high rainfall events, although theft and herbivory of individuals in the smaller size classes were also cited as possible causes. In contrast, the *A. plicatilis* fynbos sites are characterised by low inter-annual variation in rainfall (CV of inter-annual rainfall = <25 to <35%) compared with Succulent karoo and Nama-karoo karroo sites where *A. pillansii* occurs (>35%) (Schulze, 1997a).

Venter and Witkowski (2010) obtained mostly bell-shaped and positively skewed SCDs in a study of the population size structure of baobabs (*Adansonia digitata* L.) in South Africa. Due to the long-lived nature of baobabs and their extremely low adult mortality and recruitment rates, Venter and Witkowski (2010) suggest that a deviation from an inverse-J SCD may not necessarily indicate an unstable or declining population. Other studies on slow-growing, long-lived species for which populations are characterised by adult persistence have also obtained SCDs that deviate from the classic inverse-J, and are notably bell-shaped or J-shaped. Seven populations of the succulent plant *Haworthia koelmaniorum* Oberm. & D.S.Hardy were all strongly bell-shaped (Witkowski and Liston, 1997), as were those of the cactus *Pterocereus gaumeri* (Britton & Rose) MacDougall & Miranda (Méndez et al., 2004), the tree succulent *Pachypodium namaquanum* (Wyley ex Harv.) Welw. (Midgley et al., 1997) and *Aloe petricola* Pole-Evans (Wiesser and Deall, 1989). A similar trend was observed for a population of *Encephalartos cycadifolius* (Jacq.) Lehm., a long-lived, slow-growing cycad (Raimondo and Donaldson, 2003). A population of *Aloe peglerae* Schönland monitored for 10 years by Scholes (1988) consistently exhibited a strong J-shaped SCD, which was thought to be typical of the species and representative of a stable population. Recruitment patterns in these species may therefore be rare and/or intermittent, with population viability hinging on adult persistence rather than regular large-scale recruitment.

However, SCDs obtained for other similar long-lived species such as cacti (e.g. Godínez-Alvarez and Valiente-Banuet, 2004), cycads (e.g. Negrón-Ortiz and Breckon, 1989; Watkinson and Powell, 1997; Raimondo and Donaldson, 2003; Pérez Farrera and Vovides, 2004), palms (e.g. Barot and Gignoux, 1999) and tree succulents (e.g. Midgley et al., 1997; Bolus et al., 2004; Duncan et al., 2006) were a mixture of inverse-J, bimodal, bell-shaped and J-shaped, the majority being bimodal. Many species were said to display episodic recruitment, which may account for the dominance of bimodal distributions. Moreover, bell-shaped and bimodal SCDs are not exclusive to slow-growing, long-lived plants, and have also been observed in many forest trees (e.g. Everard et al., 1995) and savanna trees (e.g. Walker et al., 1986; Helm and Witkowski, 2012). Helm and Witkowski (2012) showed that several populations of *Sclerocarya birrea* (A.Rich.) subsp. *caffra* (Sond.) Kokwaro (marula) in the Kruger National Park, South Africa, were characterised by negatively skewed bell-shaped SDr and height SCDs. These were adult-dominated populations, where circumstances that no longer prevailed (e.g. human settlement or a massive episodic recruitment event) were thought to have shaped the distributions, and where intensive browsing of seedlings resulted in a lack of recruitment (Helm and Witkowski, 2012). Pulido et al. (2001) found distinct bell-shaped SCDs in their study of the size structure of the Spanish Holm oak, *Quercus ilex* L., intensively managed in an agroforestry context by forest clearing for livestock grazing. In contrast, the SCDs of *Q. ilex* populations in nearby undisturbed woodlands were almost always inverse-J-shaped (Pulido et al., 2001). The bell shapes were attributed to continual removal of *Q. ilex* saplings to maintain the open pastures.

With *A. plicatilis*, however, none of the populations is intensively managed or affected by utilization by large herbivores. Furthermore, unlike the marula populations, the bells in the *A. plicatilis* SCDs were always centred on the intermediate size classes, mirroring the observed dominance of short, shrubby plants in many populations. Two major factors that may be responsible for the preponderance of medium-sized *A. plicatilis* plants in many populations are (a) the bonsai effect whereby restricted rooting space limits plant size and (b) strong, persistent winds, which have a 'pruning effect' on the canopy. The south-western Cape is known for its strong, persistent summer winds, with gusts of up to128 km/h recorded in Cape Town (Kruger et al., 2010). Winds of this nature may impose height restrictions on plants, with larger plants being more exposed to damage from strong winds. The succulent growth form of *A. plicatilis*, its heavy mass and shallow root system may render this species particularly vulnerable to damage from strong winds.

Plants growing in windy places are generally known to display growth patterns different from plants growing under calm conditions: trees are bent leeward, and/or grow shorter (De Langre, 2008). Neel and Harris (1971) reported that a moderate breeze in a growth chamber resulted in reduced growth of grapevines, and a study by Jaffe (1973) showed that gentle rubbing of the stems of several plant species for short periods twice daily over seven days caused a considerable decrease in stem elongation compared to control plants that were not rubbed. Mechanically manipulated plant stems grow shorter and, generally speaking, stronger (Watt et al., 2005). Hence, plants are able to adjust their height and slenderness biologically by mechanosensing physical stimuli including wind (De Langre, 2008). Wind therefore appears to play an important role in limiting the height of *A. plicatilis* individuals growing on very exposed hillsides (Fig. 6f) compared to individuals in protected rocky alcoves (Fig. 6g) or amongst shrubs and trees, which often grow much taller.

Based on measurements of *A. plicatilis* plants of known age growing at the Kirstenbosch National Botanical Garden in Cape Town, the species has a height growth rate of ±3 cm/year under garden conditions. A 0.8 m tall individual in the wild would therefore be a minimum of 27 years old, while a very large 3 m plant would be ~100 years old. As a result of these slow growth rates and considerable longevity, adult plants, which have a much higher probability of survival relative to seedlings and juveniles, would spend many years in the adult size classes before eventually senescing. Furthermore, Duncan et al. (2006) report that growth rates in *A. dichotoma* (which is functionally similar to *A. plicatilis*) depend on plant size, with larger plants generally growing slower than smaller ones. Accordingly, if an *A. plicatilis* individual were encountered during a population survey at any given time, it would be more likely to be in a medium-to-large size class than a smaller one. Measurements of several of these dominant, persisting adults would consequently result in a bell-shaped SCD. In this context, if a plant species employs an adult-persistence survival strategy, whereby populations are consistently dominated by medium-to-large adults (hence resulting in a bell- or J-shaped SCD) with very high survival probabilities, then minimal, drib-drab recruitment is not a cause for concern, so long as senescing adults are continually replaced by new recruits. However, if there has been zero recruitment for prolonged periods, which, for example, has been observed in the tree succulent *Dracaena cinnabari* Balf.f on the island of Socotra (Adolt and Pavlis, 2004; Habrova et al., 2009), this would necessitate further investigation.

Table 2 Estimated area of occupancy, two density estimates and population size estimates, and Kolmogorov- Smirnov test results for comparison of stem diameter with height size class distributions (SCDs) within 19 populations of *Aloe plicatilis* in the south-western Cape, South Africa. NS denotes a difference that is not significant.

Population[a]	Number of individuals surveyed (n)	Estimated Area of Occupancy (AOO) (ha)	Estimated density (plants/ha)		Estimated population size (number of individuals)		Kolmogorov-Smirnov test	
			Point-centred quarter	Nearest neighbour	Point-centred quarter	Nearest neighbour	*D*-value	*p*-value
AK	32	0.43	929	395	399	169	0.125	NS
BK	32	0.48	415	377	199	180	0.281	$p<0.01$
DKK	39	2.72 (9.34[b])	227	364	617 (2 119[c])	988 (3 400[c])	0.064	NS
DKM	28	2.78	224	206	623	572	0.071	NS
GB	40	0.47	1 066	635	501	296	0.125	NS
GS	62	2.04	738	247	1506	503	0.097	NS
JH	31	0.30	-	75	-	23	0.233	NS
KK	47	1.75 (102.80[b])	1 356	1 093	2 373 (139 397[c])	1 911 (112 400[c])	0.149	NS
LM	40	>3.82[d]	1 011	459	>3 862[d]	>1 753[d]	0.167	NS
SB	48	2.69	676	408	1 818	1 099	0.208	$p<0.05$
TK	24	3.46	498	293	1723	1012	0.125	NS
TW	28	0.12	-	1331	-	163	0.393	$p<0.001$
TWK	60	13.32	740	481	9 857	6 407	0.200	$p<0.02$
V1	48[e]	0.05	-	1 036	-	56	0.063	NS
V2	61[e]	0.06	-	555	-	30	0.090	NS
W1	91	8.47	301	532	2 549	4 505	0.099	NS
W2	46	0.27	549	577	148	156	0.152	NS
WL	67	0.82	-	3 043	-	2501	0.227	$p<0.002$
ZH	90	2.51	562	881	1 411	2 215	0.133	NS

[a]Key to population abbreviations in Fig. 1.
[b]Estimated maximum AOO including inaccessible parts of population not included in the population periphery GPS coordinate dataset.
[c]Estimated maximum population size using maximum AOO.
[d]Minimum AOO and estimated population size for LM, since the population extended beyond the bounds of the surveyed area.
[e]Actual population size determined by conducting counts.

3.5.3.2. Deviations from the bell-shaped distribution

A striking result in this study was that the inverse-J-shaped SCD, which has traditionally been thought to be indicative of a healthy, stable and strongly recruiting population (Weiner and Solbrig, 1984; Łomnicki, 1988; Condit et al., 1998), was absent in all except one *A. plicatilis* population (WL). Considering that bell-shaped SCDs appear to better represent stable *A. plicatilis* populations, use of the inverse-J as the only index of a healthy, stable population is questionable not only for *A. plicatilis*, but also for similar long-lived, slow-growing species. Inverse-J SCDs are characteristic of many forest tree populations (e.g. 24 out of 36 species in Everard et al., 1995; eleven species combined in Sano, 1997; 18 of 20 species in Obiri et al., 2002; 13 of 15 species in Mwavu and Witkowski, 2009), and may be considered typical of tropical trees whose seedlings and saplings can persist for long periods in the understory (Sarukhán, 1980). Long-lived, slow-growing species do sometimes exhibit inverse-J SCDs, but these are often forest species such as shade-tolerant understory cycads (e.g. Negrón-Ortiz and Breckon, 1989; Pérez Farrera and Vovides, 2004) and species from arid areas that probably show episodic recruitment (e.g. Esparza-Olguín et al., 2002; Godínez-Álvarez et al., 2003; Bolus et al. 2004). For forest trees, inverse-J SCDs may be observed year after year, but for episodic recruiters, anything from an inverse-J-shaped to a J-shaped SCD may be observed depending on how long after a previous recruitment event the population was surveyed.

Since *A. plicatilis* does not appear to be an episodic recruiter, the high recruitment observed at WL is unusual. The population last burned 12 years prior to the survey, which supports the hypothesis that recruitment in the species is not strongly linked to fire. WL covered only a single hilltop (0.82 ha), but the size of the population was fairly large and it was also the densest population surveyed (3043 plants/ha). It occurs in close proximity (<1 km) to another reasonably large population (SB), which shares very similar rainfall and temperatures, yet SB exhibits a bell-shaped SCD. It is therefore unclear why WL should be displaying such high levels of recruitment, but it may be that the hilltop offers particularly favourable microsites for seedling establishment. Out of all 19 populations WL had the second highest average rock cover (mean ± S.D. = 75 ± 20%) around sampled *A. plicatilis* individuals. Furthermore, most of the juveniles at WL were found growing amongst rocks in shady areas under large trees and shrubs. These microsite conditions were likely to have been very conducive to germination and establishment, thus resulting in an inverse-J SCD.

Aloes and succulents in general often require nurse plants for establishment in wild populations (Godínez-Álvarez et al., 2003; Cousins and Witkowski, 2012 (Chapter two)). The shade provided by these nurse plants is particularly important for aloe seedling establishment (Giddy, 1973). In cultivation, *A. plicatilis* grown under shaded greenhouse conditions show markedly enhanced vigour compared to seedlings grown in full sun (S.R. Cousins pers. obs.). However, in most populations, *A. plicatilis* individuals were found growing in full sun, with low surrounding forb cover (~20%) compared to rock cover (~60%) (Cousins et al., in prep; Chapter five). In fact, small-medium forbs acting as nurse plants may become a liability during fire (Narog and Wilson, 2005), especially considering the intensity of fynbos fires. Rocks may ameliorate stressful conditions in a similar way to nurse plants by providing shade, thus reducing ambient temperatures, evaporation and evapotranspiration, and increasing soil water retention and the accumulation of organic matter (Peters et al., 2008). Other studies on succulent plants have demonstrated the importance of 'nurse rocks' in seedling establishment (e.g. Parker, 1987; Peters et al., 2008); however, their significance in shaping *A. plicatilis* seedling recruitment patterns remains to be tested.

Only two populations displayed J-shaped SCDs (DKM and JH), and of these two, only JH appears to be in decline. DKM last burned in 2007, three years before the survey, and the presence of a number of standing dead adults suggested a hot fire. The absence of small juveniles suggests that the fire had killed them before they had grown large enough to survive. The adult plants at DKM appeared otherwise healthy, and fruit production at the time of the survey was high (S.R. Cousins, pers. obs.). A section of the population where a rockfall had occurred was missed by the fire, and a number of small *A. plicatilis* individuals were found growing between the rocks, which acted as a fire refugium. However, the sampling transect placed across the population also missed this section and hence these juveniles were not reflected in the SCD. Due to this observed recruitment, and the presence of many large, reproductive adults, DKM is not considered to be in decline.

JH was the smallest population (31 plants), by far the least dense (75 plants/ha) and had the steepest positive SCD slope. In a study of the reproductive ecology of *A. plicatilis*, Cousins et al. (2013) (Chapter four) showed that out of the populations GB, JH and W1, plants at JH exhibited the lowest seed set per plant and per population. Several plants had inflorescence abortion rates of 75-100% and inflorescences that did produce fruits were often highly predated by birds (S.R. Cousins, pers. obs.). JH appears to be displaying the Allee effect whereby the fitness of individual plants in a small and/or sparse population declines as population size or density decreases (Stephens et al., 1999).

Table 3 Permutation index (P) and diversity indices, Simpson's index (λ) and evenness (E) for the stem diameter and height size class distributions (SCDs), each grouped into low, medium and high categories for 19 populations of *Aloe plicatilis* in the south-western Cape, South Africa. Populations that share similar values for stem diameter and height are indicated in bold within each category. Key to population abbreviations in Fig. 1.

Permutation Index			Simpson's Index (λ)			Evenness measure	
Category	Stem diameter SCD	Height SCD		Stem diameter SCD	Height SCD		Stem diameter SCD	Height SCD
Low (10-20)	**AK, GB**, **KK, TK**, TW, **TWK, V1, WL**	**AK, GB,** GS, **KK, TK**, **TWK**, **V1, WL**, ZH	Low (0.1-0.15)	**AK, BK, DKK, GB, GS,** DKM, TWK, W1, **W2**	**AK, BK, DKK, GB, GS**, SB, TK, TW, V1, V2, **W2**, ZH	Low (0.7-0.9)	KK, LM, ZH	WL, W1
Medium (>20-30)	**BK, DKK**, GS, **LM, V2, W2**, ZH	**BK, DKK, LM,** TW, **V2,** W1, **W2**	Medium (>0.15-0.2)	JH, SB, TK, TW, V1, V2, WL, ZH	KK, LM, DKM, TWK, W1	Medium (>0.9-1.1)	AK, BK, DKK, **GS, JH, SB, TWK,** TW, V1, **V2,** WL, W1, **W2**	GB, **GS, JH,** KK, LM, DKM, **SB, TWK, V2, W2,** ZH
High (>30-40)	**DKM, JH, SB**, W1	**DKM, JH, SB**	High (>0.2-0.25)	KK, LM	JH, WL	High (>1.1-1.3)	GB, DKM, **TK**	AK, BK, DKK, **TK,** TW, V1

Table 4 Size class distribution (SCD) slope of the regression between size class midpoint and the number of plants per size class for stem diameter and height SCDs of 19 populations of *Aloe plicatilis* in the south-western Cape, South Africa. Significant relationships are indicated in bold.

Stem diameter SCD					Height SCD				
Slope category	Population[a]	Slope (°)	r^2	p	Slope category	Population[a]	Slope (°)	r^2	p
Steep negative	V1	-0.15	0.38	0.142	Steep negative	WL	-67.28	0.30	0.126
(-0.15 to -0.07)	WL	-0.14	0.50	**0.034**	(-70 to -30)	TWK	-52.51	0.46	0.063
	TWK	-0.10	0.60	**0.025**		V1	-46.63	0.63	**0.018**
	ZH	-0.10	0.53	**0.027**		ZH	-40.98	0.67	**0.007**
	GB	-0.08	0.64	**0.020**		GS	-30.23	0.63	**0.010**
	GS	-0.07	0.57	**0.020**		GB	-27.99	0.37	0.084
Gentle negative	KK	-0.05	0.31	0.118	Gentle negative	V2	-20.13	0.31	0.120
(>-0.07 to -0.03)	LM	-0.05	0.17	0.304	(>-30 to -3)	W1	-19.21	0.35	0.095
	TW	-0.05	0.26	0.192		TK	-17.11	0.59	**0.027**
	AK	-0.04	0.73	**0.003**		AK	-16.84	0.55	**0.022**
	TK	-0.04	0.27	0.187		KK	-16.32	0.25	0.175
	W1	-0.04	0.31	0.120		DKK	-15.78	0.39	0.071
	BK	-0.03	0.29	0.170		W2	-14.79	0.31	0.156
	DKK	-0.03	0.49	**0.035**		LM	-9.95	0.09	0.46
	V2	-0.03	0.10	0.437		BK	-7.67	0.24	0.183
	W2	-0.03	0.41	0.063		TW	-3.36	0.04	0.619
Flat	SB	-0.01	0.02	0.733	Flat (>-3 to 3)	SB	-0.46	0.0008	0.943
(>-0.03 to 0.01)	DKM	+0.01	0.15	0.301		DKM	+1.79	0.04	0.614
Steep positive (>0.1)	JH	+0.11	0.08	0.494	Gentle positive (>3)	JH	+4.84	0.26	0.159

[a]Key to population abbreviations in Fig. 1

Aloe plicatilis individuals at JH may be too few and too far apart to attract adequate numbers of pollinators, resulting in pollen and/or pollination limitation (see Wilcock and Neiland, 2002). The lack of recruitment and the preponderance of large adult plants suggest that the population may undergo local extirpation if reproductive failure persists; however, repeat surveys are required to determine whether the population consistently displays poor reproductive output.

Another population that may be in decline is V1, despite its steep negative SCD slopes and bell- and inverse-J-shaped SCDs for SDr and height respectively. Although its SCDs indicate the presence of many juvenile plants, they most likely reflect the occurrence of several older bonsai individuals instead of true juveniles. V1 therefore appears to exhibit a 'false inverse-J SCD', which gives the impression of a recruiting population, however recruitment may not have occurred in many years, and individuals that appear to be true juveniles are in fact suppressed juveniles or reproductive dwarfs exhibiting the bonsai effect. Stunting of almost all the individuals in V1 probably results from a high degree of rockiness (74 ± 20% rock cover around *A. plicatilis* individuals) and low average rainfall at the site compared to most other populations. Both V1 and V2 occur at the extreme eastern edge of the species' range and are also among the three smallest populations. Monitoring of these populations would be useful for tracking their long-term dynamics, especially in light of climate change, which is predicted to result in hotter, drier conditions in the Western Cape (Midgley et al., 2003).

The driving forces behind irregular *A. plicatilis* SCDs are unclear. Wiegand et al. (2000) note that most studies on *Acacia* Mill. demographics have reported irregular SCDs, which were ascribed to periodic regeneration. Mortality regimes and variable growth have also been suggested as factors responsible for irregular SCDs (Wiegand et al., 2000). The size structure of various species in the Cactaceae are often characterised by an uneven number of individuals distributed across the size classes (Godínez-Álvarez et al., 2003). The purported drivers behind these patterns are consistent with those of Wiegand et al. (2000), reflecting massive, infrequent recruitment events, apparently associated with periods of high rainfall, which produce conditions conducive to germination and seedling establishment (Godínez-Álvarez et al., 2003). However, mass episodic recruitment appears to be unlikely in *A. plicatilis* (Cousins et al., 2013; Chapter four), and since the populations with irregular SCDs group together with the bell-shaped SCDs in the Sørensen similarity plot, this indicates that the two SCD types are similar in structure and probably result from similar underling mechanisms. Since it appears that bell-shaped SCDs are typical of *A. plicatilis* and indicate stable populations, these more irregular or 'flatter' bell-shaped SCDs are not considered to indicate unstable or declining populations.

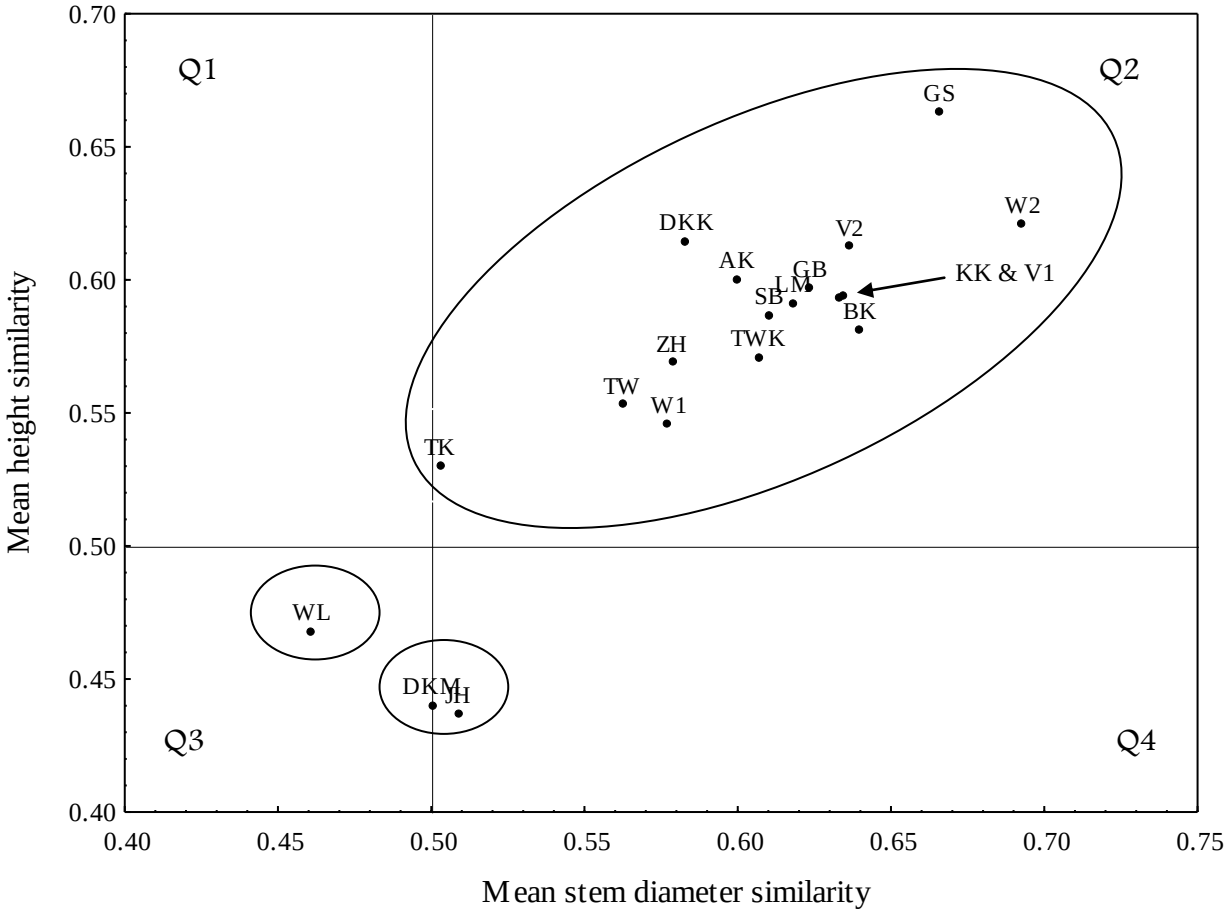


Fig. 8. Regression relationship between mean Sørensen similarity index for height and stem diameter between populations. Mean similarity values indicate the degree to which the structure of each population is similar to that of all the other populations combined.Q1: High height similarity, but low stem diameter (SDr) similarity; Q2: High height and high SDr similarity; Q3: Low height and low SDr similarity; Q4: Low height and high SDr similarity. See Fig. 1 for key to population abbreviations.

3.5.4. Within population stem diameter and height size class distribution comparisons

This is the first known study to align SDr and height SCDs for a single species and draw comparisons between them to test their level of agreement within populations. The few significant differences between SDr and height SCDs within populations (five out of 19 populations) suggest that SDr and height size class widths were well aligned using the regression relationship between SDr and height. Furthermore, few differences between SDr and height SCDs also suggest that for *A. plicatilis*, SDr and height measurements portray population structure equally well. Hence, if repeat surveys were to be conducted, one could measure either one or the other, which would limit the time and financial resources spent. However, since the height of *A. plicatilis* individuals appear to be limited by strong, persistent winds, SDr probably provides a better representation of plant size. Four of the five populations that had significantly

different SDr and height SCDs were in group 3 (bell-shaped or irregular SCDs), while the fifth was WL in group 1; however, the reasons for these differences are unclear and require further investigation.

3.6. Conclusion

This is the first quantitative description of patterns in the population size structure, density and abundance of *Aloe plicatilis* in the Cape fynbos, South Africa, encompassing a large spread of populations across its distribution. The study uncovered 21 new *A. plicatilis* populations, bringing the total number of populations currently known to 30. Population size varied between 31 and >110 000 individuals, and area of occupancy ranged from 0.05 to 103ha. Densities also varied among populations (75–3000 plants/ha) but were fairly comparable. *Aloe plicatilis* shows little support for the "abundant centre hypothesis", since populations at the centre of the distribution are not always the largest and/or densest, and those at the range edge were not consistently smaller and/or sparser.

Frequent bell-shaped size class distributions (SCD) and the occurrence of only one population with an inverse-J-shaped SCD suggest that *A. plicatilis* adopts an adult-persistence population survival strategy, whereby populations consist mainly of medium-to-large adults, with low recruitment rates and hence few juveniles, but are nonetheless stable. This finding challenges the suitability of the inverse-J-shaped size class distribution as the only indicator of a stable, 'healthy' population for slow-growing, long-lived species such as *A. plicatilis*. The growth of many *A. plicatilis* plants found in exceptionally rocky sites with limited rooting space is suppressed, resulting in a 'bonsai effect'. These bonsai individuals may be either 'suppressed juveniles' that remain as small, non-reproductive juvenile-sized plants indefinitely, or, should they eventually accumulate sufficient reserves to reproduce, they may become 'reproductive dwarfs' reproducing at a smaller size than is typical for the species

This study demonstrates the need for a well-informed, holistic approach in order to interpret snapshot data in the form of SCDs, which includes knowledge of a species' longevity, growth rate, recruitment strategy, seed storage and the local site conditions and disturbance regime in its habitat. Careful examination of SCDs in tandem with detailed field observations are required to make plausible interpretations about population structure, since the size of an individual does not necessarily always dictate its stage class. The presence of many small plants in a SCD may not necessarily reflect recent recruitment, but rather the persistence of individuals in smaller size classes due to growth suppression (bonsai plants). It is also crucial to consider the time at which a population is surveyed in relation to disturbances and hence its reproductive cycle. A bell-shaped or J-shaped SCD obtained for a long-lived, episodic recruiter long after

a reproductive event may not necessarily indicate a population that is unstable or in decline. If reproduction does not occur over very protracted periods, this may, however, be cause for concern.

The results of this study provide key baseline data on patterns in the demographics of *A. plicatilis* across its distribution. The knowledge acquired is useful for long-term monitoring and for identifying and explaining trends in the demographics of other similar slow-growing, long-lived plant taxa such as cacti, cycads and other *Aloe* species. Ultimately, an enhanced understanding of their population ecology will contribute to the successful conservation of these often threatened taxa.

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CHAPTER FOUR

Reproductive ecology of *Aloe plicatilis*, a fynbos tree aloe endemic to the Cape Winelands, South Africa

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4.1. Abstract

While the pollination ecology of many *Aloe* species is well-documented, knowledge on aloe seed ecology is limited. The aim of this study was to investigate the reproductive ecology of *Aloe plicatilis,* a Cape fynbos tree aloe endemic to the Cape Winelands, South Africa. Results from a pollinator exclusion experiment conducted at an *A. plicatilis* population on Paarl mountain suggests pollination primarily by insects, although bird visitation significantly increased seed set/fruit indicating possible co-pollination with insects. The species' long-tubed flowers and production of concentrated nectar, with observations of malachite sunbirds as the most common avian visitors to *A. plicatilis* flowers indicate the importance of long-billed specialist avian nectarivores as floral visitors. Analysis of the relationship between plant size and inflorescence production for five populations combined revealed a significant, positive linear relationship between plant size and the logarithm of the number of inflorescences/plant. Natural fruit and seed set determined for three populations (1325, 27930 and 251616 seeds/population) suggests low reproductive output compared to several other *Aloe* species. The smallest (31 individuals) and least dense (75 plants/ha) *A. plicatilis* population produced the lowest seed set/plant (128 seeds) and per population (1325 seeds), suggesting an Allee effect. Evaluation of seed dispersal potential showed that potential dispersal distances were approximately three times canopy height; however, the occurrence of *A. plicatilis*

on mountains isolated from more continuous mountain ranges on which the species also occurs suggests the possibility of long-distance dispersal by strong, gusty, summer winds. Soil seed bank samples collected from 13 populations yielded close to zero seedling emergence, indicating the absence of persistent seed banks. *A. plicatilis* seeds stored under ambient laboratory conditions for 3, 18 and 24 months were germinated in an environmental control chamber and a laboratory. High percentage germination was recorded for 18- and 24-month-seed (86 and 80%, respectively), while germination of 3-month-old seeds was three times lower, suggesting the need for after-ripening. Germination of fresh and one-year-old seed under ambient nursery conditions at the Karoo Desert National Botanical Garden in Worcester yielded emergence percentages of 67 and 44%, respectively, and were therefore less successful than germination under more controlled conditions. This is the first known study to investigate the reproductive ecology of a tree aloe species and that of a Cape fynbos aloe. The study highlights the importance of further studies on aloe seed ecology, particularly for rare and threatened species.

Key words: Allee effect; Dispersal; Flowers; Fruit set; Pollination; Seeds; Seed banks

4.2. Introduction

Knowledge of plant reproductive ecology is key to understanding many community processes such as regeneration, establishment, succession and alien species invasion, as well as species survival strategies and causes of rarity (Grubb, 1977; Bazzaz, 1979; D'Antonio, 1990; Gutterman, 1994; García-Fayos and Verdú, 1998; Kaye, 1999). Pollination, which is an integral part of plant reproductive ecology, deals with pollination strategies, flowering phenology and patterns of nectar, fruit and seed production (Lovett Doust and Lovett Doust, 1988), while seed ecology covers dispersal, dormancy and germination (Fenner and Thompson, 2006). The persistence of a plant population is a product of its constituent individuals' collective reproductive success which, in turn, is affected by factors such as plant morphology (size, shape and positioning of plant parts), competition, herbivory, population size and density, and the availability of pollen for fertilization and resources for seed production (Lovett Doust and Lovett Doust, 1988; Stephens et al., 1999; Mustajärvi et al., 2001; Wilcock and Neiland, 2002).

Each species possesses a suite (or syndrome) of floral traits that suggests adaption to a particular mode of pollination, either self- or cross-pollination (Fægri and van der Pijl, 1979; Primack, 1987; Dafni, 1992; Fenster et al., 2004). Descriptions of syndromes emphasize characteristics such as flower colour, odour, size, shape, rewards, and timing of anthesis (Primack, 1987; Dafni, 1992). Flowers pollinated by energy-

demanding vertebrates such as birds and bats are generally large and produce copious amounts of food rewards, while flowers visited by small insects tend to be smaller and produce less food rewards (Primack, 1987). Individual plant species are associated with a particular pollination system that occurs along a continuum from generalized (hundreds of pollinator species) to extremely specialized (a single pollinator species) (Johnson and Steiner, 2000). Most animal-pollinated plants exhibit moderate to highly generalized pollination systems (Waser et al., 2006); however, there is a growing body of literature documenting very specialized pollination systems in the tropics and in the species-rich temperate flora of South Africa (see citations in Johnson and Steiner, 2000). Although floral syndromes may provide clues about potential pollinators, they do not necessarily provide a foolproof means of predicting all a species' floral visitors, and visitors that do not match the species' floral syndrome may still be important and should not be overlooked (De Merxem et al., 2009).

Seeds play four important roles in the persistence of species, viz. reproduction, dispersal within the same plant community, expansion into new habitats, and survival of germplasm through seasons or environmental conditions unfavourable for growth (Vázquez-Yanes and Orozco-Segovia, 1993). Fruit and seed set, followed by seed dispersal are critical determinants of a plant's reproductive success and may influence the distribution and size of populations (Steffan-Dewenter et al., 2012). Seed set is dependent on interactions with pollinators, seed predation, nutrient availability and microclimatic site conditions (Steffan-Dewenter et al., 2012). Seed dispersal affects plant population dynamics by reducing density-dependent mortality near parent plants, expanding a species' range on a regional scale, and shaping population genetic structure (Weiblen and Thomson, 1995; Corlett, 2009; Howe and Miriti, 2004). While short-distance dispersal shapes the dynamics of local populations and communities, long-distance dispersal is central to the large-scale dynamics thereof (Schurr et al., 2009). Dispersal distances are often difficult to determine in the field, hence rate of seed descent can be used as an index of dispersal capability, which has often been related to seed size and mass (see citations in Matlack, 1987).

Sometimes dispersed seeds germinate immediately, but in most cases there is a delay, which is brought about either by quiescence or dormancy (Fenner and Thompson, 2006). Wild plant populations often form stores of dormant or quiescent seeds in seed banks, which may last for long periods of time, with intermittent germination of part of the seed bank (Murdoch and Ellis, 2000). Dormancy is caused by a block to germination within an imbibed seed (Murdoch and Ellis, 2000). Thus, dormancy is a temporary failure of a viable seed to germinate after a specified period of time under a particular set of environmental conditions (e.g. moisture availability and temperature) that later induce germination when

the restricted state has been terminated by either natural or artificial means (Vleeshouwers et al., 1995). Quiescent seeds, on the other hand, are those that remain ungerminated because the environmental conditions favourable for radicle emergence and seedling growth are lacking (Murdoch and Ellis, 2000). Seed banks comprising dormant or quiescent seeds may be transient (persisting in the soil for <1 year), short-term persistent (1–5 years) or long-term persistent (>5 years) (Bakker et al., 1996). Following this inactive state, the successful germination and survival of a proportion of seedlings is crucial for the persistence of plant populations, and underpins the development and sustainability of plant communities (Murdoch and Ellis, 2000; Leck et al., 2008).

The Allee effect is a phenomenon of prime importance when investigating reproductive ecology in plant populations, particularly in studies on species with small, sparse and/or fragmented populations and which rely on animal vectors for pollination (Stephens et al., 1999). The Allee effect refers to a positive relationship between any component of individual fitness (e.g. probability of reproducing or dying) and either numbers or density of conspecifics (Stephens et al., 1999; Berec et al., 2007). Decreases in the fitness of individuals often occur in small and/or sparse populations as population size and/or density decline (Berec et al., 2007; Kramer et al., 2009). Plants in such populations tend to receive fewer visits from pollinators, which may not only result in lower seed set (e.g. Lamont et al., 1993a), but also inbreeding depression (e.g. Groom, 1998). If populations drop below the Allee threshold – the size or density at which population growth rate becomes negative (Berec et al., 2007) – this can have dire consequences for the persistence of rare and threatened species.

Aloe L., is the largest genus in the Asphodelaceae, a family of succulent-leaved, petaloid monocots (Smith and Van Wyk, 2009), found primarily on the African continent (see distribution map in Cousins and Witkowski, 2012; Chapter two). With ±140 *Aloe* species, South Africa has the highest aloe diversity of any African country (Klopper et al., 2009). Aloes produce tubular flowers on many-flowered spikes, simple racemes, or compound racemes, which tend to be densely flowered and brightly coloured (Smith and Van Wyk, 2009). Aloes are generally self-incompatible and therefore reliant on animal floral visitors for pollination and seed set (Hoffman, 1988; Botes et al., 2009). Many *Aloe* species attract insect and bird pollinators by supplying abundant nectar primarily during winter, when alternative food sources are scarce (Beyleveld, 1973; Nicolson and Nepi, 2005; Botes et al., 2008; Symes and Nicolson, 2008; Forbes et al., 2009, Symes et al., 2011). Studies on several *Aloe* species have confirmed the existence of extensive bird pollination systems in the genus (e.g. Hoffman, 1988; Ratsirarson, 1995; Johnson et al., 2006; Forbes et al., 2009; Botes et al., 2008; Symes and Nicolson, 2008; Arena et al., 2013). Avian

pollinators are either specialist or opportunistic nectarivores, which may be filtered by specific floral traits especially nectar properties (Johnson and Nicolson, 2008). Botes et al. (2008) showed that aloes that produce long-tubed flowers with small quantities of comparatively concentrated nectar are associated with specialist long-billed sunbirds as pollinators, while those producing short-tubed flowers that yield large volumes of relatively dilute nectar are generally pollinated by short-billed occasional nectarivores.

While the majority of *Aloe* species have floral adaptations consistent with bird pollination, insects are also frequent visitors to some of these species, usually nectar- and/or pollen-collecting bees (Hoffman, 1988; Hargreaves et al., 2008; Human and Nicolson, 2008; Botes et al., 2009; Symes et al., 2009; Wilson et al., 2009). However, *Aloe* species appear to show extensive variation in the contribution that bees make to pollination (Wilson et al., 2009). They may be exclusive pollinators (e.g. Hargreaves et al., 2008), co-pollinators with birds (e.g. Human and Nicolson, 2008; Symes et al., 2009), or resource robbers that contribute very little towards, or compromise, pollination success (e.g. Hargreaves et al., 2010). In some cases where bees co-pollinate with birds, the bees' contribution to reproductive success may equal or exceed that of the birds' (e.g. Symes et al., 2009).

Aloe seeds are typically 3–5mm long, two-winged, smooth and triangular-elliptical in shape (Kamstra, 1971). They are wind-dispersed and in some *Aloe* species they possess a third wing, which may increase travelling distances (Jordan, 1996). The seeds of other *Aloe* species lack wings, probably resulting in poor dispersal, and hence the establishment of dense seedling stands close to parent plants (Jordan, 1996, 1999). Aloe seeds are borne in fruits which are usually three-angled oblong dehiscent capsules (Kamstra, 1971). Despite aloes producing an abundance of seeds, establishment of recruits is infrequent and appears to be dependent on rainfall, which is often scarce and erratic across much of the range of the genus (Wabuyele and Kyalo, 2008). Aloe seeds typically germinate within three weeks of dispersal and their viability is often significantly reduced after a year (Giddy, 1973; Van Jaarsveld, 1989). The germination and establishment of aloe seedlings is dependent on nurse plants, which protect against excessive heat, solar radiation, desiccation, frost and herbivory (Giddy, 1973; Smith and Van Wyk, 2009).

Studies on aloe reproductive ecology have focused primarily on pollination and to a much lesser degree on seed ecology (Smith and Correira, 1992; Symes, 2012; Arena et al., 2013). Fewer still, have addressed aloe reproductive ecology in its entirety, from pollination through to germination. Hence, there is a paucity of information on several aspects of aloe seed ecology, including dispersal, dormancy, germination, longevity and seed banks. The aim of this study was to investigate the reproductive ecology

of *Aloe plicatilis* (L.) Mill., a fynbos tree aloe endemic to the Cape Winelands, South Africa. The objectives were to (a) determine the primary pollinator guild of the species, (b) quantify natural fruit and seed set, (c) conduct tests for the presence of seed banks, (d) investigate seed dispersal potential, and (e) conduct germination studies on fresh and stored seeds.

4.3. Materials and methods

4.3.1. Study species and area

Aloe plicatilis (L.) Mill. (Asphodelaceae: Alooideae) is one of six tree aloes indigenous to South Africa and the only tree aloe that occurs in the Cape fynbos (Van Wyk and Smith, 2008). The species has a restricted distribution in the mountainous parts of the Cape Winelands (also known as the "Boland") in the south-western Cape (Fig. 1). The region is characterized by a Mediterranean climate with hot, dry summers (average midsummer temperatures = 15–25°C) and cool, wet winters (average midwinter temperatures = 7–15°C) (Manning, 2007). *A. plicatilis* grows in well-drained, acidic soils on steep rocky slopes and outcrops that offer protection from fires (Van Jaarsveld, 1989; Carter et al., 2011). The Cape fynbos has a crown fire regime, with fires occurring primarily during summer, at intervals of 10–30 years depending on the vegetation type (Keeley et al., 2012).

Aloe plicatilis occurs at altitudes of 200–950 m, with average monthly wind speeds of 4.5–10.4 km/h and average annual rainfall and temperatures of 420–1900 mm/year and 14–18°C, respectively (Cousins et al., submitted; Chapter three). *A. plicatilis* is relatively long-lived and slow-growing, with dichotomously branching stems, each of which ends in a set of 12–16 alternate, succulent leaves in a fan-like arrangement (Van Wyk and Smith, 2008; Carter et al., 2011) (Fig. 2c,d). Most *A. plicatilis* individuals reach reproductive maturity at ~15 cm stem diameter and ~0.8 m in height (Cousins et al., submitted; Chapter three). Adult plants average ~1.5 m in height, but exceptionally large individuals may reach up to 5 m (Van Wyk and Smith, 2008).

The flowers are simple, cylindrical and slightly acuminate, ±5 cm long and scarlet in colour, arranged in laxly flowered racemes (25–30 tubular flowers/raceme) that are 15–25 cm long (Reynolds, 1969) (Fig. 2a,f). *A. plicatilis* flowers from August–October (occasionally November) and the fruiting season starts in early November, with fruit capsules dehiscing from December–January (Van Wyk and Smith, 2008). The fruits are longitudinally dehiscent capsules, approximately 20 mm long and 16 mm in diameter (Killick,

1988) (Fig. 2d). They are green with a pinkish tinge when fresh and pale manila-coloured when dehiscent (Killick, 1988). The winged seeds are dark brown to black (Killick, 1988).

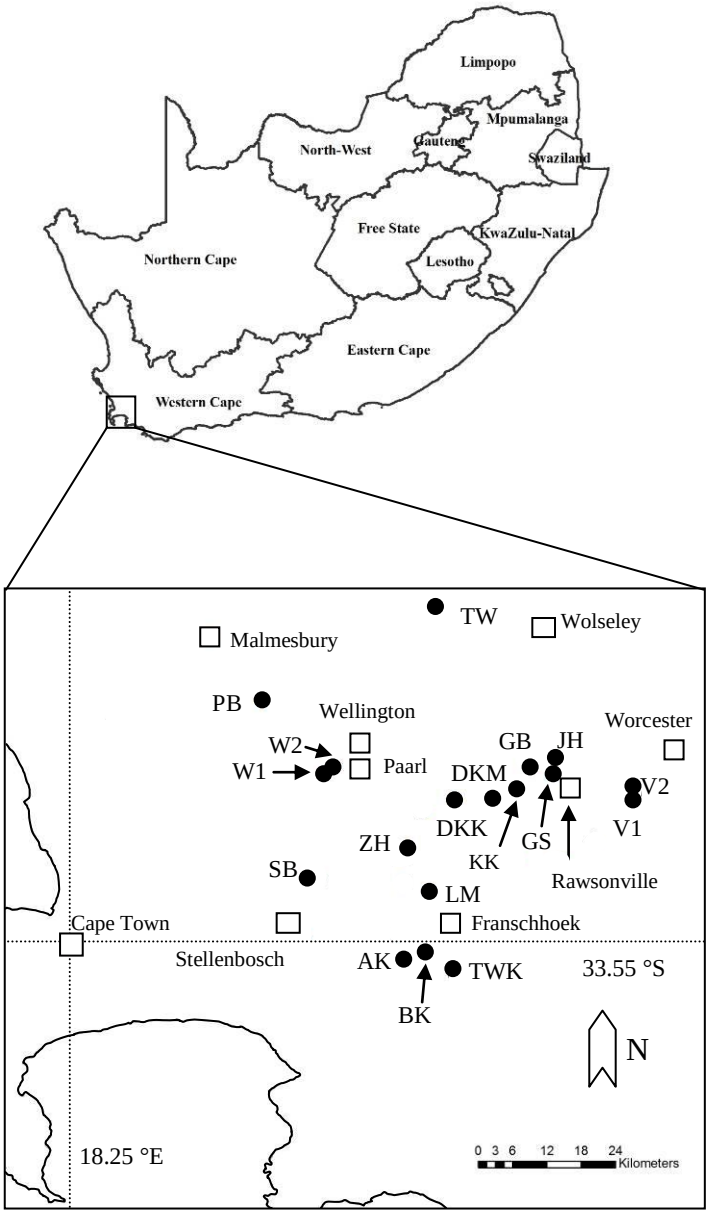


Fig. 1. Distribution map of *Aloe plicatilis* in the south-western Cape, South Africa showing the populations sampled in this study. Population abbreviations: AK=Assegaaiboskloof, BK=Bosjemanskloof, DKK=Du Toit's Kloof Krom River, DKM=Du Toit's Kloof Molenaar's River, GB=Goudini Badsberg, GS=Goudini Spa, JH=Jason's Hill, KK=Kliphoutkloof, LM=La Motte, PB=Paardeberg, TW=Tulbagh Waterfall, TWK=Theewaterskloof, V1=Voorsorg 1, V2=Voorsorg 2, W1=Windmeul 1, W2=Windmeul 2 and ZH=Zachariashoek.

4.3.2. Pollination ecology

A pollinator exclusion experiment was conducted at a population of *A. plicatilis* on Paarl Mountain (W1, Fig. 1 & 2b) in order to determine whether the species is predominantly bird or insect pollinated. Three treatments were applied to three different inflorescences on 17 plants: total exclusion, partial exclusion and a control (Fig. 2b). Exclusion of all potential visitors (i.e. birds, insects and mammals) was achieved by placing a fine gauze bag (±0.25mm mesh shade cloth) over each inflorescence and the leaf cluster from which it emerged. For the partial exclusion treatment, a cage made of rigid ±2 cm gauge wire mesh was placed around the inflorescences, allowing unrestricted access by bees and other insects, but excluding birds and small mammals. The control involved marking one inflorescence with identifying tape on each individual sampled, allowing unrestricted access by all floral visitors. The experiment commenced at the onset of the flowering season in August 2010 when flowers were at the bud stage so as to avoid any temporal bias. The plants were revisited during the fruiting season in December 2010 to collect the fruits and determine fruit and seed set. Fruit set was calculated as the percentage of pedicels on each inflorescence that bore fruit (which included both visible remains of pedicels and evidence of pedicels as scars on the raceme where flowers were attached). Seed set was determined per inflorescence and per fruit by counting the number of seeds per fruit for all fruits present on the inflorescence.

Four Bushnell® 8 Mega pixel camera traps were set up for observations of animal visitors at the *A. plicatilis* population on the Paardeberg (PB; Fig. 1) for one week from 5–12 November 2012 during the peak flowering period. Each camera was positioned so as to encompass an entire *A. plicatilis* individual, but where possible, clumps of aloes were included in order to maximize the likelihood of observing floral visitors.

Standing crop nectar concentration was measured at two populations of *A. plicatilis* using an Eclipse® handheld refractometer. Measurements were taken mid–late morning (10h00–12h00) at W1 on 8 October 2011 and at PB on 29 October 2012. At W1, four flowering plants were selected, and for each plant two flowers on two different inflorescences were sampled, giving four flowers/plant and a total of 16 flowers. At PB, 10 individual flowering plants were selected, and 2–3 flowers from one inflorescence on each plant were sampled, giving a total of 26 flowers. Flowers were selected at a stage in their development corresponding with the flower indicated with an arrow in Fig. 2f. Observations of insect visitors at the inflorescences sampled for nectar concentration were recorded.

4.3.3. Relationship between plant size and inflorescence production

The relationship between plant size (stem diameter and height) and inflorescence production was determined from five *A. plicatilis* populations where data on flowering were available (DKK, DKM, GB, GS and V1) (see Fig. 1 for key to all population abbreviations). For all populations, individuals were sampled along transects using the Point Centred Quarter Method (Cottam and Curtis, 1956), with points spaced at 15–20 m intervals, except for V1 where all individuals were measured due to small population size (n=48 individuals). Stem diameter was measured 10cm above ground level using tree callipers and stem height (at the point of leaf emergence on the tallest stem) with a tape measure. The number of inflorescences was counted on each flowering individual, and the mean height of flowering individuals was calculated for three populations, viz. GB, JH and W1.

4.3.4. Natural fruit and seed set

Natural fruit and seed set were determined for GB, JH and W1. At each population, one inflorescence from ≥13 individuals was randomly selected, and for each inflorescence the following was counted: (a) the number of pedicels present (indicative of the number of flowers produced/inflorescence), (b) number of fruits/inflorescence, and (c) the number of seeds within each fruit. Fruit set/inflorescence was calculated as the percentage of flowers that produced fruit. Seed set was calculated as the mean number of seeds/fruit and mean number of seeds/inflorescence. Mean seed set/inflorescence was used together with mean fruit set/inflorescence and number of inflorescences/plant to estimate total fruit and seed production/plant. Total seed production/population was calculated by multiplying the percentage of flowering plants in each population by the average seed production/plant and the estimated population size.

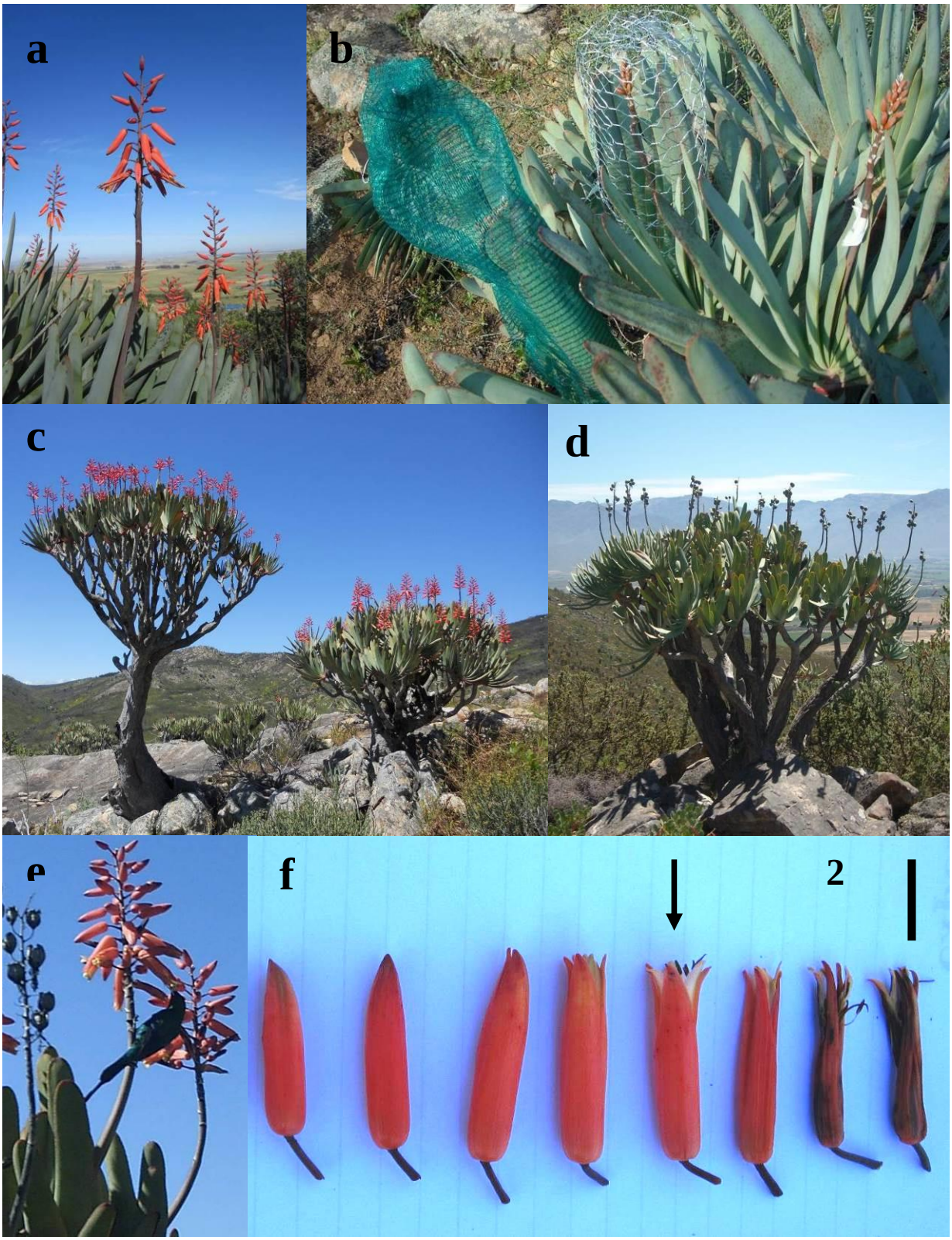


Fig. 2. (a) Close-up of mature *Aloe plicatilis* inflorescences taken at W1 on Paarl Mountain, south-western Cape, South Africa. (b) The three pollinator exclusion treatments applied to an *A. plicatilis* individual at W1. From left to right: 'no visitors' (±0.25mm mesh bag), 'insects only' (± 2 cm wire cage), and 'all visitors' (tagged). (c) Reproductively mature *A. plicatilis* individuals on the Paardeberg (PB). (d) Fruiting individual at GB. (e) A malachite sunbird (*Nectarinia famosa)* visiting an *A. plicatilis* inflorescence at PB. (f) Developmental stages of *A. plicatilis* flowers indicating the stage at which nectar concentrations were measured at PB and W1. Photographer: S.R. Cousins.

4.3.5. Seed dispersal potential

Fresh *A. plicatilis* seeds were collected from PB in January 2012 to investigate seed dispersal potential. In May 2012, thirty seeds were weighed and their terminal velocity determined as an index of air lift for ease of dispersal using the method in Lamont et al. (1993b). The seeds were dropped individually from a height of 3 m in still air, while two observers measured the time taken for each seed to reach the ground using a stopwatch accurate to 0.01 s. Data on wind speed and direction at seven stations within the distribution of *A. plicatilis* were obtained from the Agricultural Research Council of South Africa. Potential dispersal distances were calculated for *A. plicatilis* individuals of three different sizes (a) the mean height at which the onset of reproductive maturity occurs i.e. 0.8 m, (b) the maximum recorded height for *A. plicatilis*, i.e. 4.0 m (S.R. Cousins, unpublished data), and (c) the mean height of flowering individuals calculated using height measurements and flowering data from V1, DKK, DKM, GS and GB Distances were estimated using the following formula from Stokes and Yeaton (1995):

$$d = \frac{1}{V_t}(h.V_w)$$

Where d = potential dispersal distance from an individual aloe in metres, V_t = terminal velocity of 2.7 m/s (calculated for *A. plicatilis* using the method in Lamont et al., 1993b), h = plant height (m), and V_w = average wind speed (m/s) at each wind station over the month of December, when seed dispersal is at its peak.

4.3.6. Soil seed banks

The presence of soil seed banks was determined on two separate occasions for a total of 13 populations. The first set of soil samples was collected from four populations (DKK, DKM, JH and W2) during the dry season in December 2010 – one year post-dispersal in 2009 and shortly pre-dispersal in 2010. The second set was collected from nine populations (AK, BK, GB, LM, SB, TK, TWK, V2 and ZH) during the rainy season in June 2011 – six months after seed dispersal in 2010. At each population samples were collected from beneath the canopies of five randomly selected, large, reproductively mature individuals. Soil samples were extracted using a hand trowel at ≥5 points beneath the canopy to a depth of ±5cm at each point. Approximately 120g of soil was removed per individual, totalling ca. 600g per population. The samples from individual plants were pooled for each population and then placed into seedling trays

lined with newspaper in the greenhouse at the University of the Witwatersrand, Johannesburg, within two to three weeks of collection. Shade cloth (30%) was placed over the glass roof of the greenhouse and plants were watered to saturation using automatic watering set at approximately 10 minutes once a day. Emergence of *A. plicatilis* seedlings was observed once a week over a period of six months.

4.3.7. Germination experiments

4.3.7.1. Germination under controlled and ambient laboratory conditions

A sample of fresh *A. plicatilis* seeds was collected from approximately 2–3 inflorescences on ~40 plants at KK in December 2010. A second sample was collected in the same month *ad hoc* from three inflorescences on a single plant from each of the DKK, DKM and JH populations, which were also used as voucher specimens. The seeds from these three populations were pooled and used with the separate batch of seeds from KK to conduct seed viability tests after three different storage durations. The seed lots were stored in brown paper bags under ambient conditions in a cool, dry place, out of direct sunlight in a laboratory at the University of the Witwatersrand, Johannesburg.

The water content of a subset of 100 seeds from KK was determined on a fresh mass basis in the first week of March 2011. Seeds were weighed on a *Precisa 92SM-202A* scale correct to four decimal places, and then reweighed after oven-drying at 80°C for 24 hours (a temperature and duration similar to those used for determining the water content of other orthodox seeds e.g. Hay and Probert (1995) and Farrant and Walters (1998)).

Seed viability after three months storage was determined by germinating n=300 seeds from KK in March 2012. Germination, which was defined as emergence of the radicle, was monitored once a week. The seeds were germinated in an environmental control chamber set at a light/dark cycle of 12 h/12 h, with temperatures at a constant 25°C during the day and 15°C at night, and a constant relative humidity of 50%. Light was supplied by fluorescent bulbs at ~650 nm. Seeds were placed in 90mm diameter petri dishes, 25/dish. The 18-month-old seeds (n=60 seeds; 30/dish) were germinated under ambient conditions on an east-facing laboratory windowsill in June 2012, since the environmental control chamber was not available. The 24-month-old seeds (n=75; 25/dish) were germinated in December 2012 under the same conditions in the environmental control chamber described for the 3-month-old seeds.

For all three seed lots, the seeds were placed on two sheets of filter paper, covered by a third sheet and supplied with ±10 ml distilled water (or until the filter paper was saturated). The filter paper and distilled water were sterilized in an autoclave prior to use. Watering took place every 3–4 days; existing water was left in each dish and supplemented with fresh water until the filter paper was re-saturated. The seeds were inspected for germination once a week until cumulative germination was fairly constant (i.e. ≤2 new seeds germinating per week for ≥2 weeks). Accordingly, the 3-, 18-, and 24-month-old seeds were monitored over six, three and seven weeks, respectively. Germinated seeds were removed and planted in seedling trays to be grown for *ex situ* conservation in botanical gardens and private collections.

At the end of each experiment, standard tetrazolium tests were used to determine the viability of ungerminated seeds (Savonen, 1999). The seeds were sliced in half, keeping only one-half, which was placed in a 1% 2, 3, 5-Triphenyl-tetrazoliumchloride solution and stored under ambient, dark conditions for 24 hours after which they were inspected for signs of viability. Embryos and storage tissues turned pinkish-purple if viable or remained white if dead.

Germination rate as mean weeks to germinate for each treatment was calculated using the formula: Mean weeks to germination $= \frac{\sum_{i=1}^{n}(q.i)}{N}$, where n = total number of weeks, q = number of seeds germinated in the i^{th} week, i = number of weeks and N = total number of seeds tested.

4.3.7.2. Germination under ambient nursery conditions

Two seed lots were collected from KK, one in December 2010 and the other in November 2011. The seeds were collected from 2-3 inflorescences on 40 different individuals on each occasion. Seeds were stored under ambient conditions in a laboratory before sowing in the first week of January 2012. Germination tests were carried out in seedling trays under shade netting in ambient conditions outside at the Karoo Desert National Botanical Garden in Worcester, Western Cape, approximately 15 km from KK. Three growing media were used: (a) coarse river sand, (b) 50% fine sieved river sand mixed with 50% fine sieved compost, and (c) soil collected from KK. Fifty hard, undamaged seeds were sown in each medium (25 seeds collected in 2010 and 25 collected in 2011), giving a total of six trays of 25 seeds each. Trays received 7 ml of water twice daily at 09h00 and 14h00 using a mist irrigation system. Temperatures

during the germination period ranged between <20°C and 38°C and relative humidity between 25 and 50%. The total number of emerged seedlings was determined on 25 June 2012.

4.3.8. Statistical analyses

Analyses were conducted in Statistica 6.0 (StatSoft, Tulsa, OK, USA, 2002). Regression analyses were used to explore the relationship between plant size and inflorescence production. Initially, a curvilinear relationship provided the best fit, but residuals plotted against the independent variable (plant size) showed a random pattern. This pattern was indicative of the data exhibiting heteroscedasticity and therefore necessitated transformation to produce a linear fit (Zar, 1999). Hence, a logarithmic transformation of the flowering data was performed as this yielded the highest coefficient of determination. For the exclusion experiments, one-way ANOVAs compared fruit set/inflorescence and number of seeds/inflorescence, while the number of seeds/fruit was compared using a Kruskal-Wallis test. Post-Hoc Tukey tests were applied to statistically significant results. Student t-tests compared differences between (a) the nectar concentrations and (b) nectar volumes at PB and W1. A χ^2 test with Yates correction compared the germination of fresh and one-year-old seed under nursery conditions. Values are presented as $\bar{x}$ ± S.D. except for the exclusion experiment where $\bar{x}$ ± S.E. was used.

4.4. Results

4.4.1. Pollination ecology

Fruit set/inflorescence differed between treatments ($F_{2,51}$=8.46, p=0.0007), being significantly lower for inflorescences where all visitors were excluded. Exclusion of birds and mammals did not affect fruit set/inflorescence (Fig. 3a). Seed set/inflorescence followed the same pattern as fruit set ($F_{2,48}$=6.77, p=0.003), with the 'all visitors' and 'insects only' treatments both being significantly higher than the 'no visitors' treatment (Fig. 3b). Seed set/fruit also differed between treatments ($H_{2,51}$=12.19; p=0.0023), with 'all visitors' being significantly higher than both 'insects only' and 'no visitors' and 'insects only' significantly higher than 'no visitors' (Fig. 3c). The only bird species observed visiting *A. plicatilis* flowers were three individual malachite sunbirds (*Nectarinia famosa*), one each at GB, PB and W1 (Fig. 2e). Numerous bees were observed entering *A. plicatilis* flowers at GB, one of which was identified as a honeybee (*Apis mellifera)*.

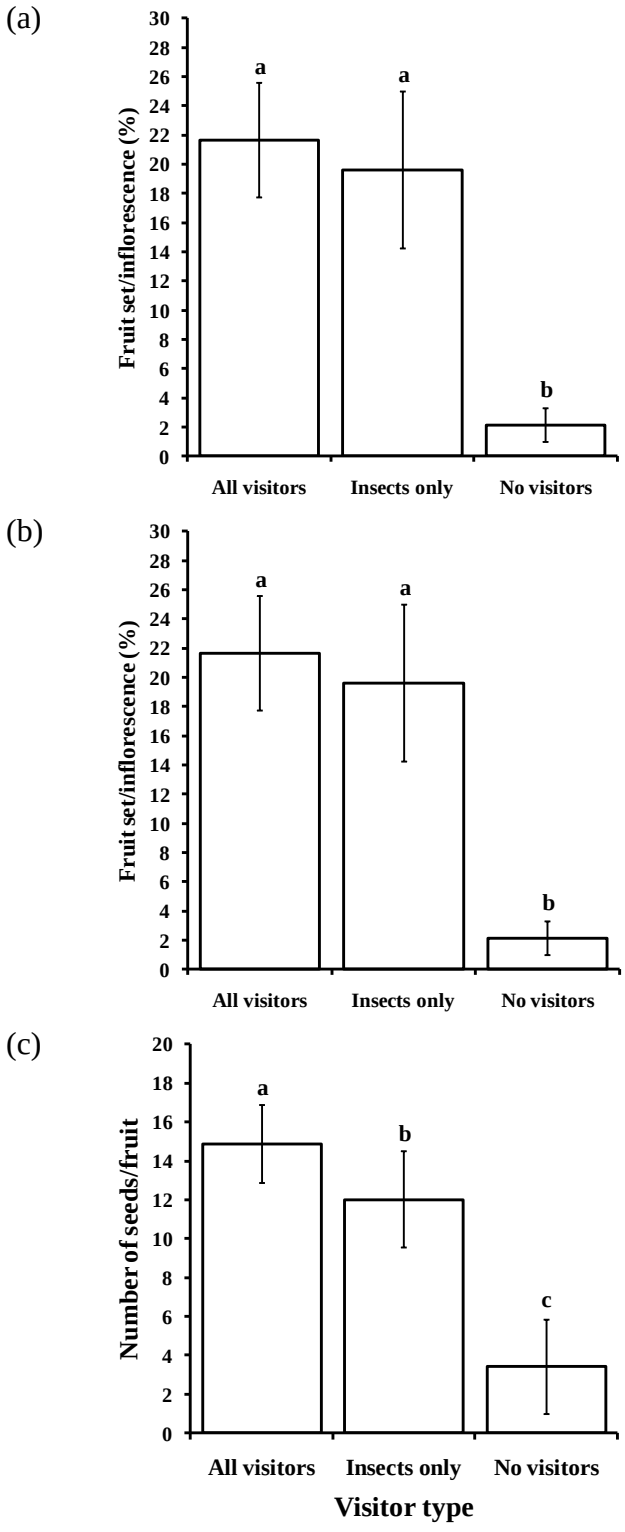


Fig. 3. Fruit and seed set ($\bar{x}$ ± S.E.) from the pollinator exclusion experiment at the *Aloe plicatilis* population at W1, south-western Cape, South Africa. The three treatments used were: (1) complete exclusion ('no visitors'), (2) exclusion of birds and mammals ('insects only') and no exclusion ('all visitors') (n=17 plants for each treatment). (a) Percentage fruit set per sampled inflorescence per plant, (b) seed set (number of seeds) per inflorescence and (c) seed set per fruit. Different letters indicate significant differences between treatments (Tukey HSD, $p<0.05$).

A single monkey beetle species (Scarabeidae, Tribe Hopliini) and a second unidentified beetle species were observed on two different *A. plicatilis* flowers at W1. Mean standing crop nectar concentration at PB was significantly higher than at W1 (PB: 30.8 ± 7.91%, range = 21.0–46.0%; W1: 15.8 ± 3.1%, range = 9.5–21.5%) (t_{41}=7.45; p<0.0001). Overall nectar concentration for PB and W1 combined was 28.1 ± 12.0%.

4.4.2. Relationship between plant size and inflorescence production

There was a significant positive linear relationship between plant size and the logarithm of the number of inflorescences, with larger plants generally producing more inflorescences than smaller plants, however the relationship was stronger for stem diameter than for height (r^2= 0.56 and 0.45, respectively) (Fig. 4).

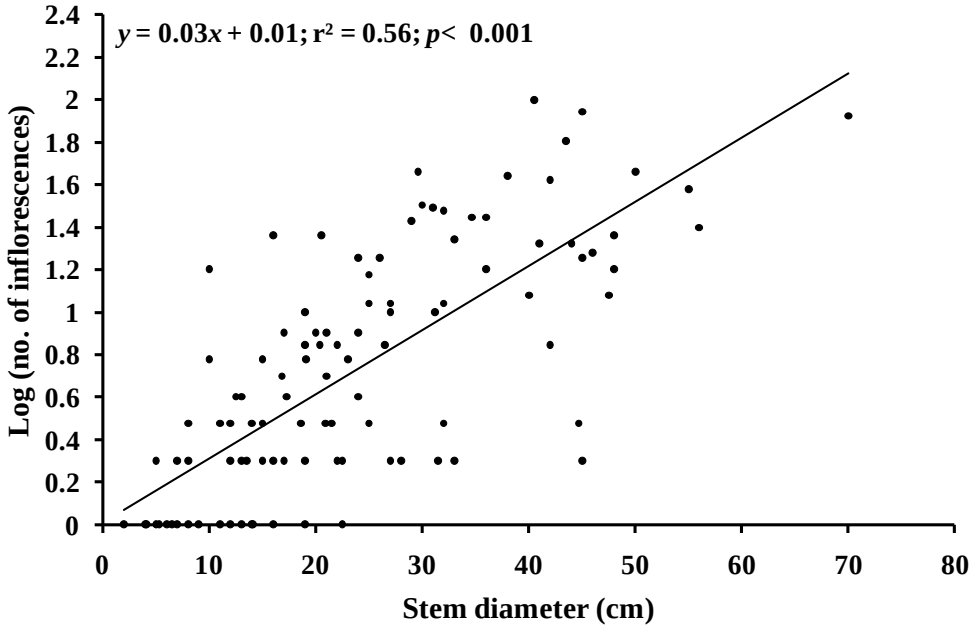
4.4.3. Natural fruit and seed set

There were no significant differences in fruit set/inflorescence between populations (17% at both W1 and GB and 13% at JH) (Table 1). Mean number of seeds/fruit ranged from 7–15. Total seed production/inflorescence ranged from 16 at JH to 50 at GB. Flowering plants were significantly taller at JH than at GB and W1. Mean number of inflorescences/individual ranged from 4 at GB to 8 at JH. W1 showed the highest calculated seed production/population due to its large estimated population size (3527 plants) and high seed production/individual. Calculated seed production/population at JH was lowest because of its small population size (31 plants) and low seed production/individual despite the larger plants (Table 1).

4.4.4. Seed dispersal potential

The seeds used for the terminal velocity test had a mass of 6.8 ± 1.0 mg and terminal velocity of 2.70 ± 0.41 m/s. Potential dispersal distances increased linearly with plant height (r^2=0.86; p<0.0001), ranging from 1.3 m for 0.8 m individuals at LM near Franschhoek where the average monthly wind speed was lowest (4.5 ± 1.0 km/h), to 15.3 m for 4 m individuals in populations near Paarl (W1 and W2) where the average monthly wind speed was highest 10.4 ± 0.9 km/h (Table 2).

(a)



(b)

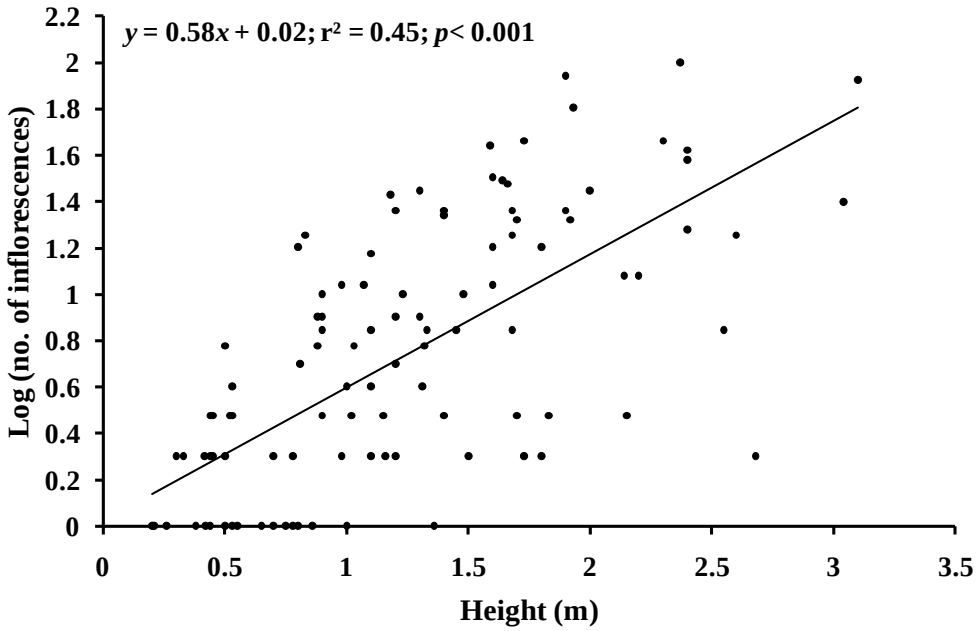


Fig. 4. Relationship between plant size and inflorescences/plant (log_{10} transformed) for (a) stem diameter and (b) height, from the five *Aloe plicatilis* populations in the south-western Cape, South Africa, where data on flowering were available (DKK, DKM, GB, GS and V1), combined.

4.4.5. Soil seed banks

Soil samples collected a year after seed dispersal yielded no seedlings, suggesting the absence of a persistent seed bank. The second sample set collected six months post-dispersal yielded only four seedlings – two from ZH and one each from GB and SB, suggesting the presence of only a transient seed bank.

4.4.6. Germination

Seed water content prior to storage was 6.91 ± 1.83%. Mean weeks to germination for 3-, 18-, and 24-month-old seeds were 0.8, 2.5 and 2.3 weeks, respectively; hence 3-month-old seeds germinated approximately three times faster than 18- and 24-month-old seeds. Total germination of 3-month-old seeds after six weeks (28%) was approximately one-third that of the 18- and 24-month-old seeds (86% after three weeks and 80% after seven weeks, respectively). Nevertheless, the viability of the ungerminated 3-month-old seeds was high (59%). The percentage of non-viable, empty seeds was similarly low for all three treatments (±11%).

Seeds sown in trays under nursery conditions emerged erratically up to six months after sowing. There was no association between percentage emergence of fresh and one-year-old seed and germination medium (χ^2_2 =0.104; p>0.90) (Table 3). Higher emergence percentages were obtained using fresh seed for all soil media compared with one-year-old seed, and fresh seed also yielded the highest average emergence across the three soil media (67%). Highest emergence/treatment was achieved using fresh seed in coarse river sand and soil from KK (both 72%).

4.5. Discussion

4.5.1. Pollination ecology

The pollinator exclusion results suggest that *A. plicatilis* is predominantly pollinated by insects. Differences in fruit and seed set/inflorescence were not significant between the 'all visitors' and 'insects only' treatments, which suggests that the contribution of birds to reproductive success is minimal. The relative abundance of honeybees (*Apis mellifera*) observed at GB and the general scarcity of birds at GB, PB and W1 would appear to support this interpretation. Other insects such as the two beetle species observed at W1 may also supplement pollination in *A. plicatilis*. Symes et al. (2009) showed that honeybees were largely responsible for the pollination of *Aloe greatheadii* var. *davyana* Schönland, and Wilson et al. (2009) confirmed the importance of insects in the pollination of *Aloe pruinosa* Reynolds. *A. greatheadii* var. *davyana* and *A. pruinosa* were also visited by sunbirds, which would be expected due to their low nectar volumes and high sugar concentrations compared to other *Aloe* species (14.8µl and 19.7% for *A. pruinosa*, and 15 µl and 20% for *A. greatheadii* var. *davyana*) (Human and Nicolson, 2008; Wilson et al., 2009). Human and Nicolson (2008) emphasise that even when floral characteristics are

suggestive of specialist nectarivore pollination (e.g. by sunbirds) (as in *A. greatheadii*, var. *davyana*), honeybees can be the primary pollinators and their contribution to pollination in aloes in general should therefore not be discounted.

The accessibility of nectar to pollinators is important to consider when determining the pollinator guild of a particular species (Arena et al., 2013). In *Aloe pluridens* Haw. and *Aloe lineata* (Aiton) Haw. var. *muirii* (Marloth) Reynolds, for example, the anthers are included and adpressed at the mouth of the perianth, thus forcing bees to crawl over them to reach the nectar (Botes et al., 2009). Hence, these species are more likely to be pollinated by nectar-feeding bees than species with strongly exserted anthers such as *Aloe africana* Mill., *Aloe ferox* Mill. and *Aloe speciosa* Baker. Since the anthers and stigmas of *A. plicatilis* flowers are only slightly exserted (1-2 mm and 3-5 mm, respectively) (Reynolds, 1969) (Fig. 2f), they are therefore similar to the flowers of *A. pluridens* and *A. lineata* var. *muirii,* further supporting the results of this study that suggest that bees may be important pollinators for this species.

Nonetheless, the significantly greater number of seeds/fruit in the 'all visitors' treatment possibly implies that despite the apparent importance of insects for the overall reproductive success of *A. plicatilis*, the bird contribution to pollination is significant at the level of the individual fruit. It is also possible that birds were able to extend their beaks through the cages of the 'insects only' treatment (as Stokes and Yeaton (1995) observed in *A. ferox*) and hence may have elevated pollination success in these inflorescences. Furthermore, of the six South African tree aloe species, the floral morphology of *A. plicatilis* and *Aloe tongaensis* Van Jaarsv. (i.e. long, slightly curved flowers on laxly-flowered racemes that become pendent when open) suggests sunbird pollination in both species (Van Jaarsveld, 2011). By contrast, the Northern Cape quiver trees (*Aloe dichotoma* Masson, *Aloe pillansii* L.Guthrie and *Aloe ramosissima* Pillans) and *Aloe barberae* Dyer have short, cylindrical-ventricose flowers on densely-flowered racemes and are purportedly pollinated largely by opportunistic nectarivores (Van Jaarsveld, 2011), although they are also visited by sunbirds and honeybees (Tribe and Johannsmeier, 1996).

Geerts and Pauw (2009) showed that a large group of Cape plants with long (35–58 mm) tubular flowers are apparently adapted for pollination exclusively by malachite sunbirds, which also appear to be the most common avian visitors to *A. plicatilis*. The long tube lengths of *A. plicatilis* flowers (±50 mm) are consistent with pollination by long-billed nectarivores, since short-billed nectarivores would be unable to reach the nectar at the base of the flower.

Table 1. Differences in population size, nearest neighbour distance, natural fruit and seed set, flowering height, and total seed production in three populations of *Aloe plicatilis* in the south-western Cape, South Africa. Population size estimates were determined using a combination of the point-centred quarter (PCQ) and nearest neighbour methods. Fruit set is expressed as the percentage of pedicels/inflorescence that produced fruit and seed set as the mean number of seeds/fruit and number of seeds/inflorescence. Data are presented as $\bar{x} \pm$ S.D., ranges are shown in brackets, and bold text indicates a significant difference.

	Windmeul 1 (W1) (3527 plants)	n	Jason's Hill (JH) (31 plants)	n	Goudini Badsberg (GB) (399 plants)	n	df	*F*	*p*
Nearest neighbour distance (m)	2.59 ± 2.14	85	6.88 ± 7.91	29	2.33 ± 2.10	26	2, 137	100.25	**<0.001**
Pedicels bearing fruit/inflorescence (%)	17 ± 11	15	13 ± 17	17	17 ± 16	13	2, 42	0.51	0.606
Number of seeds/fruit	8 ± 8	15	7 ± 12	17	15 ± 7	13	2, 31	1.86	0.173
Height of flowering individuals (m)	1.37 ± 0.43	23	1.89 ± 0.51	14	1.33 ± 0.39	14	2, 48	7.45	**0.002**
Number of inflorescences/individual = [A]	6 ± 5 (1-22)	23	8 ± 9 (1-32)	14	4 ± 3 (1-13)	14	2, 48	1.69	0.195
Number of seeds/inflorescence = [B]	41 ± 51 (6-146)	15	16 ± 27 (4-84)	17	50 ± 49 (9-146)	13	2, 42	2.60	0.086
Number of seeds/plant = [A] x [B] = [C]	246 (41-902)	-	128 (16-512)	-	200 (50-650)	-	-	-	-
Seed production/population = [C] x (population size) x (percentage of flowering plants in population)	251616	-	1325	-	27930	-	-	-	-

Table 2. Summary of wind conditions at weather stations throughout the range of *Aloe plicatilis* in the south-western Cape, South Africa and potential seed dispersal distances for plants of three different heights. Wind conditions include annual predominant wind direction, mean monthly wind speed during the peak seed dispersal period (December), and the percentage of this period during which windless conditions prevailed. Potential seed dispersal distances were calculated using the formula in Stokes and Yeaton (1995). (Plant heights: 0.8 m = average height of *A. plicatilis* at the onset of reproduction, 1.23 m = mean height of reproductively mature individuals at populations DKK, DKM, GB, GS and V1 (see Fig. 1) and 4.0 m = height of the tallest *A. plicatilis* individual encountered in this study.

Nearest town (station name)	Altitude (m)	Predominant wind direction	Windless conditions (%)	Mean ± S.D. monthly wind speed (km/h)	Potential dispersal distance (m)		
					0.8 m tall individuals	1.23 m tall individuals	4.0 m tall individuals
Franschhoek (La Motte)	207	NW and SW	60.8	4.5 ± 1.0	1.3	2.1	6.7
Grabouw (Eikenhof)	365	SE	34.2	7.8 ± 2.6	2.3	3.5	11.5
Paarl (Môrewag)	201	S	9.2	10.4 ± 0.9	3.1	4.7	15.3
Rawsonville (Blaarfontein)	276	SE	40.2	-	-	-	-
Stellenbosch (Nietvoorbij)	149	SW	21.0	9.9 ± 1.6	2.9	4.5	14.6
Wolseley (LaPlaisant)	283	E	29.2	10.0 ± 1.5	3.0	4.6	14.9
Worcester (Nuy)	225	SE	27.2	9.1 ± 1.4	2.7	4.1	13.5

The Cape sugarbird *(Promerops cafer)* has a bill equally as long as that of the malachite sunbird (Geerts and Pauw, 2009), and has also been observed visiting *A. plicatilis* flowers (Nicolson and Roets, 2012). Other specialist nectarivores that occur within the distribution of *A. plicatilis* and are therefore possible visitors and/or pollinators include *Cinnyris chalybeus* (southern double-collared sunbird) and *Anthobaphes violacea* (orange-breasted sunbird), while *Zosterops pallidus* (Cape white-eye) is a possible opportunistic nectarivore visitor (Rebelo, 1987; Sinclair et al., 2011). However, these three species have short bills that are unlikely to reach the base of *A. plicatilis* flowers, and possibly rob nectar by piercing through the corolla tube as has been observed in other Cape plant species with similarly long corolla tubes (e.g. *Chasmanthe floribunda* (Salisb.) N.E.Br.) (Geerts and Pauw, 2009).

Mean nectar concentration at PB was double that at W1, suggesting some variability between populations. Overall nectar concentration was high (28%), and exceeded the upper limit of the range generally produced by flowers pollinated by specialist nectarivores (15–25% w/w) (Symes and Nicolson, 2008). Hence, in terms of the bird contribution to the pollination of *A. plicatilis*, the species' floral morphology, its concentrated nectar, and observations of sunbirds and sugarbirds as floral visitors support the hypothesis that specialist long-billed nectarivores are more important than short-billed occasional nectarivores. However, further floral visitor observations and exclusion experiments at various *A. plicatilis* populations over several flowering seasons would help clarify its pollination system further, particularly patterns in the relative contributions of birds and insects to reproductive success.

Table 3. Total percentage emergence of *A. plicatilis* seedlings after six months in three different germination media under ambient nursery conditions at the Karoo Desert National Botanical Gardens in Worcester, Western Cape, South Africa.

Germination medium	Emerged seedlings (%)	
	Fresh seeds (1-month-old)	1-year-old seeds
Coarse river sand	72	44
50% fine river sand and 50% fine compost	56	36
Soil from wild population	72	52
Average percentage emergence	67	44

In terms of the potential for self-compatibility in *A. plicatilis*, the total exclusion treatment yielded very low fruit and seed set (mean of 2% fruit set and 7 seeds/inflorescence), which suggests a small degree of autonomous self-pollination. However, low reproductive success at JH suggests an inability to self-pollinate, for if isolated flowering plants were self-compatible, greater fruit and seed set in these

individuals would be expected. Self-incompatibility is widespread in the genus *Aloe*; though some recent studies suggest this may not be the case for certain species. Autonomous self-pollination has been observed in *Aloe maculata* All., *Aloe krausii* Baker, (Hargreaves et al., 2012), *and Aloe peglerae* Schönland (Arena et al., 2013). However, seed set/fruit was very low in all three species, especially *A. maculata* and *A. krausii* (0.02 and 0.11 seeds/fruit, respectively). While self-compatibility appears to be possible in *A. plicatilis*, detailed supplemental self- and cross-pollination experiments are necessary to confirm its breeding system.

4.5.2. Relationship between plant size and inflorescence production

Plant size is generally closely correlated with total flower production, with the largest plants in a population usually being the most floriferous (Ollerton and Lack, 1998). This relationship was evident in *A. plicatilis*, with larger plants (as measured by stem diameter and height) having more inflorescences than smaller ones. A similar trend has been demonstrated in studies on other long-lived succulent plants that are functionally similar to *A. plicatilis*: Pfab and Witkowski (1999) found a significant, positive relationship between canopy area and flower and fruit production in *Euphorbia clivicola* R.A. Dyer, while McIntosh (2002) showed that the number of flowers produced by two *Ferocactus* species (Cactaceae) increased with plant size. In terms of other *Aloe* species, Hoffman (1988) recorded a significant positive linear relationship between plant height and raceme number, raceme length and fruit set in *A. ferox*, and Symes (2012) demonstrated that larger *Aloe marlothii* A. Berger individuals produced more seeds than smaller ones.

Klinkhamer et al. (1992) suggested that the relationship between plant size and reproductive output is curvilinear. Initial curvilinear relationships between plant size and inflorescence production determined for *A. plicatilis* produced a good fit, but the coefficient of determination was stronger using a linear regression with the dependent variable logarithmic transformed. Bazzaz et al. (2000), however, cautioned that the reproductive individuals in a population can vary enormously in size, owing to fine-scale environmental heterogeneity and competitive interactions, which leads to inequalities in the distribution of resources within a population. Hence, while the relationship between plant size and flower production in *A. plicatilis* is curvilinear, large plants may not always produce more flowers than smaller ones owing to differences in local environmental conditions (e.g. climate, shading by other species and nutrient availability).

4.5.3. Natural fruit and seed set

Natural fruit set at GB, JH and W1 was comparable to that measured for *Aloe divaricata* A.Berger, *Aloe linearifolia* A.Berger and *A. marlothii* (15, 19 and 12–18%, respectively) (Ratsirarson, 1995, Botes et al., 2009; Symes et al., 2009), but was less than half that of *A. greatheadii* var. *davyana, A. pruinosa* and *A. peglerae* (45–55, 41 and 40%, respectively) (Symes et al., 2009; Wilson et al., 2009; Arena et al., 2013). Number of seeds/fruit, was, however only comparable to that found for certain grass aloe species e.g. *A. inconspicua, A. minima* and *A. linearifolia* (ca. 3.5, 10 and 13.5 seeds/fruit, respectively) (Hargreaves et al., 2008; Botes et al., 2009), and was 2–9 times lower than that of *A. peglerae, A. greatheadii* var. *davyana, A. marlothii* and *A. pruinosa* (all >34 seeds/fruit) (Symes et al., 2009; Wilson et al., 2009; Arena et al., 2013). Furthermore, estimated seed production/plant in *A. plicatilis* was far lower than that estimated for *A. marlothii* (95148 for individuals <2.5m and 167 549 for individuals >2.5m; Symes, 2012) and *A. peglerae* (3869; Arena et al., 2013). However, all the above-mentioned species are variable in terms of growth form, inflorescence size and shape and number of flowers/inflorescence, making comparisons between species difficult. Nonetheless, seed production in *A. plicatilis*, both at the level of individual fruit and whole plant, does appear to be markedly low relative to the size of flowering individuals.

JH exhibited the highest number of flowers/plant, but also the lowest fruit set/inflorescence and the lowest seed set/plant and per population. At GB and W1, almost all inflorescences on flowering individuals produced at least one fruit, whereas a remarkably large proportion of inflorescences on most flowering individuals at JH died-back after flowering (i.e. functional in terms of producing pollen, but not fruiting). Post-survey analyses of fruiting plants at JH for which photographs were available (n=8; 57% of all flowering plants in the population) revealed an average of 63% dead inflorescences/plant, and dead inflorescences comprised 77% of the total number of inflorescences of all eight plants combined.

Furthermore, inflorescences that did produce fruit were often highly predated by birds (S.R. Cousins pers. obs.). Due to the uncertainty regarding the season in which the dead inflorescences were produced, only inflorescences that bore at least one fruit were sampled in order to determine fruit and seed set. Thus, while measures of reproductive output at JH were not significantly different from those of GB and W1, the results for JH probably overestimate the overall reproductive success at this population due to the unsampled dead inflorescences. Another indicator of reproductive failure at JH is

that recruitment appears to be deficient, as surveys of population size structure (S.R. Cousins, unpublished data) revealed steep J-shaped stem diameter and height size class distributions indicating a preponderance of large adults and very little recent recruitment. Furthermore, plants at JH were, on average, 7 m apart, which differed significantly from the much shorter nearest neighbour distances of 2.6 m and 2.3 m measured for W1 and GB, respectively (S.R. Cousins, unpublished data), and JH comprised only 31 plants, compared to 399 at GB and 3527 at W1 (Table 1).

Due to poor reproductive output, a lack of recent recruitment, small population size and large inter-plant distances at JH, it appears that the population is displaying the Allee effect. *A. plicatilis* individuals at JH may be too few and too far apart to attract sufficient pollinators, resulting in pollen and/or pollination limitation and consequent reproductive failure (Kunin, 1992; Ågren, 1996; Wilcock and Neiland, 2002). Furthermore, since aloes are generally self-incompatible, and the pollinator exclusion results suggest that this is likely the case for *A. plicatilis*, reproductive failure may be exacerbated as isolated individuals cannot self-pollinate for reproductive assurance (Knight et al., 2005). JH may have reached its Allee threshold (see Berec et al., 2007), and could undergo local extirpation if reproductive failure persists. However, repeat surveys of this population's size structure and reproductive output may help to determine whether it displays poor annual reproductive success, and may assist in establishing how fruit and seed set relate to recruitment patterns and population structure.

4.5.4. Seed dispersal potential

Seed terminal velocity of 2.7 m/s for *A. plicatilis* was comparable to the 2.0m/s calculated for *A. candelabrum* seed by Stokes and Yeaton (1995). Potential dispersal distances were similar across the study area within plant height categories, and were approximately three times greater than plant height on average. Direct measurements of wind dispersal of the seeds of many plant species in the field show that most are dispersed very short distances, and usually fall near parent plants (Fenner and Thompson, 2006; Howe and Miriti, 2004; Corlett, 2009). Seed shadow patterns for all modes of dispersal are generally described by negative exponential functions (Willson, 1993), with the modal distance of wind-dispersed seeds being approximately equal to canopy height (Nathan et al., 2002). However, the estimated potential dispersal distances for *A. candelabrum* seeds calculated by Stokes and Yeaton (1995) were three-fold the height of seed release – a result that concurs with that calculated for *A. plicatilis*. This difference may possibly be due to aloe seeds generally possessing wings that aid wind

dispersal (Jordan, 1999) and are therefore likely to travel further than seeds without any wind dispersal adaptations.

While short-distance seed dispersal influences the local dynamics of plant populations, long-distance dispersal is integral to their large-scale dynamics (Schurr et al., 2009). The "Cape Doctor", or south-easterly wind, blows over the south-western Cape during summer, when seed dispersal in *A. plicatilis* occurs, and is known to be persistent and often very gusty, with gusts of up to 35 m/s (128km/h) recorded in Cape Town (Kruger et al., 2010). Since the geographical distribution of *A. plicatilis* is very patchy, with many populations separated by large distances, it is possible that these isolated populations arose due to long-distance dispersal events caused by strong gusts of wind. Arguably, isolated *A. plicatilis* populations that occur on continuous mountain ranges such as the Du Toit's Kloof and Franschhoek mountains may once have been connected and subsequently become fragmented due to changing climatic conditions over time (see citations in McLachlan and Clark, 2004).

However, the occurrence of populations on mountains completely disconnected from other more continuous mountain ranges e.g. PB on the Paardeberg and W1 and W2 on Paarl Mountain raises questions regarding the possibility of long-distance dispersal. Schurr et al. (2009) noted that for a plant species to persist in a fragmented landscape (such as a mosaic of mountain and lowland habitats), local extinction from occupied habitat fragments must be balanced by the colonisation of unoccupied fragments, which requires long-distance dispersal to those fragments. Horn et al. (2001) emphasized that many of the aerodynamic mechanisms that facilitate long-distance dispersal in light, fluffy or plumed seeds may also apply to heavier winged seeds (such as aloe seeds) at somewhat different scales. Furthermore, turbulence and variations in wind velocities may more frequently and more extensively promote extreme dispersal than retard it despite reducing the modal dispersal distance on average (Horn et al., 2001). However, in order for seeds to be dispersed long distances they must be captured in convection cells of the scale of hundreds of meters to kilometres (Horn et al., 2001).

Since *A. plicatilis* occurs exclusively on well-drained, rocky mountain slopes that act as fire refugia, it is unlikely that it historically occurred in the less-rocky lowland fynbos between the Paardeberg, Paarl Mountain and the Du Toit's Kloof/Franschhoek mountains. Furthermore, both the Paardeberg and Paarl Mountain occur north-west of several other large *A. plicatilis* populations (e.g. LM, TWK and ZH), from which seed may have been transported by strong south-easterly winds. Testing this hypothesis may prove challenging, as long-distance dispersal events are very rare and difficult to track (Horn et al.,

2001; Nathan et al., 2002), although analyses of population genetic variation (e.g. He et al., 2004) may provide a feasible approach.

4.5.5. Seed banks and seedling recruitment

The total absence of seedling emergence from the soil samples from most populations of *A. plicatilis* suggests that the species forms only transient seed banks that last for <1 year after dispersal. There was also little or no evidence of recruitment *in situ* or in the soil samples collected below plants that had many spent inflorescences beneath them (S.R. Cousins, pers. obs.). These results are consistent with those of Symes (2012), who assessed the formation of soil seed banks in *A. marlothii* using soil samples collected pre-dispersal at various distances from an aloe stand on two consecutive years. Samples from both years combined yielded only one seedling during a three month germination trial, while samples collected at the same site directly after dispersal yielded far greater numbers of seedlings (Symes, 2012). The absence of persistent seed banks in *A. plicatilis* is not unexpected, since the presence of persistent seed banks in any plant species is strongly associated with long-term dormancy, and the seeds of most *Aloe* species are known to have a short viability period of approximately one year (Giddy, 1973). However, being wind-dispersed, the aloe seeds are likely to be caught up against barriers such as surrounding vegetation or rocks, which may not have been captured in the sampling design. Thus, soil sampled from such sites may have yielded greater numbers of seedlings.

The Cape fynbos is dominated by sclerophyllous evergreen vegetation that dries sufficiently during the summer dry season to produce a predictable and extended wildfire season (Keeley and Bond, 1997). Many fynbos species (e.g. *Protea* and *Erica*) regenerate 1–2 years post-fire, since fire stimulates flowering, seed release from serotinous cones, and breaks seed dormancy through heat or chemicals in charred wood or smoke (Pierce and Moll, 1994; Keeley and Bond, 1997). Disturbance-dependent fynbos species typically produce strongly dormant seeds with germination triggered by heat or chemicals, while species with 'disturbance-free' recruitment produce non-refractory seeds that lack deep dormancy and therefore have transient seed banks (Keeley and Bond, 1997). In the case of aloes, Wabuyele and Kyalo (2008) note that although most species produce an abundance of seeds, recruitment in wild populations is only occasional.

Despite *A. plicatilis* occurring in the Cape fynbos, where many other plant species reseed *en masse* after fire, recruitment in the species is probably erratic and 'disturbance-free' and therefore similar to

that of other *Aloe* species, most of which occur in arid or semi-savanna (Van Jaarsveld, 1989). Out of the 19 *A. plicatilis* populations surveyed for population size structure in Cousins et al. (submitted), 50% displayed bell-shaped size class distributions, while only one exhibited a steep inverse-J distribution indicating recent recruitment. Seedlings at this population occurred mostly in moist, shaded, rocky sites surrounded by dense vegetation on a hilltop that had not burned in 10 years, strongly suggesting establishment in the absence of a major disturbance event. Moreover, zero seedling recruitment was observed during a seedling search at KK 22 months after fire (S.R. Cousins, pers. obs.), thus supporting the hypothesized absence of mass post-fire recruitment. Other studies on *Aloe* population structure have found bell- or J-shaped distributions suggesting a survival strategy based on adult persistence and drib-drab recruitment (e.g. Scholes, 1988; Weisser and Deall, 1989). Notwithstanding, further investigations on the specific period during which *A. plicatilis* seeds germinate in the wild is key to understanding its reproductive ecology and population dynamics.

In terms of seedling establishment in *A. plicatilis*, consistent water availability and shading appear to be important. Wind-dispersed *A. plicatilis* seeds would probably be trapped in surrounding vegetation or rock crevices where suitable microsites for seedling establishment may occur. Aloe seedlings generally require nurse plants for protection from harsh, direct sunlight (Giddy, 1973; Smith and Correira, 1992; Smith and Van Wyk, 2009) and such conditions may also potentially be provided by nurse rocks that afford stress amelioration and protection from fire (e.g. Peters et al., 2008). Smith and Correira (1992) showed that *A. greatheadii* var. *davyana* seeds sown outdoors in seed beds either under an organic mulch or under shade netting exhibited greater rates of seedlings emergence, and the seedlings leaves were considerably greener, more turgid and approximately four times longer than the those of seedlings grown in full sun.

Similar observations were made for shaded versus non-shaded *A. plicatilis* seedlings growing in an environmental control chamber and greenhouse (S.R. Cousins, pers. obs.), and for *A. peglerae* under the same conditions (G. Arena, pers. comm.). Rodrígues-García et al. (2007) found that the new leaves of *Aloe vera* Mill. plants are sensitive to water stress and Bairu et al. (2009) showed that regular watering of *Aloe ferox* Mill. seedlings enhanced most of the growth parameters studied. *A. plicatilis* seedlings in cultivation also respond well to regular watering and may show considerably reduced turgidity after ±2 weeks without watering (S.R. Cousins, pers. obs.). These findings suggest that despite having succulent leaves that act as a buffer against desiccation, in order for *A. plicatilis* seedlings to establish and persist in wild populations they require substantial, consistent rainfall over winter and

probably into spring and early summer to accumulate sufficient water reserves to survive the subsequent summer drought.

4.5.6. Germination trials

4.5.6.1. Controlled and ambient laboratory conditions

Despite the 3-month-old *A. plicatilis* seeds germinating approximately three times faster than both the 18- and 24-month-old seeds, total germination in the former was three-fold less than the latter two. The tetrazolium tests showed that 100% of the remaining ungerminated 3-month-old seeds that were not empty were viable. These findings suggest that *A. plicatilis* seeds undergo after-ripening – a progressive loss of primary dormancy in air-dry seeds, which is a function of environmental variables and time (Murdoch and Ellis, 2000). Bairu et al. (2009) suggested the need for an after-ripening period in *A. ferox* seeds, since total germination at various temperatures, light intensities and concentrations of plant growth regulators was <80% after ±1 month, although 95% of ungerminated seeds were viable. Staggered germination was also observed in *A. greatheadii* var. *davyana* and *A. marlothii* seeds, some of the former still germinating in the second season after sowing (Smith and Correia, 1992; Symes, 2012). Eloff and Liede (1987) reported increased percentage germination in *A. dichotoma, A. speciosa, Aloe thraskii* Baker and *Aloe vryheidensis* Groenew. seeds stored for ± 16 months under ambient conditions compared to those stored for only four months. However percentage germination in other *Aloe* species studied either decreased or remained fairly consistent over time.

Although the vigour of the 18- and 24-month-old *A. plicatilis* seeds in this study decreased slightly (indicated by slower germination rates), their viability was maintained. This result is, however, in stark contrast to the extremely poor germination of 0.5% Eloff and Liede (1987) obtained for *A. plicatilis* seed stored for 16.5 months under ambient laboratory conditions. However, the initial viability of that particular seed lot was unknown and the reasons for germination failure were therefore unclear. While the potential longevity of seeds stored in an air-dried state in a laboratory may provide clues about their longevity in the field, laboratory-stored seeds are exposed to much smaller variations in temperature, moisture and solar radiation compared to those in habitat (which are also vulnerable to predation). Seeds dispersed in habitat therefore probably survive for much shorter periods. Differences in viability between laboratory-stored seeds and those in the wild have been shown for marula (*Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro), which remain viable for many years in a laboratory,

but form small, short-term persistent seed banks in the wild (Helm et al., 2011). In addition, Mbalo and Witkowski (1997) demonstrated the effect of simulated high soil surface temperatures on seeds of *Acacia karroo* Hayne, *Acacia tortilis* (Forssk.) Hayne subsp. *heteracantha* (Burch.) Brenan and *Chromolaena odorata* (L.) K. & R., which all declined in seed viability with increasing duration of exposure at 70°C. While the viability of *A. plicatilis* seeds in the wild is most likely restricted to <1 year, seed storage and germination experiments *in situ* would help validate this deduction and thus contribute to our understanding of regeneration and establishment not only in *A. plicatilis*, but also aloes in general.

The percentage of one-year-old seeds that germinated and emerged under nursery conditions was fairly low (44%) compared with fresh seeds (67%), which suggests that some of the one-year-old seeds may have lost viability during storage or during the germination trials. The two germination media that appeared to favour the germination and emergence of *A. plicatilis* seedlings were coarse river sand and soil from the wild population, as they both yielded higher percentage emergence than the mixture of fine river sand and compost. The low percentage emergence of seeds under nursery conditions may have been due to fluctuating temperatures and relative humidity outside in the Karoo Desert National Botanical Garden, compared with seeds germinated under more stable conditions in the environmental control chamber and laboratory. For optimal germination and emergence it is therefore recommended that *A. plicatilis* seeds less than one year old be sown under controlled conditions in a growth chamber or greenhouse.

4.6. Conclusion

Aloe plicatilis appears to be pollinated primarily by insects; however, bird visitation significantly increased seed set/fruit, suggesting co-pollination with insects. Malachite sunbirds appear to be the most common avian visitors to *A. plicatilis* flowers – an observation that is consistent with the species' floral morphology and concentrated nectar which suggest pollination by specialist avian nectarivores. Natural seed set at three populations varied by orders of magnitude, and reproductive success was poorest at the smallest and least dense population. The reproductive failure evident at this population suggests a possible Allee effect, but this requires further investigation. Potential seed dispersal distances in *A. plicatilis* were estimated to be approximately three times canopy height, consistent with a negative exponential seed shadow. However, the species' occurrence on isolated mountains that are disconnected from more continuous mountain ranges where the species also occurs suggests that long-

distance dispersal by strong, gusty summer winds is possible. Seed banks in *A. plicatilis* populations appear to be transient, lasting for <1 year, and recruitment is likely erratic and 'disturbance free'. *A. plicatilis* seeds stored under ambient laboratory conditions for 18 and 24 months maintained high viability with total germination at ≥80%, while that of 3-month-old seed was three times less, suggesting the necessity for after-ripening. Emergence of *A. plicatilis* seeds under nursery conditions was not as successful as germination under controlled conditions in a growth chamber and laboratory. Further pollinator exclusion experiments and floral visitor observations will help verify the species' pollinator guild, and detailed supplemental self- and cross-pollination experiments are required to confirm its breeding system. Very little is known about the germination ecology of *A. plicatilis* (and most other aloes) in habitat. Further studies on germination requirements and recruitment patterns in the genus *in situ* would be especially beneficial for the conservation of rare and threatened *Aloe* species.

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CHAPTER FIVE

Beating the blaze: fire survival and resprouting in the succulent plant *Aloe plicatilis,* a Cape fynbos endemic tree aloe

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5.1. Abstract

Fire is central to Cape fynbos ecology and plays a major role in shaping vegetation patterns in the region. Studies on the fire ecology of fynbos species have focused primarily on the Proteaceae, but little is known about the fire ecology of succulent fynbos plants. This study investigated the fire ecology of an arborescent succulent monocot, *Aloe plicatilis*, a Cape fynbos endemic. Habitat suitability was assessed to determine whether the species tolerates or 'avoids' fire, and plant traits associated with fire survival (bark thickness and tissue water content) were measured. The population size structure and density of three *A. plicatilis* populations were assessed after a natural fire. Resprouting after stem removal was investigated, as was post-fire regrowth from burned plants. *Aloe plicatilis* adopts a dual fire survival strategy, occupying rocky sites to 'avoid' fire and possessing morphological features that promote fire tolerance e.g. well-protected apical meristems and thick corky bark. High tissue water contents may confer fire retardant properties. Bark thickness of burned individuals was similar to that of unburned plants, suggesting that *A. plicatilis* bark provides effective insulation against fire. All three populations showed reduced plant density post-fire. Mortality rates at populations decreased as the degree of rockiness increased; however, within populations, live plants had similar surrounding rock cover to dead individuals. Small plants appear most vulnerable to fire damage due to lower absolute bark thickness and heights within the flame zone. Small individuals,

may, however survive in very rocky sites, while larger plants in less-rocky sites with more surrounding flammable biomass may be killed. *Aloe plicatilis* is an 'apical sprouter', recovering post-fire by onward growth from surviving stem apices. Like all other dichotomously branching tree aloes, *A. plicatilis* seldom resprouts after stem removal or top-kill, and post-fire population persistence hinges on seed dispersal from surviving plants.

Key words: bark thickness, density, fynbos, height, resprouting, rock, size class distribution, stem diameter, succulent plant

5.2. Introduction

Fire is an important part of the ecology of Mediterranean-type climate (MTC) regions, where plants possess a range of morphological and physiological traits that confer fire survival, but are not necessarily fire adaptations *per se*, e.g. resprouting, serotiny, physical dormancy, post-fire flowering and smoke-induced germination (Le Maitre & Midgley, 1992; Bradshaw et al., 2011; Keeley et al., 2012). Both winter growing conditions and summer droughts contribute to making MTC regions among the most fire-prone ecosystems in the world (Keeley et al., 2012). Furthermore, most MTC regions experience extreme wind events that typically last several days and when coincidental with droughts and ignitions, they are associated with severe fires (Keeley et al., 2012). Crown fires are frequent in MTC regions, and shrubs are often either killed outright by burning (non-sprouters or seeders, which re-establish post-fire by seedling recruitment), while others recover vegetatively from roots or stems (sprouters) (Bond & Midgley, 2001; Keeley et al., 2012).

The Cape Floristic Region (CFR) in South Africa's south-western Cape is the smallest of the world's five MTC regions (Keeley et al., 2012). Covering approximately 90000 km^2, with ~9000 indigenous vascular plant species, 69% of which are endemic, the CFR is one of the richest regions globally in terms of floral diversity (Goldblatt & Manning, 2000). Fires are more common in the fynbos than any other MTC region (Manning, 2007), and play a central role in determining major vegetation patterns in the region (Keeley et al., 2012). Fynbos is extremely flammable when dry, with most fires occurring during summer at intervals of 10–30 years depending on the vegetation type (Keeley et al., 2012). Under experimental conditions, fynbos fire intensities range from 500–20000 kWm^{-1}, with flame heights of 2–7 m and rates of spread of 0.04–0.89 ms^{-1} (Van Wilgen et al., 1985).

The susceptibility of plants to fire-induced injury or death depends primarily on the degree to which live buds are protected from heat (Bond & Van Wilgen, 1996). Other important factors include the nature and distribution of critical tissues, stem diameter (SDr) and bark insulating quality (which is affected by bark composition, structure, density, specific gravity, thickness, moisture content and flammability) (Hare, 1965; Gill, 1995; Pinard & Huffman, 1997). Susceptibility is also influenced by pre-fire plant vigour, plant moisture content, resprouting ability, ambient temperatures, fuel loads, fire intensity, duration of heat exposure, and the distribution and value of fire temperatures (Gill, 1995; Bond & Van Wilgen, 1996; Pinard & Huffman, 1997). High fuel loads, for example, result in more intense fires, thus increasing the likelihood of plant death (Bond & Van Wilgen, 1996). Plants with high moisture content act as fire retardants (Montgomery and Cheo, 1969), but are generally killed at lower temperatures than those with lower moisture content (Bond & Van Wilgen, 1996).

Two hypotheses have been proposed as explanations for fire survival in trees: (a) "Escape diameter hypothesis" – large individuals possess thicker bark than smaller ones and are therefore better insulated from the heat of a fire (Wilson and Witkowski, 2003; Balfour & Midgley, 2006) and (b) "Escape height hypothesis" whereby plants grow quickly in order to reach a height at which vulnerable apical buds avoid fire damage (Higgins et al., 2000). However, Lawes et al. (2011a) suggest that absolute bark thickness (BT) is the most important factor that determines fire survival, since it is positively correlated with cambial resistance to fire damage (Martin, 1963; Hare, 1965; Vines, 1968; Hengst & Dawson, 1993; Bond & Van Wilgen, 1996). BT varies according to the bark's position on the plant and its fire history, and may increase linearly (e.g. Hengst & Dawson, 1993; Williams et al., 2007; Brando et al., 2012) or non-linearly (e.g. Wilson & Witkowski, 2003; Lawes et al., 2011a) with SDr, but tends to decrease progressively with increasing height on a stem (e.g. Gill & Ashton, 1968; Williams et al., 2007). Hence, since BT is generally positively correlated with SDr, resistance to stem death is suggested to be a function of basal SDr (Gignoux et al., 1997). The thickest bark generally occurs at the plant's base where fire intensity is highest and is therefore where the plant is most susceptible to hydraulic damage (e.g. Wilson et al., 1996; Midgley et al., 2011).

Resprouting is a common plant response to injury from a variety of causes; hence, resprouting is not considered a specific adaptation to fire (Bradshaw et al., 2011). In order to resprout, a plant requires surviving meristems (especially buds or bud-forming tissues) and stored reserves to support growth (Bond & Midgley, 2001; Clarke et al., 2012). Resprouting post-fire may occur above ground (axillary, branch epicormic, or stem epicormic), at the plant's base, or below ground, and varies among species

and with disturbance severity (Bond &Van Wilgen, 1996; Bond & Midgley, 2001; Clarke et al., 2012). Resprouters are well-represented in the Cape fynbos, constituting 50% of the 4418 fynbos species described in Le Maitre and Midgley (1992) and 70% of the 201 species sampled in Van Wilgen and Forsyth (1992). Most fynbos resprouters regenerate from the base, but a few woody species resprout from epicormic buds on branches that survive fire (e.g. *Protea nitida*), although this is very rare (Keeley et al., 2012).

Many succulent plants naturally occur and persist in fire-prone landscapes (Thomas, 1991). Post-fire mortality in succulent plant populations is variable and may be >50%, but is rarely total (Thomas, 1991; Thomas & Goodson, 1992). Thomas & Goodson (1992) suggested that succulents survive fire either by fire 'avoidance' in refugia or by fire tolerance. Fire refugia may be (a) low fuel refugia, e.g. rocky sites or bare ground, (b) accidental refugia, where plants growing in flammable vegetation may survive in unburned patches missed by chance or protected by discontinuities in fuel or topographical barriers, and (c) man-made fire suppression refugia (Thomas, 1991). Succulent species that are fire-tolerant often rely on bark for insulation and usually have well-protected apical meristems that allow post-fire regrowth from above or below ground; hence, survival is dependent on fire frequency and intensity (Thomas, 1991; Thomas and Goodson, 1992). The high water contents of succulent plants make them unlikely fuel plants (Thomas, 1991; Wilson et al., 1996), since moist materials have considerable fire resistance properties (Jin et al., 2000). Consequently, succulents rarely actually burn, but the plant body will usually scorch and blister (Thomas, 1991). The primary cause of mortality is therefore suggested to be cell death in the photosynthetic and underlying cambial tissue (Thomas, 1991). Succulents often show delayed death due to fire (e.g. Bunting et al., 1980), sometimes taking up to six years to die; hence, mortality rates may be grossly underestimated immediately post-fire (Thomas, 1991). Midgley et al. (2011) argued that in most plant taxa, if stem apices survive fire initially but subsequently die, this may be due to hydraulic failure (damage to the xylem) lower down on the stem, where fire intensity is highest, and hence the plant dies from dehydration.

Aloes are generally intolerant of fire, which has a major influence on their local distribution (Jordan, 1996). However, aloes vary extensively in their sensitivity to fire and survival depends on the species, its habitat and the prevailing disturbance regime (see Table 1 in Cousins & Witkowski, 2012; Chapter two). In southern Africa many *Aloe* species inhabit areas regarded as fire-free, such as parts of the Great Karoo, where fuel loads are insufficient and inter-plant distances too great for the development and spread of fires (Smith & Van Wyk, 2009). Aloes are also a key component of Eastern Cape

succulent thicket, where plants with stout, moisture-filled leaves prevent the ignition of fires (Bond, 1983; Smith & Van Wyk,, 2009). Other fire intolerant aloes occur in fire-prone vegetation, but typically grow in soil pockets in rock fissures, on cliff faces, or on bare ground (Jordan, 1996). By contrast, some aloes occur in habitats that are subjected to regular fires (Smith & Van Wyk, 2009). These aloes are usually fire-tolerant or fire-dependent (e.g. grass aloes) and occur in grasslands, savannas and the CFR (Craib, 2005; Jordan, 1996; Smith & Van Wyk, 2009).

Substantial work has been conducted on the fire ecology of the Cape fynbos; however, studies have often focused on members of the Proteaceae, while the fire ecology of fynbos succulent plants, particularly aloes is under-researched. Furthermore, little is known about the fire resistance of plants with dispersed vascular bundles (Gill, 1995), especially arborescent monocots. The aim of this study was to investigate the fire ecology and resprouting behaviour of *Aloe plicatilis*, a tree aloe endemic to the Cape fynbos. Objectives included assessments of: (a) habitat suitability for the species in relation to fire occurrence, (b) plant characteristics that confer fire survival, (c) size-related fire survival, (d) impacts of fire on population density, (e) post-fire recovery, and (e) resprouting capacity after stem removal.

5.3. Methods

5.3.1. Study species

Of the six tree aloe species indigenous to South Africa, *Aloe plicatilis* (L.) Miller (Asphodelaceae: Alooideae) is the only one that occurs in the Cape fynbos (Van Wyk & Smith, 2008). It is a slow-growing, well-branched succulent monocot, with dichotomously branching stems, each ending in 12–16 distichous linear to lorate leaves in a fan-like arrangement (Carter et al., 2011) (Fig. 1 a, d). On average, adult plants range from 1.5–2 m in height, but exceptionally large individuals may reach 4–5 m. *Aloe plicatilis* flowers from August – October and fruit capsules dehisce from December – January (Van Wyk & Smith, 2008). The comparatively small, winged seeds are wind-dispersed (Van Wyk & Smith, 2008). The species grows in well-drained, acidic soils on steep rocky slopes and outcrops in areas of moderate–high winter rainfall (Van Wyk & Smith, 2008; Carter et al., 2011). *Aloe plicatilis* occupies rocky sites that offer some protection from fires and it is the only aloe known to have relatively thick, corky bark, which provides additional fire protection (Van Jaarsveld, 1989).

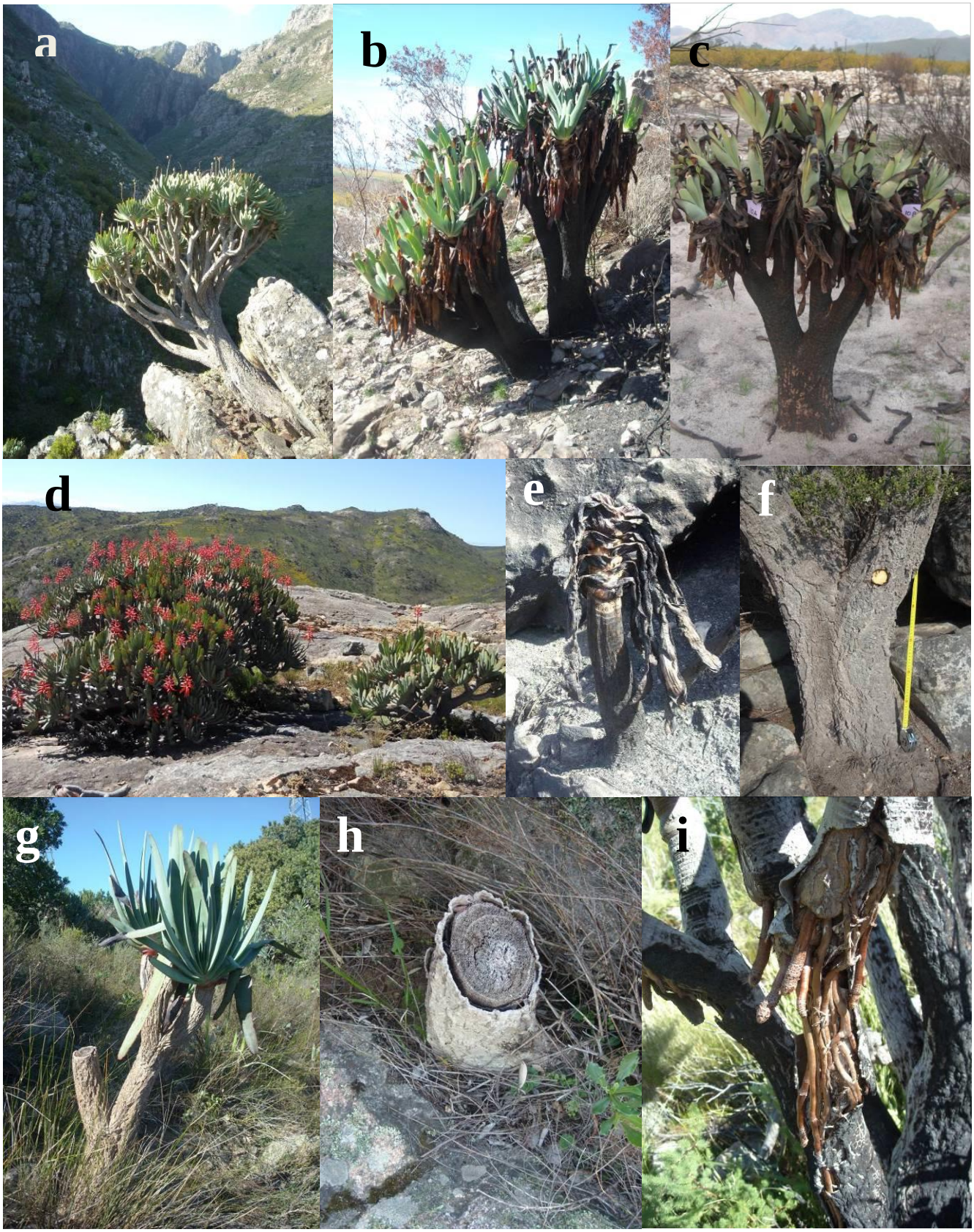


Fig. 1. (a) Unburned adult *Aloe plicatilis* individual growing in a protected rocky site. (b) Live burned adult showing onward growth from its stem apices. (c) Live burned adult six months post-fire. The plant was dead after 22 months post-fire. (d) Two unburned shrub-like, multistemmed individuals 22 months post-fire. (e) Dead juvenile six months post-fire. (f). Adult *A. plicatilis* individual with a scar at 0.5 m where a bark sample was removed. *Aloe plicatilis* individuals with (g) 50% and (h) 100% of branches removed showing no signs of resprouting 10 months post-harvesting. (i) Aerial rooting

occurring on parts of an *A. plicatilis* stem damaged by fire. Photograph locations: (a, i) Du Toits Kloof Kromriver, (b, c, e, f) Kliphoutkloof, (d) the Paardeberg, (g, h) Paarl mountain, south-western Cape, South Africa. Photographer: S.R. Cousins.

5.3.2. Study area

Aloe plicatilis is endemic to mountain fynbos in the Cape Winelands (also known as the "Boland") in the south-western Cape, South Africa (Van Wyk and Smith, 2008). Its distribution extends from the Franschhoek Mountains near Villiersdorp in the south, to the Grootwinterhoek and Elandskloof Mountains near Tulbagh in the north (Van Wyk and Smith, 2008). East to west, it occurs from the Du Toit's Kloof Mountains near Worcester to the Paardeberg between Wellington and Malmesbury. Populations occur at altitudes of 190–950 m, with average annual temperatures of 14–18°C and average rainfall of 400–1900 mm/year (Schulze, 1997). Mean monthly wind speeds within the species' distribution range from 4.5–10.4 km/h (Agricultural Research Council, South Africa). *Aloe plicatilis* occurs primarily in Hawequas and Kogelberg Sandstone fynbos, but some populations also occur in Granitic vegetation types (Mucina & Rutherford, 2006). Major mountain ranges in the region are dominated by Table Mountain sandstone, which is acidic and nutrient-poor (especially nitrogen and phosphorus), with outcrops of Cape granite to the west and southwest (Witkowski & Mitchell, 1987; Manning, 2007).

5.3.3. Micro-habitat in relation to fire

In order to determine whether *A. plicatilis* exhibits fire tolerance or fire 'avoidance' as per the hypothesis proposed by Thomas & Goodson (1992) for fire survival in succulent plants, the percentage aerial cover in a 1 m radius around *A. plicatilis* individuals at 16 unburned and 4 burned populations was visually estimated. Aerial cover was classified as rock, forbs, grass, gravel and bare soil/litter. To test for a relationship between the prevalence of rock cover around each plant and its exposure to fire, the maximum height of fire damage on the stem was measured using a tape measure. The total stem height of the plant was also measured up to the point of leaf emergence and the percentage of stem height that was fire-damaged was calculated. The relationship between the height of fire damage and percentage rock cover was then determined using linear regression.

5.3.4. Bark thickness (BT) of burned and unburned plants

SDr and BT were measured for 40 burned and 40 unburned *A. plicatilis* individuals >1m in height at a population at Kliphoutkloof, six months post-fire. The closest branch on the east-facing side of each plant was selected and its diameter measured at 0.5 m above ground level using a tree calliper. A bark sample was taken from each plant at 0.5 m by hammering a sharp-ended metal pipe 40 mm in diameter into the stem until the cortex was reached and removing the bark disc using a chisel (Fig. 1f). Since *A. plicatilis* produces fissured bark, the thickness of each bark disc was measured at both its thickest and thinnest points using Vernier callipers. Wounds were then sealed with Virikop® anti-fungal powder to prevent infection.

5.3.5. Plant tissue moisture content

A single branch was removed from 20 unburned *A. plicatilis* individuals >1m tall at Kliphoutkloof in November 2012. A section of each branch ±10 cm long and 3-4 cm diameter was then sliced off for measurements of stem and bark water content. The leaf clusters at the end of the harvested branches were replanted *in situ* in suitable rocky sites. A single fully-developed leaf was also removed from a healthy leaf cluster on each of the 20 plants sampled for stem tissue. Single samples of burned bark (outer and inner) were collected from the stems of 10 individuals using a hammer and sharp-ended metal pipe as described above. The bark on each harvested unburned stem section was stripped, and its fresh mass determined, as was the fresh mass of burned bark, bark-stripped stem pieces and leaf material, correct to two decimal places. The stem, bark and leaf material was oven-dried for 96 hours at 80°C and reweighed to determine the oven-dried mass. Percentage moisture content was calculated on a dry mass basis for each plant part type using the formula:

Percentage moisture content = [(fresh mass – oven-dried mass)/(oven-dried mass)]*100

In addition, the relative cross-sectional proportions of bark, cortex and pith that constitute total SDr were determined for 17 of the stem pieces for which water content was determined. The SDr and thickness of each tissue type was measured using a Vernier calliper correct to two decimal places. All measurements were taken at a cleanly cut, wet surface at the end of each stem piece.

5.3.6. Population size structure and density

Three *A. plicatilis* populations were surveyed after a natural fire in January 2011, viz. Kliphoutkloof, $Voorsorg_1$ and $Voorsorg_2$. Localities and environmental and climatic conditions associated with each population appear in Table 1. All three populations occur in Hawequas Sandstone fynbos (Mucina & Rutherford, 2006). $Voorsorg_1$ was surveyed in May 2011 and Kliphoutkloof and $Voorsorg_2$ in November 2012. *Aloe plicatilis* individuals at each population were recorded as dead or alive and measured for SDr and height using tree callipers and a tape measure respectively. At $Voorsorg_1$ (47 plants) and $Voorsorg_2$ (50 plants) all individuals were measured, while at Kliphoutkloof (>112 400 plants) a 100 m transect was walked through part of the population. The point centred quarter method (PCQ) (Cottam & Curtis, 1956) was used to sample individual plants, with points set at 15 m intervals along the transect. Both the nearest live and the nearest dead plant were measured in each of the four quadrants at every PCQ point.

Table 1. Localities and environmental and climatic conditions associated with the three *Aloe plicatilis* populations surveyed post-fire in the south-western Cape, South Africa. Rainfall and temperature data were obtained from the Schulze Climate Database (Schulze, 1997).

Population	Long term average annual rainfall (mm)	Long term average monthly temperature (°C)	Latitude and Longitude	Altitudinal range (m)	Predominant Aspect	Years since previous burn
Kliphoutkloof	652	15	33.70°S; 19.27°E	213-340	East	±30
$Voorsorg_1$	422	15	33.78°S; 19.38°E	443-485	North	10
$Voorsorg_2$	426	15	33.72°S; 19.38°E	458-542	North	10

SDr and height size class distributions (SCD) were constructed for live and dead plants post-fire at Kliphoutkloof, $Voorsorg_1$ and $Voorsorg_2$ using the methods described in Cousins et al. (submitted) (Chapter three). All individuals (dead and alive) were combined to reconstruct pre-fire SDr and height SCDs for each population, with the caveat that the reconstructed SCDs would exclude individuals that were completely incinerated and hence undetectable post-fire, and all dead individuals post-fire were assumed to be alive pre-fire. The same applied to pre- and post-fire density calculations.

Pre- and post-fire densities (in m^2) at Kliphoutkloof were estimated using the formula:

$$\text{Density} = \frac{1}{q^2}$$

where '*q*' is the mean distance from each PCQ point to the centre of the nearest *A. plicatilis* individual in each of the four PCQ quadrants. Densities at Voorsorg_1 and Voorsorg_2 were determined by dividing the total number of plants in each population by its spatial extent. Spatial extent was determined by recording GPS coordinates around the periphery of each population and calculating the area of its distribution polygon in ArcMap version 9.2.

5.3.7. Post-fire growth

The recovery of burned plants by means of apical sprouting (onward growth) was assessed at Kliphoutkloof 22 months post-fire in November 2012. For each living individual sampled on the PCQ transect, the closest leaf cluster to the PCQ point was selected and the distance from the branch end to the point of leaf emergence was measured. Each sampled individual was also inspected for signs of basal and epicormic sprouting.

5.3.8. Resprouting from cut stems

The ability of *A. plicatilis* to resprout basally or epicormically after the removal of branches was assessed at a population on Paarl Mountain. Twenty adult individuals were selected, all 1–2m tall and of similar structure (i.e. single emergent stem that branched higher up). Each plant was tagged and its GPS coordinates recorded. Individuals were then randomly assigned to one of four harvesting treatments: 0% (control), 25%, 50% and 100% stem removal, with five plants per treatment. Half the cuttings removed from the harvested plants were planted *in situ* at suitable sites and the remainder were taken for *ex situ* conservation purposes.

5.3.9. Statistical analyses

Regression analyses were used to determine the relationship between (a) flame height and percentage rock cover and (b) BT and SDr for burned and unburned plants. For the latter, a modified t-test (Zar, 1999) compared (a) the slopes and (b) elevations of the linear fits between burned and unburned plants. One-way ANOVA and Post-Hoc Tukey tests compared (a) rock cover around *A. plicatilis* individuals

at Kliphoutkloof, $Voorsorg_1$ and $Voorsorg_2$ and (b) plant tissue water contents. Two-way ANOVA tested for an interaction between populations and the size of dead and live individuals therein. Within populations, t-tests tested for differences in (a) pre- and post-fire interplant distances and (b) percentage rock cover around dead versus live plants. χ^2 tests compared proportions of dead and live plants between populations. Kolmogorov-Smirnov tests compared pre- and post-fire SCDs within populations (SCDs not presented here) and those of dead plants between populations. Statistical tests were conducted in Statistica 6 and STATPAK.

5.4. Results

5.4.1. Micro-habitat in relation to fire

Aloe plicatilis individuals occupied sites with substantially higher rock cover (59% and 56% in burned and unburned populations, respectively) than other aerial cover types (Fig. 2). Most of the remaining aerial cover surrounding *A. plicatilis* individuals was dominated by forbs in unburned populations (22%), and bare soil in burned populations (22%) (Fig. 2). Bare soil was significantly higher in burned populations ($t_{2,18}$=-3.66; p=0.002), and plant cover (grasses/restios and forbs combined) in unburned populations was significantly higher than that of burned populations ($t_{2,42}$=3.69; p=0.0006).

Aloes surrounded by higher rock cover tended to have flame scars covering proportionally less of their stem heights than those in less rocky sites (Fig. 3). However, the stems of some individuals in sites with 95% rock cover were completely damaged by fire, while other plants growing in areas where rock was absent showed no evidence of fire damage. Mean rock cover around all *A. plicatilis* individuals differed between Kliphoutkloof, $Voorsorg_1$ and $Voorsorg_2$ ($F_{2, 147}$=49.57; p<0.001) (Fig. 4); however, there were no differences between rock cover around live versus dead plants within all three populations combined (p=0.141).

5.4.2. Bark thickness (BT) and plant tissue water content

Both minimum and maximum BT showed a significant, positive relationship with SDr, although the coefficients of determination were low ($r^2 \leq 0.26$) (Fig. 6). The slopes of the linear fits for burned versus unburned plants for both minimum ($t_{2,74}$=-0.81) and maximum ($t_{2,75}$=-1.03) BT were not significantly different (p>0.05). Differences between the elevations of the linear fits were also not significant

(minimum BT, $t_{2,75}$=-0.51; maximum BT, $t_{2,76}$=-1.68; p>0.05). Water content differed significantly between plant tissue categories ($F_{3,66}$=962.08; p<0.0001), being highest for leaves (1375±126%) and lowest for burned bark (75±48%) (Fig. 7). Minimum BT constituted 9.7±4.6% of total SDr, while maximum BT constituted 17±7%. Cortex comprised 20.4±4.1% of total SDr, while pith made up the largest part of SDr at 68±5%.

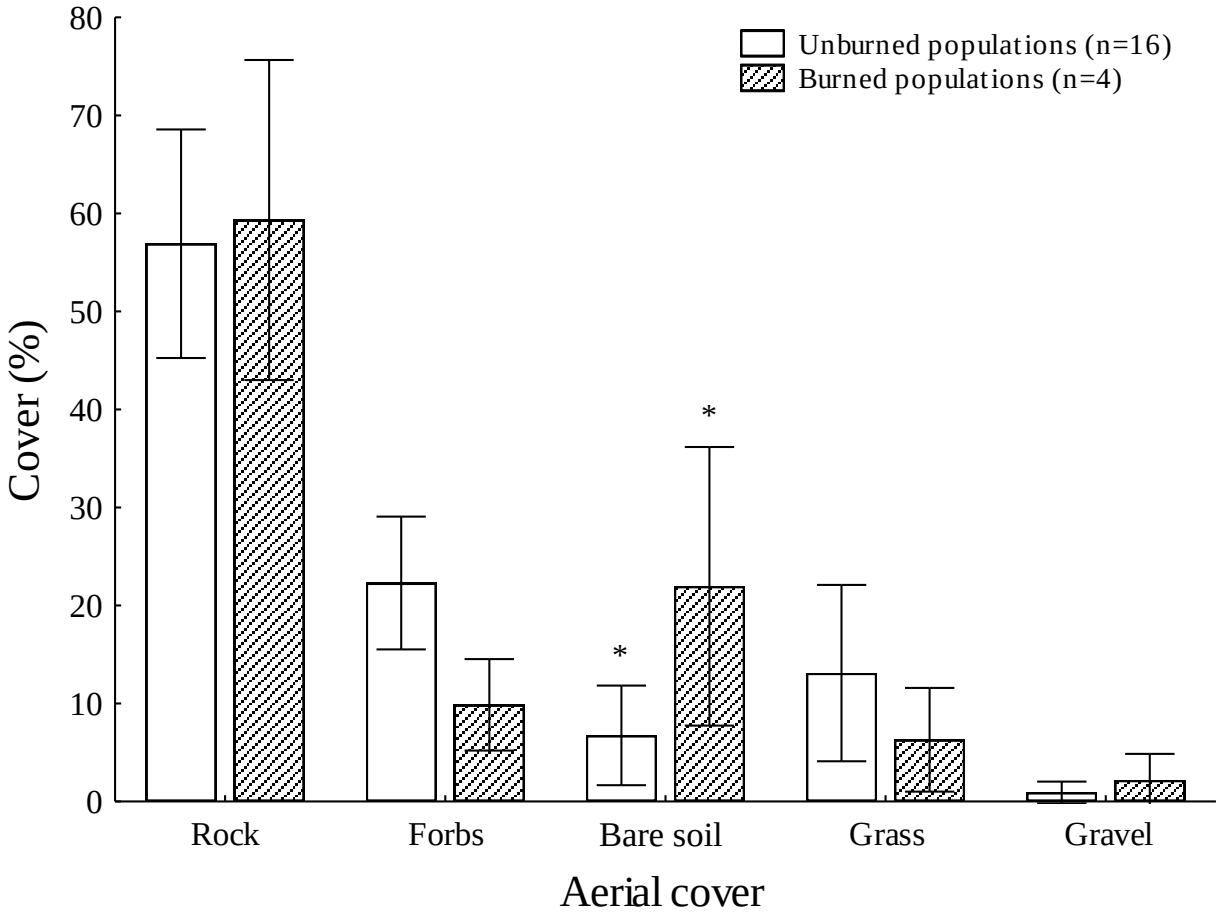


Fig. 2. Mean estimated percentage aerial cover (mean±S.D) within a 1 m radius of *Aloe plicatilis* individuals sampled at 20 populations in the south-western Cape, South Africa. Nineteen populations surveyed in total, but one population was surveyed both before and after fire, hence n=20 combined; 16 unburned, 4 burned.*Denotes a significant difference between burned and unburned populations within an aerial cover category.

5.4.3. Population size structure and density

Pre- and post-fire SDr SCDs were significantly different at Kliphoutkloof, as were height SCDs at both Kliphoutkloof and Voorsorg$_2$ (Table 2; Fig. 5). There were significant differences in both the SDr and height SCDs of dead plants between all three populations (Table 2).

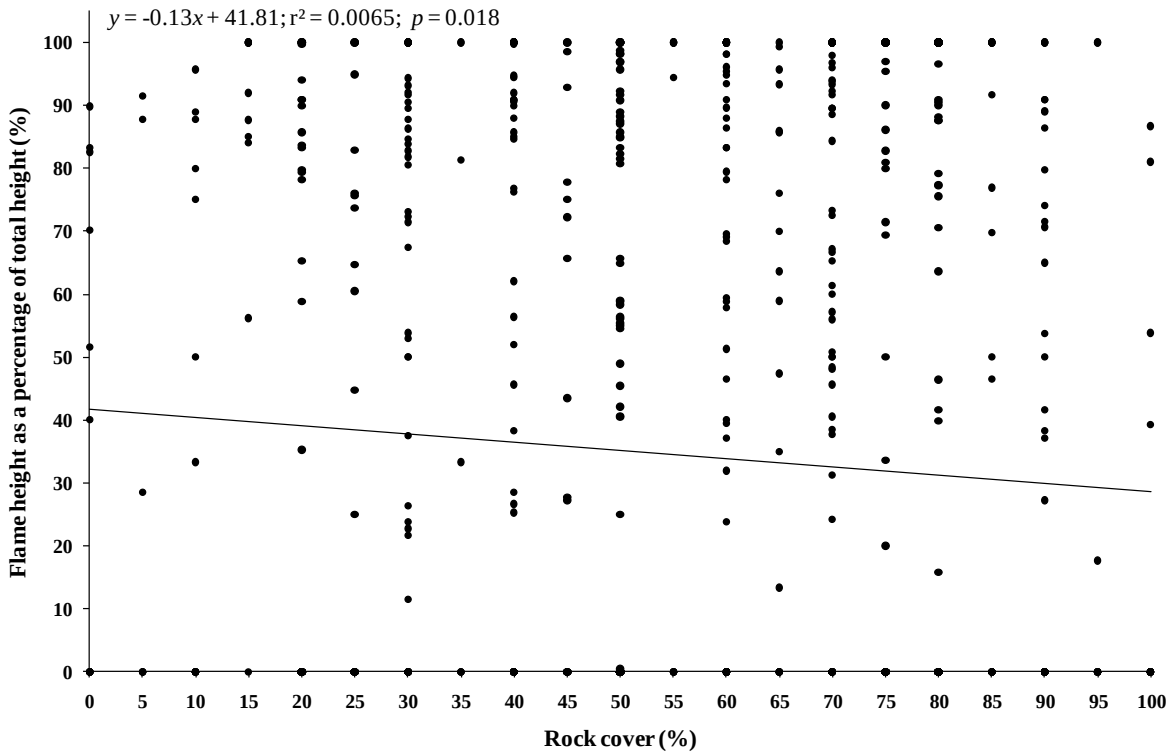


Fig. 3. Regression relationship between maximum height of fire damage and percentage rock cover within a 1m radius of *Aloe plicatilis* individuals sampled at 15 populations where there was evidence of historical fire occurrence, in the south-western Cape, South Africa (n=723 plants).

There was a significant interaction between populations and the sizes of dead versus live plants for both SDr ($F_{2,147}$=12.37; p=0.00001) and height ($F_{2,147}$=9.53; p=0.0001) (Fig. 5). The sizes (both SDr and height) of dead versus live plants within populations were significantly different at both Kliphoutkloof and Voorsorg$_2$, with live plants being larger than dead plants at Kliphoutkloof, while the opposite applied at Voorsorg$_2$ (Table 3; Fig 5). Mean SDrs of dead plants differed between populations, with those at Kliphoutkloof significantly lower than at Voorsorg$_2$. Live plants at Kliphoutkloof were significantly larger than those at both Voorsorg$_1$ and Voorsorg$_2$.

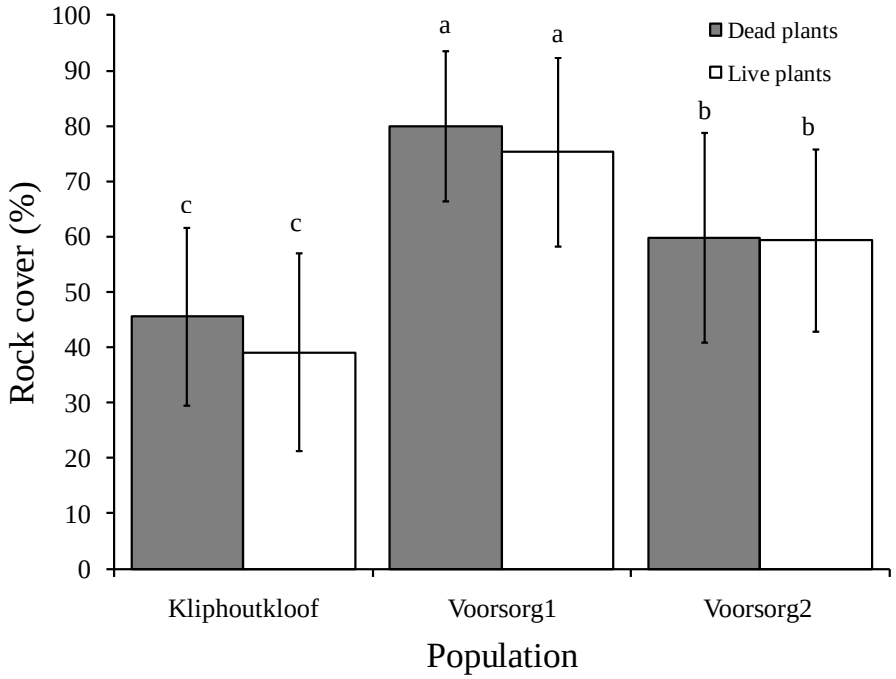


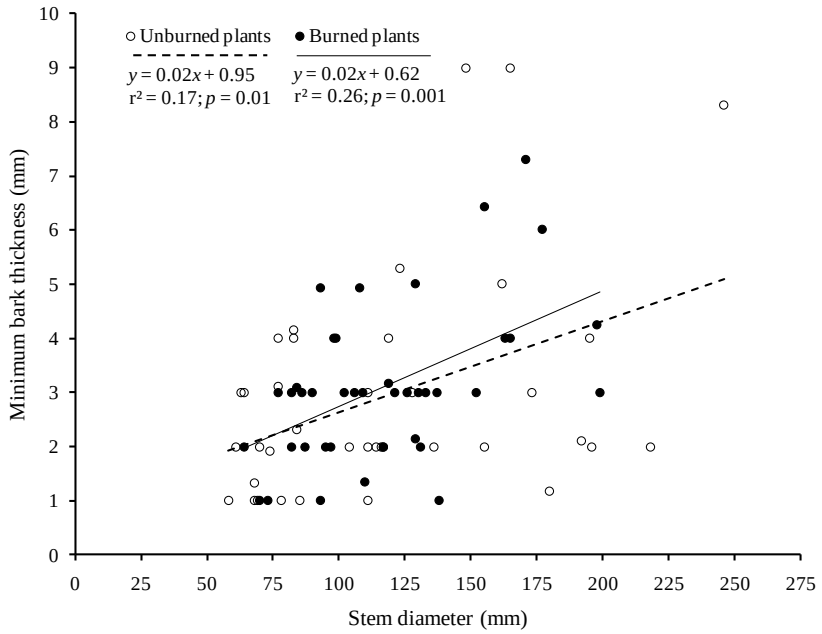
Fig. 4. Percentage rock cover (mean ± S.D.) within a 1 m radius around both live and dead *Aloe plicatilis* individuals at Kliphoutkloof, (n=56) and $Voorsorg_2$, (n=50) (both 22 months post-fire and $Voorsorg_1$ (n=47) (six months post-fire), in the south-western Cape, South Africa. Different letters indicate significant differences (Post-hoc Tukey).

Kliphoutkloof had a higher proportion of dead plants than both $Voorsorg_1$ (χ^2_1=17.10; p<0.0001) and $Voorsorg_2$ (χ^2_1=3.32; p=0.068) (Fig. 8). $Voorsorg_2$ had a higher proportion of dead plants than live plants compared with $Voorsorg_1$ (χ^2_1=4.60; p=0.011) (Fig. 8). All three populations showed decreases in the density of live plants post-fire (Table 4). Density decreased by 43%, 17% and 40% at Kliphoutkloof, $Voorsorg_1$ and $Voorsorg_2$ respectively. Mean post-fire PCQ distance at Kliphoutkloof increased significantly from 2 m pre-fire to 2.6 m post-fire (p=0.048).

5.4.3.4. Post-fire growth and resprouting

The *A. plicatilis* branches measured for post-fire apical growth at Kliphoutkloof increased in height by 7.4±2.6 cm (mean±S.D.) over the 22 month post-fire period (4.04 cm/year). No signs of basal or epicormic sprouting were found on any of the fire-damaged surviving plants in any of the three populations. Similarly, none of the *A. plicatilis* individuals from which stem material was harvested showed any signs of resprouting after nine months (Fig. 1g). All five individuals that were cut at the base (100% stem removal) were dead after nine months (Fig. 1h), while the plants used for the other treatments all persisted.

(a)



(b)

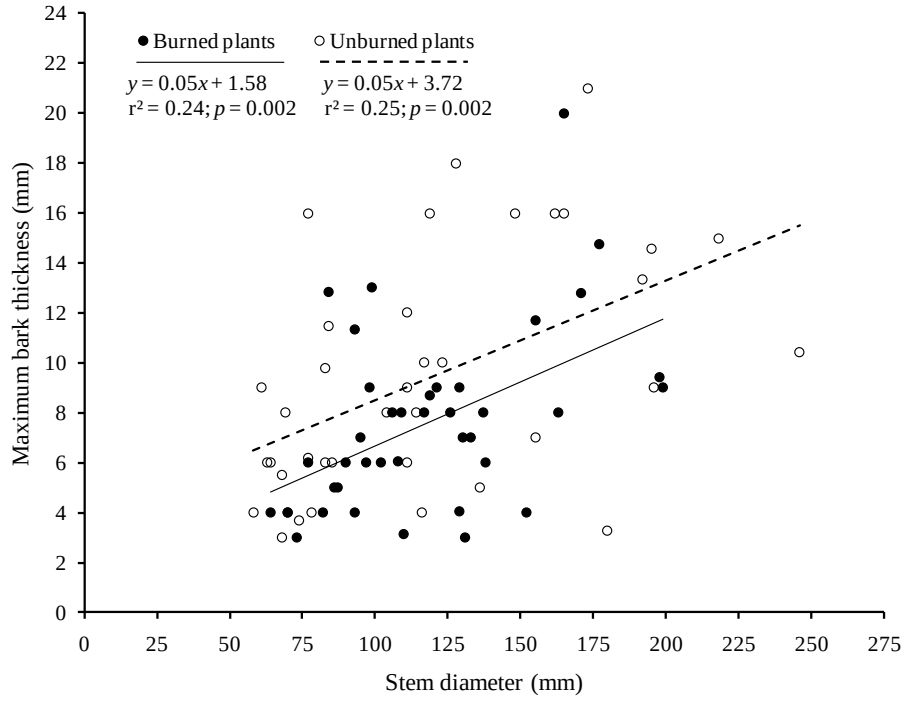


Fig. 6. Regression relationships between stem diameter and (a) minimum and (b) maximum bark thickness for n=40 burned and n=40 unburned *Aloe plicatilis* individuals at Kliphoutkloof, south-western Cape, South Africa.

5.5. Discussion

5.5.1. Plant traits that confer fire survival

There has been recent increased research into how fires actually cause plant death (e.g. Balfour and Midgley, 2006; Kavanagh et al., 2010; Midgley et al., 2011). Previous studies have often assumed that post-fire mortality results from the death of canopy buds or from cambium necrosis (e.g. Hengst and Dawson, 1993; Bond and Van Wilgen, 1996), but cambium death would likely result in a delayed response due to disrupted xylem and phloem differentiation sometime after the fire (Balfour and Midgley, 1996; Midgley et al., 2011). Evidence from stem heating experiments suggests that plants suffer more immediate impacts and that burned plants are subjected to water stress through heat-induced xylem malfunction (Balfour and Midgley, 2006). Even if delayed fire-induced mortality occurs, this is likely due to xylem malfunction as opposed to cambium necrosis (Kavanagh et al., 2010).

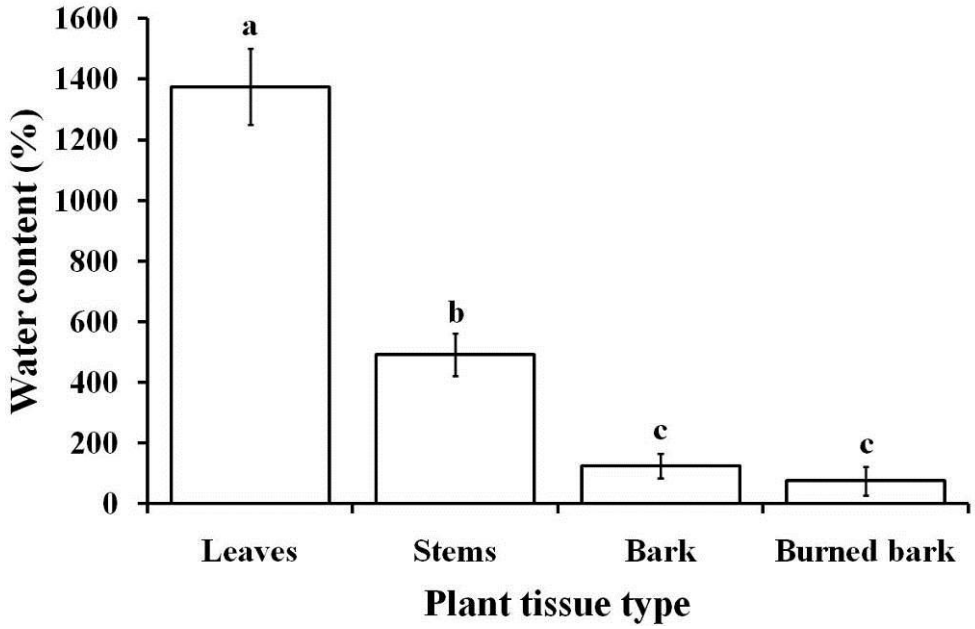


Fig. 7. Moisture content of *Aloe plicatilis* leaves, stems, unburned bark and burned bark (mean ± S.D.) calculated on a dry mass basis. Different letters indicate significant differences (Post-hoc Tukey).

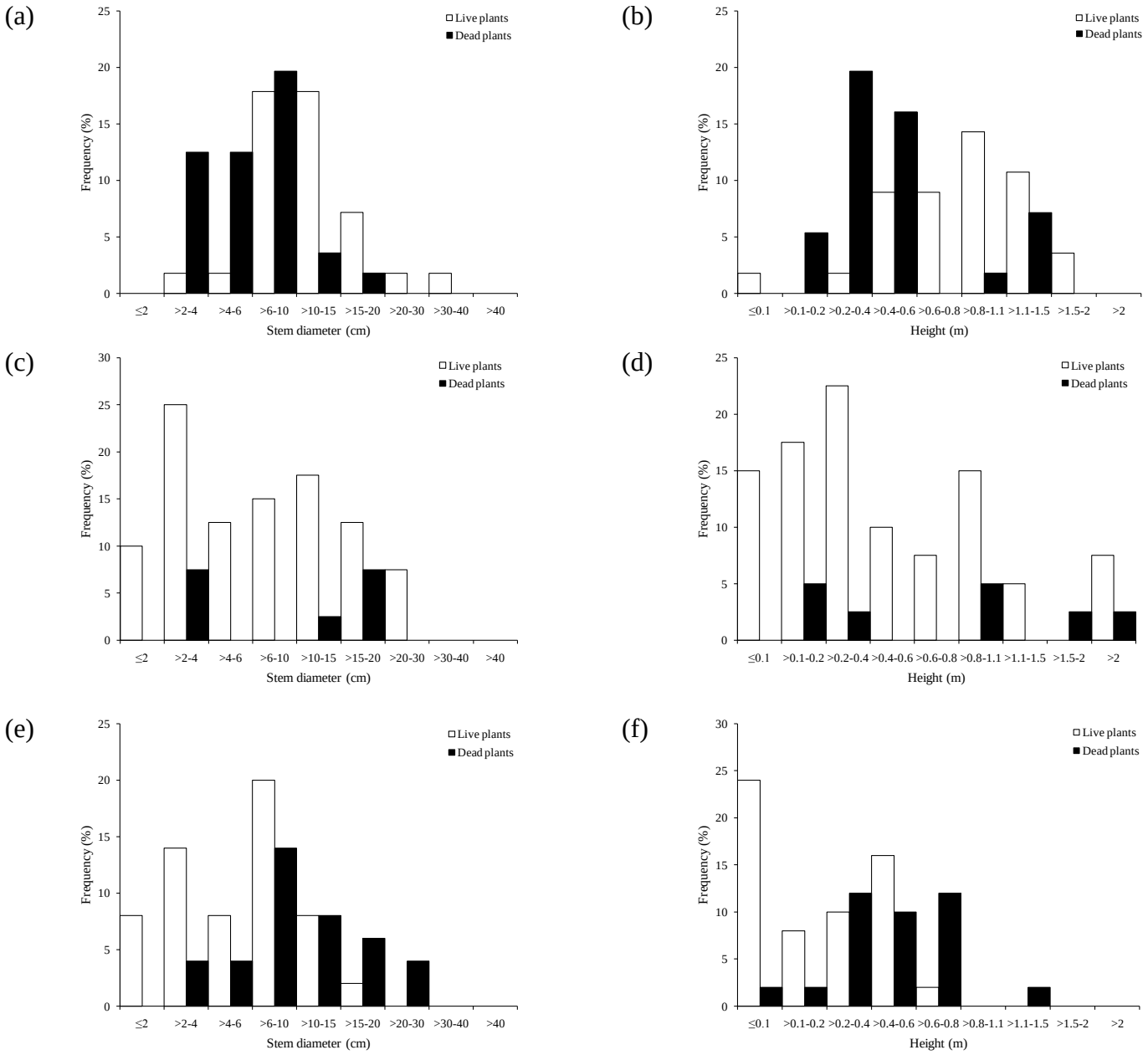


Fig. 5. Stem diameter and height size class distributions showing percentages dead and live *Aloe plicatilis* individuals at (a, b) Kliphoutkloof, (c, d) Voorsorg$_1$ and (e, f) Voorsorg$_2$ in the south-western Cape, South Africa.

Table 2. Comparisons of the size class distributions (SCD) (both stem diameter and height) of three *Aloe plicatilis* populations in the south-western Cape, South Africa, using Kolmogorov-Smirnov tests: (a) live plants pre- and post-fire within populations and (b) dead plants post-fire between populations. NS denotes no significant difference.

Population	Stem diameter SCDs pre- vs. post-fire			Height SCDs pre- vs. post-fire		
	D	d.f.	*p*	*D*	d.f.	*p*
Kliphoutkloof	0.479	28	<0.001	0.443	28	<0.001
$Voorsorg_1$	0.034	47	NS	0.044	47	NS
$Voorsorg_2$	0.120	100	NS	0.173	100	<0.005
Population comparison	Stem diameter SCDs of dead individuals post-fire			Height SCDs of dead individuals post-fire		
	D	d.f.	*p*	*D*	d.f.	*p*
Kliphoutkloof vs.$Voorsorg_1$	0.516	18	<0.001	0.460	18	<0.001
Kliphoutkloof vs.$Voorsorg_2$	0.744	40	<0.001	0.239	40	<0.020
$Voorsorg_1$ vs. $Voorsorg_2$	0.329	40	<0.001	0.521	40	<0.001

Since BT is generally considered to be the most important plant trait that confers fire survival (Vines, 1968; Hengst and Dawson, 1993; Pinard and Huffman, 1997; Lawes et al., 2011b; Catry et al., 2012), the function of the thick bark in *A. plicatilis* (compared to dicotyledonous trees, e.g. Hengst and Dawson, 1993) is likely to protect stems against fire-induced necrosis, and hence reduce the chance of heat-induced xylem cavitation and resultant hydraulic failure (see Midgley et al., 2011). *Aloe plicatilis* is therefore similar to other plant taxa with dispersed vascular bundles e.g. palms, bamboos, cycads, ferns and grasstrees, which rely on strongly insulative, thick bark or persistent leaf bases to protect underlying stem tissues (Gill, 1995).

Although it was not possible to measure the extent to which *A. plicatilis* bark insulates internal stem tissues from temperature increases, BT was not significantly reduced post-fire, suggesting the bark is capable of withstanding extremely high temperatures. The burned outer bark does, however, flake off when rubbed, but would likely be replaced by new living bark provided the underlying cork cambium is still functional. A notable feature of *A. plicatilis* bark is its cork-like nature, which is absent in other *Aloe* species (Van Jaarsveld, 1989). Cork has low density, owing mainly to the high gas content of its small cells (typically 40 µm long), which results in very poor heat transfer properties (Silva et al., 2005). The bark of *Quercus suber* (cork oak), for example, is known to have excellent insulation properties (Catry et al., 2012). Although the similarity of *A. plicatilis* bark to true cork is yet to be determined, its cork-like nature together with absolute BT may be the most important traits for fire survival.

Fire survival in leaf succulents is also conferred by well protected apical meristems, which allow post-fire regrowth from above or below ground (Thomas, 1991; Thomas and Goodson, 1992). In the case of *A. plicatilis*, small, sensitive young leaves at the stem apices are protected by tightly packed larger leaves with extremely high water content (1375%), which likely results in substantially reduced flammability. *Aloe plicatilis* stems and bark also contain large amounts of water (493 and 126%, respectively); however, the role of stem and bark moisture content in the fire survival of *A. plicatilis* is unclear, since although water acts as a fire retardant (Montgomery and Cheo, 1969; Jin et al., 2000), it has a higher thermal conductivity than air (Vines, 1968), and may therefore improve heat conduction through moist plant tissues. Whelan (1995) notes that metabolically inactive or dehydrated plant tissue can tolerate greater heating than metabolically active hydrated tissue, thus making succulents very susceptible to fire damage.

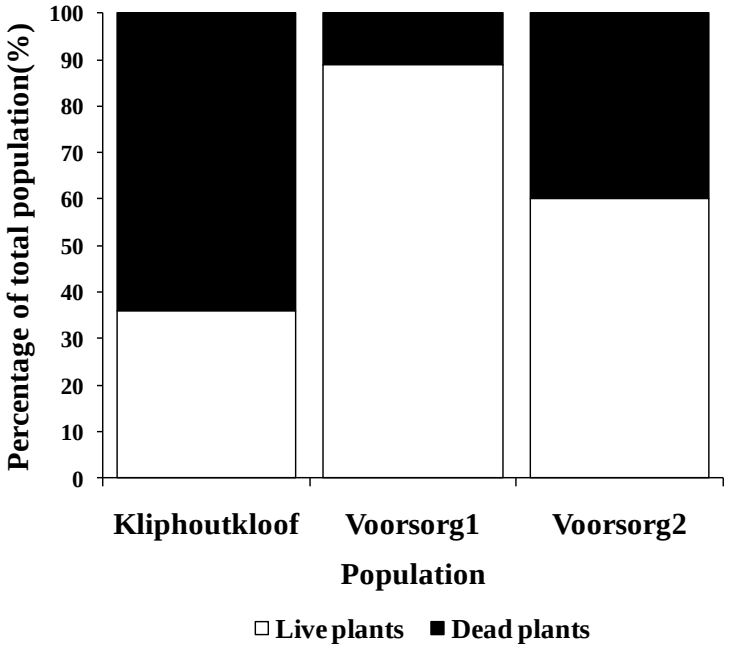


Fig. 8. Percentages of live versus dead *Aloe plicatilis* individuals at three populations post-fire in the south-western Cape, South Africa.

Brando et al. (2011) showed that water contained in the bark of tropical forest trees significantly reduced the temperature difference between the vascular cambium and an experimentally applied heat source, possibly because of water's high latent heat of vaporization (i.e. the quantity of heat absorbed during a phase change from liquid to gas). However, Pinard and Huffman (1997) found only a weak positive correlation between bark moisture content and time to peak cambial temperature, and other studies indicate that the insulating quality of bark is less strongly affected by bark properties (including moisture content) than by BT (Martin, 1963; Vines, 1968; Hengst and Dawson, 1993). In *A. plicatilis*, the insulating properties of the species' thick, corky bark may override the influence of its high water content, thus rendering the heat-conducting capacity of the water negligible, however this requires further investigation.

5.5.2. Habitat suitability

Bond (1983) showed that fire tolerance in southern African single-stemmed aloes and tree aloes is strongly related to the degree to which their stems are protected by persistent skirts of dead leaves, which form effective compact insulators. Bare-stemmed species generally occur in fire-free environments, or where fires are rare or of low intensity, whereas species with dead leaf skirts mainly

occur in fire-prone habitats (Bond, 1983). Of the six South African tree aloe species (*sensu* Van Wyk and Smith, 2008), all of which have bare stems, *A. plicatilis* is the only one that occurs in a fire-prone habitat and the only one that possesses thick corky bark (Smith and Van Wyk, 2009). Although fire survival in *A. plicatilis* does not appear to be heavily dependent on rock cover at the individual plant scale, at the population level, high rock cover is generally associated with higher fire survival rates (Thomas and Goodson, 1992). Variability in the fire survival of individual plants may be explained by the mosaic of rock and vegetation cover in their surroundings. Individuals in less-rocky sites may occur on vegetated islands surrounded by protective rock sheets (S.R. Cousins, pers. obs.) and may therefore survive, while plants with a large amount of rock cover in their immediate surroundings may be growing near to large flammable shrubs. When ignited, the flames emanating from these shrubs may bend towards adjacent aloes during strong wind events, which are very common during fynbos fires (Keeley et al., 2012). These individuals may therefore be damaged or killed despite the rockiness of their immediate surroundings.

Table 3. Post-fire stem diameter (cm) and height (m) (mean ± S.D.) of dead versus live individuals at three *Aloe plicatilis* populations in the south-western Cape, South Africa. Significant differences within stem diameters and heights are indicated by different letters (Post-hoc Tukey).

Population	Stem diameter (cm)		Height (m)		n	
	Dead	Live	Dead	Live	Dead	Live
Kliphoutkloof	6.5 ± 3.9^{a}	12.4 ± 6.8^{b}	0.50 ± 0.37^{a}	0.90 ± 0.42^{c}	28	28
$Voorsorg_1$	10.9 ± 7.2^{ab}	8.4 ± 6.6^{a}	0.93 ± 0.80^{cd}	0.58 ± 0.59^{bd}	7	40
$Voorsorg_2$	10.9 ± 5.9^{ab}	6.2 ± 3.7^{a}	0.50 ± 0.27^{ad}	0.24 ± 0.22^{a}	20	30

The other *Aloe* species that occur in the Cape fynbos appear to either tolerate fire (*A. commixta*, *A. juddii* and *A. gracilis* var. *decumbens* (rambling aloes) and *A. haemanthifolia* (stemless aloe)), or occupy fire refugia (*A. perfoliata* (creeping aloe) and *A. brevifolia* (dwarf aloe)) (Cousins and Witkowski, 2012; Chapter two). However, the traits *A. plicatilis* possesses that confer fire survival, combined with its occupation of predominantly rocky sites, suggests that it adopts a dual fire survival strategy: (a) fire avoidance in rocky refugia and (b) a degree of fire tolerance by means of thick, corky, protective bark and stem apices that are protected by fleshy outer leaves. *Aloe plicatilis* is not, however, the only aloe that appears to have a dual fire survival strategy. *Aloe marlothii* is similar in that many populations are confined to rocky fire-protected islands within fire-prone vegetation (Bredenkamp and Van Vuuren, 1987), but the species also possesses persistent dead leaf skirts that afford it additional protection from fires (Bond, 1983).

5.5.3. Population size structure and density

At the population level, *A. plicatilis* mortality rates decreased as percentage rock cover increased, so that Kliphoutkloof, which occurred at the least rocky site had the highest mortality (64%), followed by $Voorsorg_2$ (40%) and $Voorsorg_1$ (11%). Decreasing mortality with increasing rockiness is expected, since rocky sites offer fire refugia (Thomas, 1991). Kliphoutkloof and $Voorsorg_2$ showed contrasting size-related mortality patterns, with most dead individuals at Kliphoutkloof in smaller size classes, while at $Voorsorg_2$ most dead plants were in larger size classes. Forty-two percent of the dead plants at $Voorsorg_2$ had SDrs ≤10cm compared to 89% at Kliphoutkloof. However, these figures exclude small plants that possibly existed pre-fire but were completely incinerated and therefore undetectable post-fire.

Table 4. Area of Occupancy (AOO), pre- and post-fire densities of live plants and mean Nearest neighbour (NN) or point-centred quarter (PCQ) distances (mean ± S.D.) of live plants post-fire for three *Aloe plicatilis* populations in the south-western Cape, South Africa.

Population	AOO (ha)	Pre-fire density (plants/ha)	Post-fire density (plants/ha)	Pre-fire NN or PCQ distance[a]	n	Post-fire NN or PCQ distance[a]	n	*t*	*p*
Kliphoutkloof	1.75	2532	1440	1.99 ± 0.91	28	2.64 ± 0.68	10	-2.045	**0.048**
$Voorsorg_1$	0.05	960	800	2.07 ± 2.12	47	1.96 ± 1.92	40	0.258	0.797
$Voorsorg_2$	0.06	833	500	1.68 ± 2.52	50	1.12 ± 2.10	30	1.015	0.313

[a]PCQ distance for Kliphoutkloof; NN distance for $Voorsorg_1$ and $Voorsorg_2$.

Smaller plants are generally the most impacted by fire as their entire above-ground biomass is within the flame zone and they have smaller SDrs and hence thinner, less protective bark than larger individuals (Gignoux et al., 1997; Lawes et al., 2011a). Furthermore, an individual with a large SDr would serve as a greater heat sink, thus reducing the likelihood of heating through the stem (Uhl and Kauffman, 1990). In succulent plant species, taller individuals often show lower fire-induced mortality than shorter ones (e.g. Bond, 1983; Weisser and Deall, 1989; Witt and Nongogo, 2011). The high mortality of juveniles at Kliphoutkloof is most likely due to the tall, dense pre-fire vegetation at the site, which had not burned in ±30 years. Small plants would have been totally engulfed by the flames (Lawes et al., 2011a) and both their stems and apical meristems killed (Fig. 1e).

These individuals probably established in less rocky and therefore more vulnerable sites after the previous fire, but were unable to grow large enough to withstand the very intense subsequent fire. Larger plants (>10cm SDr; >0.6m height) at Kliphoutkloof had most likely been persisting in comparatively rockier sites for many years, and showed much higher survival rates since they were less exposed to fire, they possessed thick bark that provided adequate insulation and their sensitive growing points were well protected by large, fleshy outer leaves (Fig. 1b). Of the live plants at $Voorsorg_2$, 83% were ≤10cm SDr, compared to only 42% at Kliphoutkloof. These small live plants at $Voorsorg_2$ either occupied rocky sites (average rock cover = 60%), or occurred in more vegetated patches that were surrounded by rock sheets (S.R. Cousins, pers. obs.), which may explain their survival.

Aloe plicatilis densities decreased at all three populations post-fire, most markedly at Kliphoutkloof. By contrast, Wilson et al. (1996) showed that initial post-fire mortality of *Carnegiea gigantea* (Superior giant saguaro cactus) was only 19%. However, of the living saguaros 80% were completely stem girdled and eventual mortality was predicted to be >80%. Delayed plant death was observed in *A. plicatilis* at Kliphoutkloof. During a preliminary visit to Kliphoutkloof six months post-fire, several large individuals were still alive (Fig. 1c), but had very flaccid, dull leaves and were dead 22 months post-fire (S.R. Cousins, pers. obs.). Hence, the densities at Kliphoutkloof and $Voorsorg_2$ likely represent true post-fire densities as they allowed for a time lag (22 months post-fire), whereas the comparatively smaller density reduction at $Voorsorg_1$ (six months post-fire) may have increased had the survey been conducted later.

5.5.4. Resprouting

The stem harvesting experiments and observations of stem-damaged *A. plicatilis* individuals in many populations indicate that the species does not have latent bud banks in its stems or roots and therefore cannot resprout epicormically, basally or from below ground. *Aloe plicatilis* is therefore an unusual fynbos plant in that it is neither a sprouter *sensu stricto* (see Clarke et al., 2012), nor an obligate seeder (non-sprouter). It belongs to a specialised subset of aerial sprouters that survive fire through protection of apical buds and do not resprout *per se* (Clarke et al., 2012). These so-called 'apical sprouters' include other arborescent monocots e.g. grasstrees and palms, as well as tree ferns and cycads, the apical meristems of which are protected with tightly clustered leaf primordia and the leaf bases of mature leaves (Clarke et al., 2012). In addition to protected apical buds, these species' hydraulics are

also well-protected by thick bark (or persistent old leaf bases) and therefore have high fire survival probabilities (Clarke et al., 2012).

Non-sprouting appears to be common to all dichotomously branching tree aloes, viz. *A. dichotoma, A. pillansii, A. plicatilis* and *A. ramosissima* (Cousins and Witkowski, 2012; Chapter two). These species appear to have an absence of bud banks in their stems and therefore cannot resprout if branches are removed. By contrast, the tree aloe *A. barberae* resprouts vigorously when above-ground biomass is removed (Cousins and Witkowski, 2012; Chapter two). In general, resprouting appears to be most common in rambling and grass aloes (Cousins and Witkowski, 2012; Chapter two), which often occur in fire-prone environments where resprouting is key to their survival (Craib, 2005; Smith and Van Wyk, 2009). For plant species that do not resprout or maintain persistent seed banks, post-fire recovery is largely dependent on seed dispersal from surviving plants (e.g. Rogers, 1985). Like most aloes, *A. plicatilis* appears to maintain only transient seed banks (<1 year) (Cousins et al., 2013) and since burned individuals cannot resprout if they are top-killed, population persistence is heavily reliant on the survival of adult plants within safe sites. Furthermore, since it is a slow-growing species, population recovery after a very damaging fire is likely to be slow.

Although *A. plicatilis* cannot resprout from cut/wounded stems, it displays an unusual response to stem damage that may assist in post-fire population recovery. Stem damage by fire, snapping by chacma baboons (*Papio ursinus*), or bark removal by rock hyraxes (*Procavia capensis*) often induces the production of numerous aerial epicormic roots around the wounded area on *A. plicatilis* stems (i.e. aerial rooting) (Fig. 1i). These roots usually remain <20 cm long if suspended in the air, but if contact with the plant's stem is made, they may grow all the way down the stem until they reach ground level (S.R. Cousins pers. obs.). It is thought that these roots form in preparation for the impending fall of the damaged branch. Since *A. plicatilis* propagates easily from stem cuttings both in cultivation and *in situ* (S. R. Cousins, unpublished data), once on the ground, the aerial roots on fallen branches likely serve a propagative purpose, enabling the branch to establish as a new individual, resulting in asexual reproduction (Jeník, 1994).

5.6. Conclusion

This appears to be the first known study on the fire ecology of an arborescent succulent monocot in a Mediterranean-type climate region. *Aloe plicatilis* appears to adopt a dual fire survival strategy, displaying fire 'avoidance' in rocky refugia and a degree of fire tolerance by means of thick corky bark. Sensitive apical meristems are protected by fleshy outer leaves that are unlikely to burn. Survival of stem apices facilities onward growth or 'apical sprouting' post-fire. Small *A. plicatilis* individuals appear to be most vulnerable to fire-induced injury or death since they are completely within the flame zone and have lower absolute bark thickness than larger individuals. However, small individuals in very rocky sites with low surrounding biomass may survive fire, while larger plants in comparatively less-rocky sites with higher surrounding biomass may be killed, especially in a very intense fire. Hence, there appears to be a trade-off between plant size and fire protection, since although individuals growing in very rocky sites are protected from fire, they are often kept in a stunted 'bonsai' state due to restricted rooting space, whereas plants growing in deeper soil in less rocky sites are often able to attain larger sizes, but are more vulnerable to fire. *Aloe plicatilis* is similar to other dichotomously branching tree aloes in that it cannot resprout from cut stems. Since burned *A. plicatilis* individuals do not resprout if they are top-killed, and the species does not maintain persistent seed banks, population persistence depends largely on the survival of adult plants within safe sites. Due to the species' slow-growing nature, population recovery post-fire may take several years. The formation of aerial roots on damaged branches may, however, enhance population recovery if these branches fall to the ground and establish as new individuals.

5.7. Acknowledgements

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CHAPTER SIX

General discussion

A thorough understanding of plant ecology at any scale requires an unravelling of the complex interactions between a wide array of variables that shape the system and contribute to the state in which it is currently observed. By splitting complex systems into their component parts and examining them in detail individually, inter-linkages within the system become apparent. These relationships can then be assembled and studied in concert in order to comprehend the system as a whole, and illuminate gaps in current understanding.

By selecting a study species that represents a group of taxa either with unusual and appealing characteristics that make them desirable among plant collectors (e.g. succulents, cycads and orchids), or traits that endow them with medicinal or cultural value, a detailed study on the species' ecology may reveal key insights that can be extrapolated to benefit the conservation biology of the group as a whole (Hall et al., 1984). Furthermore, if selection criteria include species that are popular, but not particularly threatened, and hence have comparatively large population sizes, then intensive broad-scale sampling can help to fully elucidate patterns that might not otherwise be detectable in highly impacted species whose ranges have been severely reduced, hence resulting in small population sizes and disrupted ecological processes.

Aloe plicatilis fits these criteria well and thus provided a suitable candidate for plant ecological research. The broad themes covered in this study facilitated the development of an over-arching understanding of the species' ecology, but not without a considerable level of detail. The findings not only enhance current knowledge of the ecology of *A. plicatilis*, but have potential for considerably wider application within the genus *Aloe* as well as other similar long-lived, slow-growing taxa. The synthesis that follows assembles and integrates the salient findings from investigations on the population structure, reproductive ecology and fire ecology of *A. plicatilis* and interprets them within a broader context of aloe ecology and plant ecology in general. The synthesis is followed by a discussion of the implications of the species' name change from a conservation perspective, recommendations for population monitoring and management, and an evaluation of the study's major contributions to the field and its uncertainties. The chapter concludes with directions for future research on the species.

6.1. Synthesis

Long-lived, slow-growing plant taxa present considerable challenges when studying their ecology and conservation biology due to slow growth rates, reliance on adult persistence for population viability and slow recovery rates following severe disturbances such as over-exploitation (e.g. Pfab and Scholes, 2004; Cousins et al., 2011). Marked responses to changes in certain abiotic factors (e.g. climate change) and biotic factors (e.g. disease, alien invasions) at local and regional scales may be slow (i.e. years to decades) (e.g. Jack, 2012; Marler and Lawrence, 2012). Hence, major changes in population structure and function due to slow-acting disturbances may be unobservable over short study periods (1–3 years). However, sudden, severe disturbance events such as fire or exploitation may result in drastic changes to populations, which are easily observed before and after the event (e.g. Donaldson and Bösenberg, 1999; Sivinski, 1999).

The most pervasive disturbance in the Cape fynbos is fire. Fire is more common in the fynbos than any other Mediterranean-type climate region (Manning, 2007), and plays a pivotal role in shaping the major vegetation patterns within the Cape Floristic Region (Keeley et al., 2012). Extreme changes in both the structure and floristic composition of fynbos communities occur post-fire; plants of many species are killed outright, regenerating later by reseeding, while others are top-killed and resprout from rootstocks or other underground storage organs (Keeley et al., 2012). Post-fire regeneration of an entire community takes substantially longer in the fynbos than grassland and savanna systems. It is therefore not surprising that fire is the primary driver behind the most obvious, immediate and long-lasting changes in *A. plicatilis* population structure and function. In populations where fires have not occurred for long periods (20–30 years), population size may be reduced by >50% and regeneration considerably hindered by the elimination of a large proportion of juveniles by fire. Too-frequent fires may hamper recruitment even more severely, and may also cause long-term damage to the large reproductive adults upon which population persistence is heavily dependent. Severe fire-related reductions in plant density may also induce or enhance Allee effects in small and/or sparse populations, thus exacerbating general reproductive success within these populations.

The impacts of other disturbances on *A. plicatilis* population structure and function are much less pronounced than the effects of fire. Pathogens in the form of scale insects, black spot and aloe cancer were observed on *A. plicatilis* individuals at some populations, but were seldomly present on all plants in the population. Evidence of senescence or death as a result of heavy infestation was absent. Invasive

alien plant species did not pose a threat to a large majority of the populations surveyed (see population monitoring and management recommendations later in this chapter). While harvesting of whole plants or parts thereof by plant collectors is difficult to detect, especially a long time after the event has occurred, no signs of harvesting were observed in the form of holes in the ground or cut stems at any of the populations surveyed during the study; hence, harvesting does not appear to be affecting *A. plicatilis* population structure and function at present.

Apart from occasional bark removal by rock hyraxes (*Procavia capensis*), herbivory on *A. plicatilis* plants is almost entirely absent. However, chacma baboons (*Papio ursinus*) frequently snap branches on large individuals, seemingly for amusement only, as leaf damage and/or remains of eaten foliage and branches under affected plants has not been observed. The impact of stem snapping is unlikely to compromise the health or reproductive success of adult *A. plicatilis* individuals except at extremely high levels, where most or all branches are removed (100% branch removal was observed on a plant at Du Toit's Kloof Kromrivier (DKK)). By contrast, if snapped stems fall to the ground and land in a suitable microsite, they may form roots and establish as new individuals, thus contributing to regeneration within the population. This phenomenon was observed at almost all surveyed populations where baboon damage was evident.

Fig. 6.1 illustrates progressive changes in the demography (population size, size structure and density) of a hypothetical *A. plicatilis* population as various disturbances/stressors (fire, harvesting for the horticultural trade, disease, invasive alien plant species encroachment and climate change) impact on the population and its reproductive processes over time. While these disturbances /stressors may not necessarily act in isolation, and there may be significant interactions between them, the simplified schematic representation in Fig. 6.1 emphasizes how a seemingly static population of a long-lived, slow-growing plant species undergoes changes that may not be perceptible or measureable over short time periods. Such changes are important to consider when interpreting snapshot data and making management decisions based thereon.

A striking outcome of the study on the population structure of *A. plicatilis* was the widespread occurrence of bell-shaped size class distributions (SCD). The significance of this SCD shape in terms of population health and hence population management has seldomly been emphasized in other studies (e.g. Venter and Witkowski, 2010). Bell-shaped SCDs indicate a preponderance of medium-to-large adult plants, and, for long-lived, slow-growing species they may be associated with an adult persistence

survival strategy and not necessarily a lack of recent recruitment and concomitant population decline (e.g. Raimondo and Donaldson, 2003). In *A. plicatilis*, these bell-shaped SCDs reflect populations characterized by large numbers of compact, shrubby sub-adult and adult plants, which may suggest classification of the species as a multistemmed aloe as opposed to a tree aloe (*sensu* Van Wyk and Smith, 2008). (However, adult individuals may reach 4–5 metres in height in microsites where they are well protected from strong winds and fire.)

It appears that the major factors that work in unison to bring about this bell-shaped pattern are: the species' long life-span and slow growth rate, height limitations imposed by strong, persistent winds, restrictive rocky growth substrates, and limited 'drib-drab' recruitment. Furthermore, fire may result in the elimination of exposed juveniles and small sub-adults, both of which have limited absolute bark thickness, small stem diameters, and heights within the flame zone. This reduction in the number of small individuals in a population may further accentuate an existing bell-shaped SCD and possibly shift it towards a preponderance of larger size classes. Consequently, fire may also be important in maintaining the bell-shaped size structure of *A. plicatilis* populations, but this is not always the case, especially in highly rocky populations, where many small individuals may escape fires by persisting in highly protected rocky sites as bonsai plants (suppressed juveniles or reproductive dwarfs). A prevalence of such bonsai plants may result in elevated occupation of smaller size classes, hence resulting in a deviation from the typical bell-shaped SCD

Although some *A. plicatilis* individuals growing in very rocky sites may reach considerable sizes, the significant negative linear relationship between plant size (stem diameter and height) and the degree of rock cover surrounding individual plants, combined with a similar relationship between percentage rock cover and the degree of fire damage to individual plants, points towards a trade-off between plant size and degree of fire protection. Individuals in well-protected rocky sites may repeatedly escape the damaging effects of fire, but their reproductive ability may be drastically compromised (due to size and resource limitations), thus rendering their contribution to population growth and persistence minimal. By contrast, *A. plicatilis* individuals growing in less-rocky sites with comparatively larger rooting space may attain greater sizes, but are more exposed to fire, since other vegetation can also colonise these sites and contribute to increased fuel loads. However, if such an individual is able to grow large enough to reach a height above the flame zone (or towards the upper end thereof), and develop a stem diameter and absolute bark thickness large enough to withstand fire, it may persist as a large reproductive individual that provides a significant contribution to reproductive success within the population.

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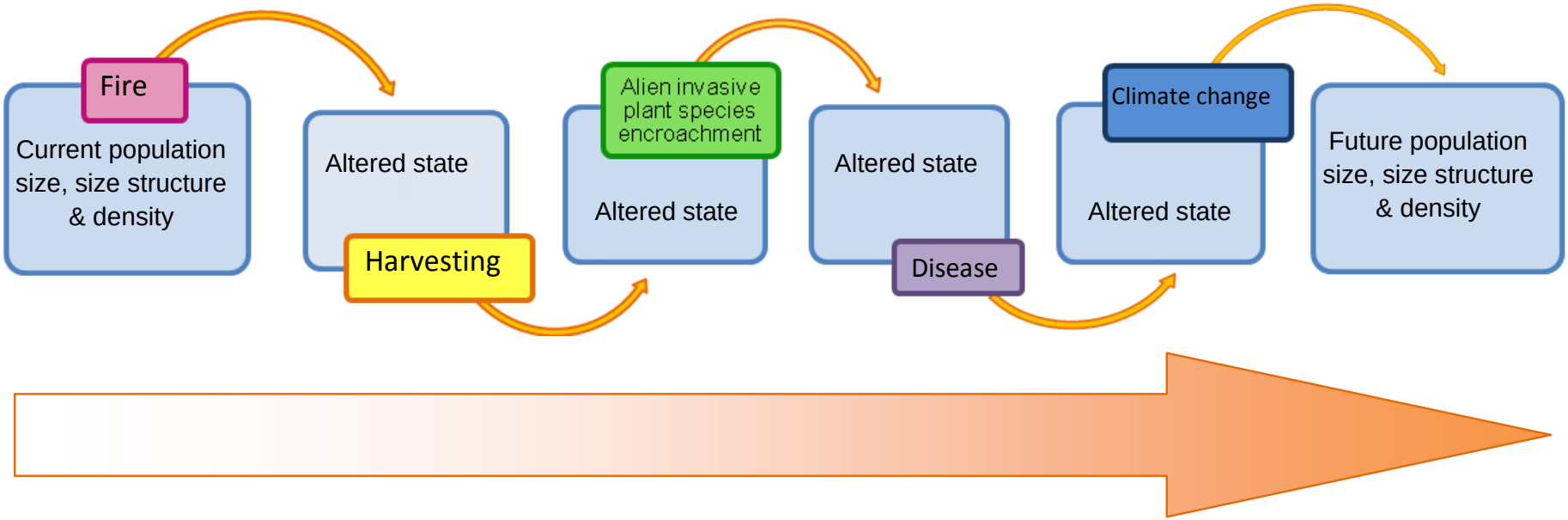


Fig. 6.1. Flow diagram illustrating a series of changes in the demographics of a hypothetical *Aloe plicatilis* over time as it is subject to various perturbations (fire, harvesting, invasive alien plant species encroachment, disease, and climate change).Some or all of the perturbations may act on the population in concert and with different outcomes, and each is also likely to influence reproductive processes within the population differently, which, in turn, will also affect the population's demography. Additional influences affecting the demographics of a population include the historical spatial arrangement of plants age differences, genetic variation, heterogeneity of resources and competition (see introduction in Chapter 3).

Aloe plicatilis appears to adopt a drib-drab recruitment strategy (i.e. erratic small-scale recruitment each season) – despite producing an abundance of seeds – a pattern which is reportedly observed across much of the genus *Aloe* (Wabuyele and Kyalo, 2008; E. Van Jaarsveld, pers. comm.). Two possible exceptions are grass aloes and species that occur in very arid environments. Grass aloes often exhibit mass flowering post-fire (e.g. *Aloe verecunda*) (Craib, 2007), which may be associated with pulsed recruitment the following summer. Species in very xeric habitats e.g. *Aloe dichotoma* and *Aloe asperifolia* may also exhibit episodic recruitment after high rainfall events when dormant seeds respond to conditions that are conducive to germination (Giddy, 1973). The drib-drab recruitment strategy in *A. plicatilis* is also reflected in the species' short-term seed banks, which appear to persist for ≤1 year. Since recruitment in *A. plicatilis* does not appear to be strongly coupled with fire, it behaves much like the forest tree species that occur in fire refugia in the Cape fynbos. Recruitment in these species is not tied to fire events but is generally associated with nucleation and habitat amelioration (Manders and Richardson, 1992).

Recruitment in *A. plicatilis* depends on the alignment of multiple factors both spatially and temporally (Fig 6.2.). First, a seed requires adequate stored food reserves to survive until the first winter rains and ensure the germination of a vigorous seedling. After release from the parent plant, the seed must escape predation by birds and other vertebrates and then land in a 'safe site' that is sufficiently far from the parent plant for the seedling to avoid competition. Such a site is important for protection of the seed from extreme heat and desiccation over the summer drought during which it is dispersed. In order for the site to offer suitable conditions from germination and establishment, it must be sufficiently rocky to act as a fire refugium and include a suitably positioned nurse object such as nurse rock(s) or nurse plant(s) to provide a shady, sheltered place where moisture and organic matter can accumulate.

Shade during the seedling phase is known to be crucial for seedling establishment across the genus *Aloe* (Giddy, 1973; Van Wyk and Smith, 2008). Seedlings and juveniles also have a greater surface-to-volume ratio than large adults and are therefore most responsive to climate and solar radiation effects, suggesting a greater sensitivity to environmental factors compared to adults (e.g. *A. dichotoma*; Jack, 2012). In addition, adequate and consistent rainfall over the successive winters post-dispersal is likely to be essential for successful recruitment, since although aloes are succulent plants (which have large water reserves in their leaves and stems) they often require regular watering in cultivation to establish (e.g. Smith and Correia, 1992). The need for regular watering (once to twice weekly) has been

observed as a crucial factor in newly germinated and establishing *A. plicatilis* seedlings grown under greenhouse conditions (personal observations).

A seed that has been dispersed locally (within the population) is more likely to experience environmental and climatic conditions (e.g. altitude, aspect, soil type, temperature and rainfall) that favour germination and establishment than a seed that has been dispersed a long distance from the source population. Moreover, long-distance dispersal events are considered to be extremely rare, and perhaps more so in aloes, which have seeds that are generally poorly-adapted for wind dispersal. Nonetheless, aloe seeds do possess wings, which likely enhance dispersability especially during strong, gusty wind events, which frequently occur in the south-western Cape during summer when *A. plicatilis* seeds are released. Many of the aerodynamic mechanisms that promote long-distance dispersal in light, fluffy or plumed seeds may also apply to heavier winged seeds (such as aloe seeds) at somewhat different scales (Horn et al., 2001). The otherwise difficult-to-explain occurrence of *A. plicatilis* on completely isolated mountains such as Paarl Mountain and the Paardeberg support the notion of possible long-distance dispersal in *A. plicatilis*.

The potential for long-distance dispersal in *A. plicatilis* has important implications for the species' response to climate change. The Cape Floristic Region is predicted to undergo major changes in floristic composition and distribution as the impacts of climate change strengthen and increase (Midgley et al., 2002; Hannah et al., 2005). Species with short life-spans such as annuals and short-lived perennials are likely to show dramatic changes more rapidly than long-lived, slow-growing taxa (REF). The potential for long-distance dispersal in the Cape flora is likely critical for determining the ability of species to undergo range shifts and colonization of suitable new habitats in a changing landscape. The magnitude and direction of changes in the distribution of *A. plicatilis* is yet to be determined, but changes will possibly be slow due to the long-lived, slow-growing nature of the species, which enables it to persist in the form of well-established mature individuals in the landscape for long periods of time (e.g. Foden et al., 2007; Jack, 2012).

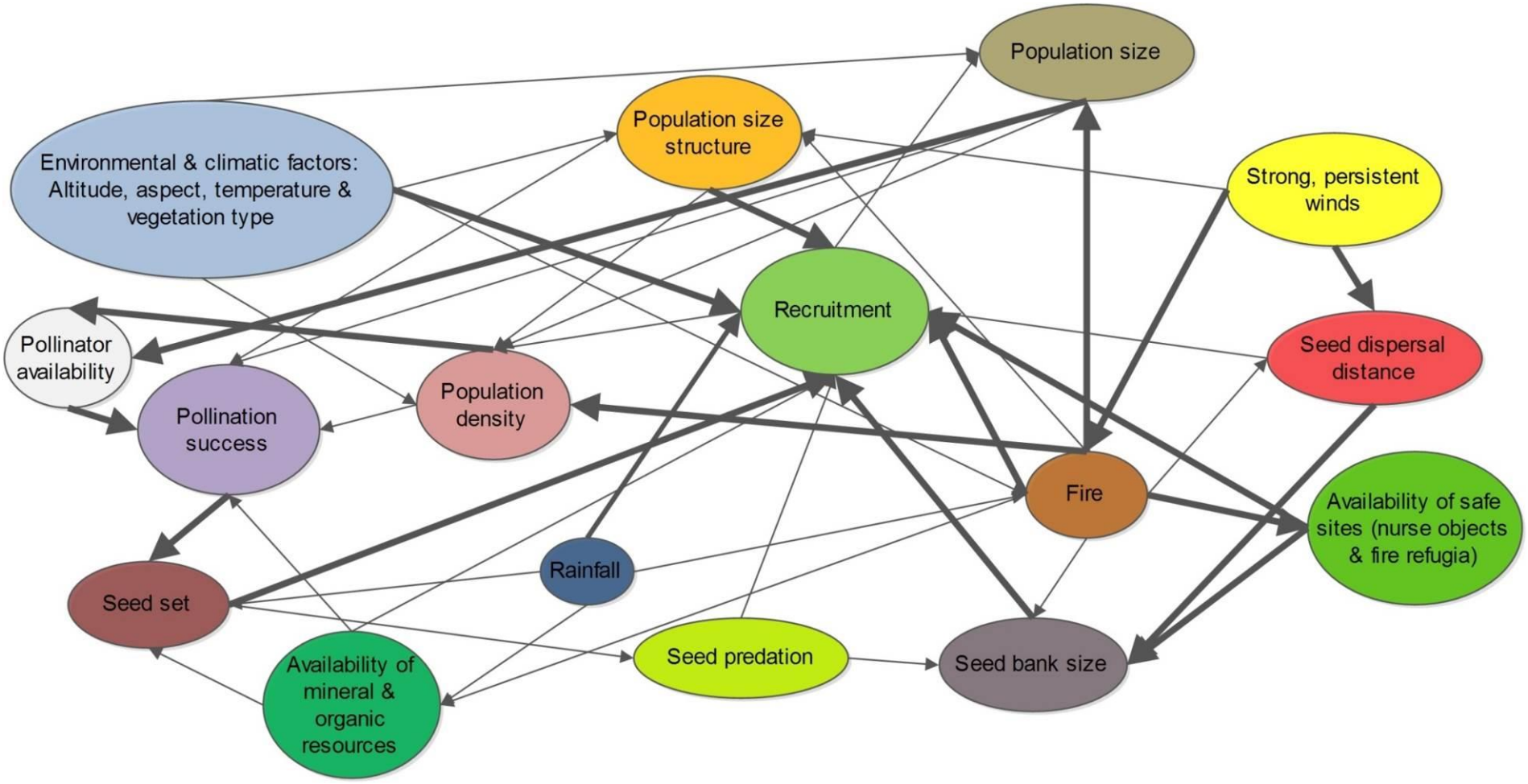


Fig. 6.2. Interactions between life history and regeneration components with environmental factors (both biotic and abiotic, including disturbance) that affect a hypothetical *Aloe plicatilis* population. Thick and thin arrows represent strong and weak interactions, respectively. The sizes of bubbles bear no relation to their relative importance in the system. Other disturbances that were not observed to be prevalent in the large majority of populations (disease, invasive alien plant species encroachment and harvesting) were excluded for the sake of simplicity.

6.2. Conservation implications of the new species designation

The name change of *Aloe plicatilis* – one species out of ±550 in the genus – to *Kumara disticha* (a monotypic genus, i.e. one that comprises a single species only) (see Grace et al., 2013) may have important implications for the species' conservation. In a study of the molecular support for a basal grade of morphologically distinct monotypic genera in the species-rich family Vanguerieae, Razafimandimbison et al. (2011) note the possibility of a monotypic genus being the sole representative of its lineage, thus carrying unique genetic information, with the consequence that extinction of the genus would result in a loss of the entire lineage. Hence, a monotypic genus may potentially be seen as a conservation priority due to its genetic isolation; however, Razafimandimbison et al. (2011) caution that this should not automatically be taken as a reason for conservation concern.

However, in the case of charismatic, unusual and attractive species such as cycads, orchids and succulent plants, a change in a species' taxonomic designation that results from recognition of its unique characters may increase its perceived rarity and/or value and desirability (Stuart et al., 2006). Courchamp et al. (2006) suggested that if consumers place disproportionate value on rare species, this could result in a 'vicious cycle' or the "anthropogenic Allee effect" as termed by the authors, whereby increases in exploitation further reduce population size, which in turn inflates the species' value and ultimately leads to its extinction in the wild. This scenario has been frequently observed in highly desirable indigenous cycad species in South Africa, especially those that naturally occurred in low abundance at the time of their discovery (e.g. *Encephalartos brevifoliolatus* and *Encephalartos nubimontanus* – both of which are now classified as Extinct in the Wild (EW) on the IUCN Red List (Raimondo et al., 2009).

Hall et al. (2008) contend that while a species' 'true' rarity implies low population size, human perception of rarity is skewed and scale-dependent. A species may be considered rare if it is widespread but at low densities throughout its range, locally scarce but more common elsewhere, or found at only a few localities (Hall et al., 2008). Although *A. plicatilis* may not necessarily be considered 'rare' in terms of its global population size and few current major threats to its persistence, it is a restricted range fynbos endemic. By placing the species in a new monotypic genus, this may lead to increased conservation efforts but its perceived uniqueness and rarity may be potentially elevated, with consequent increases in its desirability and extinction risk (Hall et al., 2008). Furthermore, since it has a shallow root system, it transplants fairly easily and grows readily from cuttings (S.R. Cousins, pers.

obs.), it is an easy target for wild collection in order to satisfy growing consumer demands. Many populations occur high up in mountain ranges that are either fairly inaccessible and/or occur in conservation areas; hence, these populations may be regarded as reasonably safe from would-be collectors. However, the more low-lying, accessible populations may be more vulnerable to harvesting.

6.3. Monitoring and management recommendations

6.3.1. Re-evaluation of the IUCN Red List status for *Aloe plicatilis*

Aloe plicatilis is currently listed as a species of Least Concern (LC) on the IUCN Red List status (Raimondo et al., 2009). However, the Area of Occupancy (AOO) calculated in this study using direct measurements of geographic extent for 19 *A. plicatilis* populations = 1.54 km^2. This value is below the threshold AOO of 20 km^2 as listed in Table 2.1 of the Guidelines for Using the IUCN Red List Categories and Criteria (2003), which may therefore require an uplisting of the species' Red List status to Vulnerable (VU D2). However, current threats to the species' persistence (mainly alien species encroachment and harvesting) are minimal, although three populations appear to be declining (Jason's Hill (JH), Voorsorg 1 (V1) and Voorsorg 2 (V2) in Table 6.1). The contributions of these threats and population declines in relation to the species' small, restricted global population need to be assessed in order to re-evaluate the Red List status fully. Furthermore, the geographic extent of the additional 11 unsurveyed populations located in this study need to be calculated in order to arrive at a more precise and up-to-date measurement of the species' AOO. Re-evaluation of the Red List status of *A. plicatilis* is also required as part of the Non-Detriment Finding (NDF) for the species.

6.3.2. Population monitoring and management

6.3.2.1. Small populations

Population monitoring is recommended for the five smallest *Aloe plicatilis* populations surveyed in this study (Table 6.1). An additional population on the Paardeberg (PB) has also been included, as although it has not been surveyed for number of individuals and the sizes thereof, it is comparatively small and occurs on the westernmost edge of the species' distribution, where future climate change may pose a threat to its persistence. JH, PB, Tulbagh Waterfall (TW) and Windmeul 2 (W2) require full counts to determine the exact number of individuals in each.

Population monitoring has already commenced at V2. In June 2011, GPS coordinates were taken for all individuals in the population, and each plant was measured for height, stem diameter and reproductive output (number of inflorescences/plant). All plants in the population were subsequently tagged, photographed and re-measured in November 2012. By the second survey, population size at V2 had decreased by a third after a fire that occurred in January 2011 (many plants that were still alive in June 2011 died in the 17 month period following that particular survey). Furthermore, only four out of 30 live plants were in flower with a total of eight inflorescences.

Both V1 and V2 are important to monitor not only due to their small population size, but also because they are at the easternmost edge of the species' distribution where climatic conditions are the most severe compared to other populations (i.e. high average annual temperatures and low rainfall). Although there is a large amount of variation in regional climate models (Tadross et al., 2005), the general consensus is that as climate change ensues, temperatures are expected to rise and rainfall to diminish in the Western Cape (Midgley et al., 2002, 2003); hence, V1 and V2 are likely to be among the first *A. plicatilis* populations to show changes in response to these new conditions.

JH is the smallest of all 19 populations surveyed (~23 individuals; Table 6.1) and appears to be in decline; however, to the author's knowledge, no historical records of population size, density and structure exist for JH for comparative purposes. The study on the population size structure and density of *A. plicatilis* (Chapter three) revealed that this population displays a steep J-shaped size class distribution, indicating a preponderance of large adult plants and very little recent recruitment. JH also had the lowest population density of all 19 surveyed populations (75 plants/ha). Furthermore, reproductive output at JH appears to be deficient compared to other populations (refer back to Chapter four) and most individuals in the population generally have low vigour (dull, flaccid leaves and a prevalence of black spot leaf disease). In light of these observations, it is recommended that JH be monitored to assess any further changes in the population.

TW is the fifth smallest *A. plicatilis* population that was surveyed in this study. The population is very dense (1331 plants/ha), but highly restricted geographically (0.12 ha). Very little recent recruitment has been observed at the site, and although there are a number of small plants in the population, there has been a dearth of recent recruitment (as indicated by the absence of individuals in the smallest size classes in the population's stem diameter and height size class distributions (refer back to Chapter

three, Fig. 3.5)). The *A. plicatilis* individuals at TW appear similar to the ones at JH and have very flaccid, dull-looking leaves, suggestive of drought stress; although the population was surveyed at the end of summer when the plants might be expected to be slightly water-stressed. This population, along with another even smaller unsurveyed population nearby (estimated 20 plants; G. Hansford, pers. comm.) should also be monitored to track any changes in population size, density and structure.

The frequency and intensity of the monitoring of these six populations will depend on the time and resources available. Monitoring could simply involve total counts, or include measurements of plant size (stem diameter or height, or both), density, population extent, and aspects of plant vigour (e.g. reproductive output, prevalence of disease, plant water balance, effects of invasive alien species encroachment and recovery after fire). Monitoring the level of alien plant invasion at these sites would also be highly beneficial.

Table 6.1. The localities and population sizes of the five smallest *Aloe plicatilis* populations that are recommended for monitoring, listed in order of decreasing population size.

Population name and abbreviation	Locality	GPS coordinates	Total number of individuals
Tulbagh Waterfall (TW)	Close to Tulbagh Waterfall, Tulbagh district	-33.3515; 19.10887	~163
Windmeul 2 (W2)	Paarl Mountain, Windmeul, Paarl district	-33.6788; 18.92298	~156
Voorsorg 1 (V1)	Voorsorg area near Rawsonville/Worcester	-33.7292; 19.37962	56
Voorsorg 2 (V2)	Voorsorg area near Rawsonville/Worcester	-33.7198; 19.38341	30
Jason's Hill (JH)	Jason's Hill wine farm, Slanghoek Valley near Goudini/ Rawsonville	-33.6671; 19.22777	~23
Paardeberg (PB)	Near Paardeberg Dam, Paardeberg, between Malmesbury & Wellington	-33.5772; 18.80838	~250*

*Paardeberg has been included as an additional population, although its size has not been quantified directly. It is, however, regarded as important for monitoring due to its comparatively small estimated population size (approximately 250 individuals based on preliminary field observations) and its occurrence at the westernmost edge of the species' distribution.

6.3.2.2. Invasive alien plant species

Invasive alien plant species do not appear to be posing a major threat to any *A. plicatilis* populations at present, except for DKK (Table 6.2), where *Acacia mearnsii* and *A. saligna* are encroaching on parts of the population. Other invasive aliens that currently occur in the vicinity of *A. plicatilis* populations include *Hakea sericea*, *Pinus pinaster*, *Pinus pinea* and *Eucalyptus* spp. (Table 6.2). A rapidly spreading *Eucalyptus* stand occurs adjacent to, and partially within Windmeul 1 (W1) on Paarl Mountain. The saplings appear to have germinated from seed dispersed from a row of large, mature

Eucalyptus trees nearby. It is recommended that all the trees and saplings are removed before the invasion poses a serious threat to the *A. plicatilis* population and the many other fynbos species that grow in the Endangered (EN) Boland Granite fynbos and Swartland Granite Renosterveld vegetation types that occur on Paarl Mountain.

At certain populations that occur on privately-owned land or in protected areas e.g. Goudini Spa (GS), Goudini Badsberg (GB) Skurweberg (SB) and Wiesenhof Lookout (WL), consultations with the relevant authorities revealed that ongoing invasive alien plant management is conducted at these sites. To the author's knowledge, there is currently no invasive alien management taking place at DKK. Alien clearing at this population will prove challenging since it occurs on very steep slopes, some of which are inaccessible by foot. This area occurs within a reserve managed by CapeNature who will be alerted to the escalating alien invasion at the site and possible management plans will be discussed. Interviews with land-owners at JH, Kliphoutkloof (KK), PB, V1 and V2 will be undertaken to ascertain whether any invasive alien species management actions are being taken. This information will form part of the NDF for *A. plicatilis* that is currently in preparation. All land-owners/custodians will be sent recommendations regarding alien plant management at the relevant *A. plicatilis* populations once the NDF has been completed.

6.3.2.3. Harvesting for the horticultural trade

Concern surrounding the illegal wild-collection of *A. plicatilis* was one of the main reasons for initiating this study. The populations that occur high up in the mountains and/or in protected areas are considered relatively safe from harvesting; however, those that are the most easily accessible by foot should be monitored more closely. These populations are DKK; -33.7262; 19.11155), Du Toit's Kloof Molenaars Rivier (DKM; -33.723; 19.16982), TW, W1 and W2 (see Tables 6.1 and 6.2 for locality details for TW, W1 and W2).

Thus far there is only one population – Kliphoutkloof (KK) – for which there are confirmed reports of historical illicit harvesting. The identity of the perpetrator and estimates of the number of harvesting events, and the quantities and sizes of plants removed, were provided by the land-owner in an interview in 2012. KK is the largest known *A. plicatilis* population (~112 000–140 000 individuals), and the illegal harvesting that occurred did not appear to have a major impact on the population (R. Hugo, pers. comm.). Furthermore, the land-owner has denied the perpetrator any further access to the site.

However, this harvesting activity will be reported to CapeNature and the South African National Biodiversity Institute (SANBI).

The other consignments of exported *A. plicatilis* individuals (see Chapter one, Fig. 1.1.) listed on the CITES trade database were either legally harvested or sold as artificially propagated plants with permits issued by CapeNature. However, a permit has not yet been located for a particular shipment of 500 reportedly wild-collected plants which was exported to Australia in 2006. Further investigations into this matter, as well as other aspects of the trade in *A. plicatilis* will be conducted and a Non-Detriment Finding (NDF) for the species is planned for completion in 2013 in order to fulfil the requirements of the SANBI Scientific Authority mandate on the research and trade monitoring of *A. plicatilis* as a "species of special concern".

6.3.2.4. Fire management

Burns at the various *A. plicatilis* populations should be set at intervals that are appropriate for the particular fynbos vegetation type that occurs at those localities. V1 and V2 occur in an ecotone between the fynbos biome and Karoo shrubland. The vegetation in this area should only be burned every 25–35 years (S. McDermott, pers. comm.). However, the interval between the two most recent burns was only 10 years as the most recent burn was an accidental runaway fire (S. McDermott, pers. comm.). Arson events and accidental runaway fires pose a challenge to the effective management of fires in the fynbos biome and the anticipated expansion of human populations in the region is expected to increase the number of ignition opportunities and the frequency of fires, with detrimental consequences for biodiversity conservation and the control of invasive alien plant species (Forsyth and Van Wilgen, 2008; Van Wilgen et al., 2010).

Table 6.2. Localities, land ownership type, alien plant species identifications and the proximity of their populations in relation to 11 surveyed *Aloe plicatilis* populations where alien plant species invasions are of concern.

Population name	Population abbreviation	Locality	GPS coordinates	Land ownership*	Species identifications	Proximity to population
Du Toit's Kloof Kromrivier	DKK	Du Toit's Kloof, old tunnel, Kromrivier hiking trail, R101/N1highway	-33.7262; 19.11155	CA (CapeNature)	*Acacia mearnsii* & *Acacia saligna*	Partially surrounding & within
Goudini Spa	GS	Goudini Spa Holiday Resort, Goudini/ Rawsonville	-33.6639; 19.2659	POL (Goudini Spa Holiday Resort)	*Pinus pinaster* & *Hakea sericea*	Partially surrounding & within
Goudini Badsberg	GB	Above Goudini Spa Holiday Resort, Goudini/ Rawsonville	-33.6621; 19.25782	POL (Goudini Spa Holiday Resort)	*Hakea sericea*	Nearby
Jason's Hill	JH	Jason's Hill wine estate, Slanghoek Valley, Goudini/ Rawsonville	-33.6671; 19.22777	POL (Jason's Hill wine estate)	*Hakea sericea*, *Acacia mearnsii* & *Pinus pinaster*	Partially surrounding & within
Kliphoutkloof	KK	Adjacent to Goudini Spa Holiday Resort, Goudini/ Rawsonville	-33.6911; 19.26448	POL (wine farms) & CA (CapeNature)	*Acacia mearnsii*, *Pinus* sp. & *Eucalyptus camaldulensis***	Partially surrounding & within
Paardeberg	PB	Paardeberg between Malmesbury & Wellington	-33.5772; 18.80838	CA (Paardeberg Sustainability Initiative)/ government land		Nearby
Voorsorg 1	V1	Voorsorg, Rawsonville/ Worcester	-33.7292; 19.37962	POL	*Hakea sericea*	Nearby
Voorsorg 2	V2	Voorsorg, Rawsonville/ Worcester	-33.7198; 19.38341	POL	*Hakea sericea*	Nearby
Windmeul 1	W1	Paarl Mountain, Windmeul, Paarl	-33.6904; 18.90998	POL & CA (Paarl Mountain Nature Reserve (CapeNature))	*Pinus* sp. & *Eucalyptus cladocalyx***	Partially surrounding & within
Windmeul 2	W2	Paarl Mountain, Windmeul, Paarl	-33.6788; 18.92298	CA (Paarl Mountain Nature Reserve (CapeNature))	*Pinus pinea* & *Eucalyptus cladocalyx***	Partially surrounding & within
Skurweberg & Wiesenhof Lookout	WL & SB	Skurweberg, Simonsberg, Wiesenhof Wildpark, Klapmuts/ Stellenbosch	-33.8538; 18.89376	CA (Wisenhof Wildpark) & POL	*Pinus* sp.	Partially surrounding & within

*CA = Conservation area; POL = Privately-owned land

**Preliminary identifications based on photographs. Species identifications will be validated after collecting voucher specimens.

Concerns about damage to infrastructure and property sometimes results in the intentional exclusion of fires from certain areas (e.g. Le Roux, 2011). However, this is not an ideal situation, since long-term exclusion of fynbos fires results in extremely large, intense and damaging fires due to the build-up of substantial amounts of highly flammable plant material. *Aloe plicatilis* populations may be severely impacted by such fires, as many seedlings and juveniles may be killed, thus retarding recruitment, and larger, more fire-resistant reproductive adults growing in comparatively exposed sites may also be destroyed or severely injured (refer back to Chapter five). Prescribed burns are recommended for the *A. plicatilis* populations at W1 and W2, which have not burned in over 10 years. These sites ought to be burned according to the fire regime appropriate for the vegetation type that occurs at each.

6.4. Major contributions of the study

- The comprehensive literature review (Chapter two) provides a synthesis of a wide range of aspects of aloe ecology, illuminating major trends and highlighting opportunities for future research. The review thus provides a useful resource to researchers and conservation practitioners working on the genus.
- The investigation of the population size structure and density of *A. plicatilis* (Chapter three) is the first known study of this nature on a broad set of populations of a monocot tree succulent in a Mediterranean–type climate region. The study introduced a novel method for aligning stem diameter and height size class distributions by using a regression relationship determined for these two measures of plant size. In turn, this technique allowed for a comparison between stem diameter and height size class distributions within populations to determine whether or not they differed from each other significantly. Furthermore, the study challenged the use of the inverse J-shaped size class distribution as an indicator of a stable and healthy plant population, especially for long-lived, slow-growing taxa.
- The study of the reproductive ecology of *A. plicatilis* (Chapter four) is the first of its kind on any tree aloe species. In particular, it contributed new insights into the seed ecology of the genus *Aloe*, especially with regard to soil seeds banks, seed longevity and germination.
- The investigation of the fire ecology of *A. plicatilis* constitutes the first known study of its kind on a monocot tree succulent in a Mediterranean-type climate region. It provided a preliminary account of the role that such species' bark and succulent leaf clusters play in their fire survival and it challenged the prevailing hypothesis of fire survival in succulent plants as being either

"fire avoidance"or "fire tolerance", since *A. plicatilis* appears to adopt both strategies simultaneously.

- On the whole, the study provides a holistic ecological understanding of a plant species that is representative of charismatic, long-lived, slow-growing taxa, which are often popular among plant collectors and sometimes threatened as a consequence thereof. Many of the insights gained in this study can be extrapolated and applied to other similar species, ultimately enhancing their conservation and management.

6.5. Uncertainties

- The snapshot study on the population structure and density of *A. plicatilis* could not reveal long-term trends or population dynamics, so interpretations of the patterns observed were fairly limited and circumspect. Furthermore, it was difficult to distinguish between the possible drivers behind the so-called 'bonsai effect' that was observed in many *A. plicatilis* populations. It appears that the two most important drivers are the pruning effect of wind and the growth limitations imposed by restrictive rooting space. The two mechanisms possibly work in concert to bring about the stunting observed in bonsai plants, but this remains uncertain and requires further investigation.
- Deductions about seed dispersal, soil seed banks, seed longevity in the field, and the timing and conditions required for germination and establishment in wild populations were somewhat speculative and uncertain. Nonetheless, these knowledge gaps provide excellent opportunities for further research as detailed in section 6.7.2.2.
- For the fire ecology study (Chapter five) it was only possible to survey the populations after they had burned and not beforehand as well. Hence, there was a degree of uncertainty in the interpretations of the pre- and post-fire size class distributions and densities, since some of the smaller individuals that were present pre-fire may have been completely incinerated and hence undetectable post-fire.

6.6. Directions for future research

6.6.1. Population dynamics

The demographic research conducted on *A. plicatilis* in this study provided a 'snapshot' assessment of the species' population structure using survey data from two-thirds of the currently known populations (refer back to Chapter three). Selection of populations across the entire range of the species allowed for an analysis of the population dynamics of *A. plicatilis* spread over space instead of time. However, monitoring of selected populations over longer periods of time will provide deeper insights into the species' long-term population dynamics. These data can then be used in conjunction with data on *inter alia*, growth rates, reproductive output, recruitment and mortality to conduct a population modelling exercise using combinations of different stressors such as fire and harvesting in order to determine the trajectory of the population(s). Such studies are very useful for predicting population trends in long-lived, slow growing plant taxa (e.g. cycads, Raimondo and Donaldson, 2003; cacti, Ferrer-Cervantes et al., 2012; and baobabs, Venter and Witkowski, 2013). For *A. plicatilis*, the outcomes of such a study could then be used to inform management decisions regarding burn intervals and harvesting intensities.

6.6.2. Reproductive ecology

6.6.2.1. Pollination ecology

- Further field pollination studies could include formal floral visitor observations in the form of field observations and camera trapping (e.g. Arena et al., 2013), and quantification of visitation rates and pollen loads per visitor (e.g. Etcheverry et al., 2012).
- Nectar volume and concentration tests could be performed on bagged and open inflorescences to determine nectar volumes and concentrations produced in the absence of visitors as well as standing crop (e.g. Symes and Nicolson, 2008).
- A flowering phenology study could be conducted at multiple populations to determine whether any differences in flowering and fruiting times exist between populations and within populations over successive years (e.g. Symes and Nicolson, 2008).
- Self compatibility tests could be conducted either in the field or under greenhouse conditions to further elucidate the species' breeding system (e.g. Hoffman, 1988).

6.6.2.2. Seed ecology

The many gaps in aloe seed ecology include knowledge on dispersal, recruitment, seed banks, potential longevity, and ecological longevity (see Vásquez-Yanes et al., 1993).

- Studies on seed dispersal *in situ* could quantify short-distance dispersal distances within and around populations (e.g. Symes, 2012), and investigations of the potential for long distance dispersal using genetic techniques (e.g. He et al., 2004). Comparative long-distance dispersal studies using for example, two species that have patchy distributions, with each species occurring in a different climatic zone where different wind conditions prevail) could help elucidate the existence of patchy distributions in the genus *Aloe* due to long-distance dispersal by wind versus changes in habitat over time (refer back to the discussion in Chapter four).
- Another important aspect of the seed ecology not only of *A. plicatilis* but the genus *Aloe* as a whole involves the timing, specific localities (microsites) and extent of germination and survivorship *in situ*. A comparison between the timing of seed germination in *A. plicatilis*, which disperses its seeds in the middle of the summer drought, and other species that disperse their seeds just before the commencement of the spring and summer rains would likely be very informative. Moreover, the timing of seedling recruitment post-fire is another important aspect of *A. plicatilis* seed ecology that deserves further attention.
- Finally, a key part of successful recruitment in the genus *Aloe* is the presence of nurse objects. Until now, there has only been mention of 'nurse plants' in the aloe literature, with little or no reference to other nurse objects such as 'nurse rocks'. However, this study and another by Arena et al. (in prep) point towards the possible use of nurse objects other than plants by aloes. The role that rocks, stone, logs and other objects play in providing shady, damp and protected sites for seedling recruitment is fairly well understood in the restoration ecology literature (e.g. Botha et al., 2008). However, a study on the relative importance of such objects for germination and establishment in various aloe species (e.g. Peters et al., 2008) would be very helpful for determining suitable localities for the relocation of threatened species impacted by human activities, for population augmentation/ re-introductions, and for predicting the habitats that may be suitable for species to colonise under climate change scenarios.

6.6.3. Fire ecology

The fire ecology of plants with dispersed vascular bundles, which includes arborescent monocots is poorly understood (Gill, 1995). This dearth of knowledge applies even more to succulent arborescent monocots and those that occur in Mediterranean-type climate regions. Hence, *A. plicatilis* is a prime candidate for continued research in this area of fire ecology; and, by building on the study presented in Chapter five, deeper insights may be gained not only into the fire ecology of *A. plicatilis*, but other similar taxa as well.

- Of particular interest is the role that the thick, corky bark in *A. plicatilis* plays in the species' fire survival. *Aloe plicatilis* is the only bare-stemmed tree aloe indigenous to South Africa that occurs in a fire-prone ecosystem. Clearly the species' unique bark has fire-resistant properties that obviate the necessity of a skirt of insulating persistent dead leaves (see Bond, 1983). The insulating qualities of the bark could be investigated by comparing its internal structure with that of other corky-barked species e.g. *Quercus suber* – the species from which commercial cork is harvested (Silva et al., 2005) and by applying various heating treatments to excised bark strips.
- At the individual plant or branch level, fire tolerance could be determined by means of stem heating experiments such as the wick technique (e.g. Helm et al., 2011) in order to simulate the effects of different burn frequencies and intensities. Temperatures at various depths within the bark and pith could be measured relative to flame temperatures, ambient temperatures, and plant tissue water content in order to determine the effects on survival (e.g. Pinard and Huffman, 1997).
- The actual cause of fire-induced plant death in *A. plicatilis* could be ascertained by applying heat to individual stems and measuring the degree of hydraulic failure in the xylem using staining techniques (e.g. Balfour and Midgley, 2006) and possibly the extent of phloem disruption and cambial damage.
- It is generally accepted that plants with high moisture contents act as fire retardants. However, detailed studies are yet to be conducted on the benefit of the fire retardant effects of large water reserves versus the potentially elevated risk of damage associated with accelerated tissue heating owing to the superior heat conductance properties of water compared to air. The succulent nature of both the stems and leaves of *A. plicatilis* makes this species a good candidate for research in this area.
- The aerial rooting phenomenon observed on the damaged stems of many *A. plicatilis* individuals reportedly occurs on other *Aloe* species (E.T.F. Witkowski, pers. comm.), but has not, to the

author's knowledge, been studied in detail in these species. A study on this phenomenon in *A. plicatilis* could involve determining its prevalence across populations, and its frequency within populations and individuals relative to damage severity. The function of this adaptation, which is hypothesized to be a strategy for asexual reproduction following damage to branches, could be elucidated in more depth. The frequency of establishment of rooting branches that eventually fall to the ground could also be investigated.

6.7.4. Species distribution modelling and climate change impacts

- The data collected for this study have excellent potential for use in a species distribution modelling study. The locality (GPS) data collected from two-thirds of the known populations across the distribution of *A. plicatilis* provide a substantial representation of the species' entire geographic range. These data can be used in conjunction with the environmental and climatic conditions at each population (e.g. rainfall, temperature, soil type, vegetation type, geology, slope, aspect, altitude and land cover type) to model the current distribution of *A. plicatilis* in order to locate further undiscovered populations. The validity of the model could then be determined by conducting a ground-truthing exercise, which would involve visits to sites where the model predicts the species to occur.

- Using the same locality data, but different climatic conditions, the model can be used to predict changes in the distribution of *A. plicatilis* under different climate change scenarios. This investigation would be very valuable for a Cape fynbos species, in light of the substantial changes to the floristic composition and distribution that are expected as a result of climate change in the region (Midgley et al., 2002; Hannah et al., 2005). Enhanced knowledge of fynbos species' responses to climate change will be beneficial for informing management decisions such as the placement of reserves. Furthermore, species distribution modelling studies on long-lived, slow-growing plant species such as *A. plicatilis* will also assist in determining the suitability of such organisms as indicators of climate change in general (see Foden et al., 2007; Jack, 2012).

6.8. References

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APPENDIX I


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Fanfare in the fynbos
The KwaZulu-Natal National Botanical Garden
Hawk moths in the garden
Unique kalkberg
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Fanfare in the fynbos



Aloe plicatilis, a unique Western Cape tree aloe

ABOVE: The Fan Aloe appears to burst into flames as it flaunts its vibrant floral display at the end of a cold winter.
Photo: Stephen Cousins.

by **Stephen Cousins,** School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg

With roots tightly wedged between the rocks, stout stems held high, each flaunting an open fan of slender blue-green leaves, the Fan Aloe is dressed to impress. Averaging heights of up to 2.5 m, these splendid succulents show off their grandeur by booking a room with a view. At lofty heights between the boulders, they find refuge from both fire and ploughs. Not only do they boast displays of fantastic fan-shaped foliage, but once a year they bedeck themselves in a cavalcade of floral finery. In the wake of a cold, inclement winter, the warmth of spring provokes an eruption of vibrant colour, and the florid fans begin to blush in a blaze of brilliant crimson. This flamboyant display attracts winged visitors, who sip at sugary cocktails from short scarlet straws. The flowers festoon the fynbos for weeks on end, illuminating the landscape and furnishing its participants with sweet nutritious nectar. With summer fast approaching, the party begins to draw to a close. The stars of the show grow weary and their rouge begins to fade. In a ruby rain of wilted petals, the flagging fans bid their friends farewell – until next spring when this floral fantasy begins again!

The Fan Aloe (*Aloe plicatilis*) is one of five tree aloes that occur in South Africa, and is the only one that grows in the Cape Floristic Region. It is restricted to a small area in the mountainous parts of the south-western Cape, from the Franschhoek Mountains in the south to the Elandskloof and Roodezands Mountains in the north. It has an affinity for well-drained, acidic soils, on steep rocky slopes in areas of high winter rainfall. The Fan Aloe exhibits a highly clumped distribution pattern, with seventeen known populations, many of which are separated by distances of more than 10 km. This attractive aloe has been described as one of the botanical treasures of the fynbos, and its striking appearance has long captivated gardeners and botanists alike. Only three other aloe species display their leaves in a fan-like arrangement, two of which occur in Madagascar, and the third - *Aloe haemanthifolia* - has a limited distribution that coincides almost exactly with that of *Aloe plicatilis*. *Aloe haemanthifolia* is the diminutive, stemless equivalent of its arborescent counterpart, with leaves that are similarly shaped but slightly larger and greener in colour.

Despite its popularity, very little is known about the ecology and population biology of the Fan Aloe. Over the two preceding decades, the Quiver Trees (*Aloe dichotoma* and *Aloe pillansii)* have received much deserved attention from local botanists due to dramatic changes in their population structures. Widespread adult mortality has been observed in *Aloe dichotoma*, and several populations of *Aloe pillansii* tell a similarly sad story. Amid this perplexing pandemonium, *Aloe plicatilis* has gone largely unnoticed, perhaps because it does not appear to be particularly threatened at present... Or does it? Recent trade statistics indicate that since 2005 there has been a major increase in the export of Fan Aloes to other countries, several hundred of which are reported to be of wild origin. This increasing trend in trade, coupled with a general dearth of knowledge on the ecology of the species called for some further investigation.

At the beginning of 2010, a Master's project on *Aloe plicatilis* was launched by the University of the Witwatersrand, the University of Johannesburg and the South African National Biodiversity Institute (SANBI) to investigate the trade in the Fan Aloe and assess the impact this might be having on wild populations, as well as to study the aloe's population structure and its general ecology. There is a marked lack of information on the re-sprouting response of aloes after disturbances, so *Aloe plicatilis* will be used as a test subject to address this issue, and the knowledge gained should lay the foundation

for future studies on re-sprouting in aloes.

All known populations of the species will be surveyed, which includes visiting historical localities where the species was known to exist in the past, but may no longer occur there. Since there is a shortage of long-term monitoring data available for *Aloe plicatilis*, an attempt will be made to use matched photographs to track changes in the various populations. In order to achieve this, historical photographs of the aloes in situ will need to be unearthed, and the precise localities where the pictures were taken, determined. If these exact positions are re-visited, matching present-day photos of the plants can then be taken from the same angle. If the historical and the present-day photos are compared, one can detect changes in the size and abundance of visible individuals in the population.

We know of seventeen localities for the Fan Aloe, three of which we discovered during a pilot study for the project and were not recorded in any of the literature on the species. If any further undiscovered sites are found, they will also be incorporated into the study. The general public is therefore requested to please contact me if they have any information on *Aloe plicatilis* – locality data, historical photographs, evidence of harvesting or any other pertinent information.

We hope that the results of this research will deepen our understanding of aloe ecology and that of *Aloe plicatilis* in particular, and help to shed light on the impact of harvesting on wild plant populations. Ultimately, this will assist in the development of better conservation and management strategies for threatened species and provide insight into the sustainable utilization of natural resources.

READING

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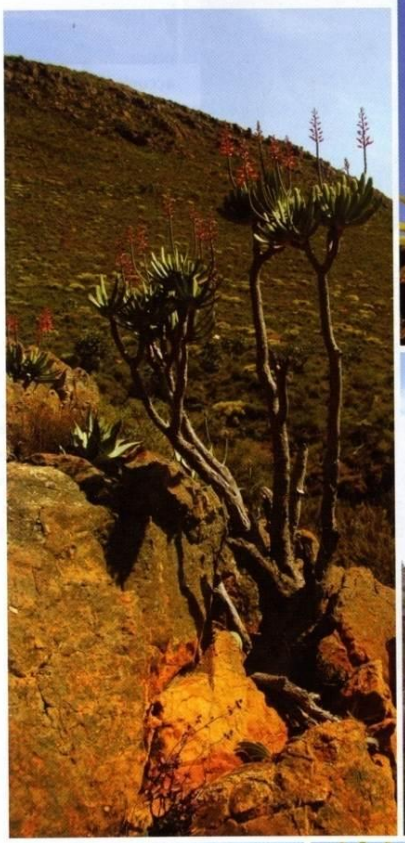
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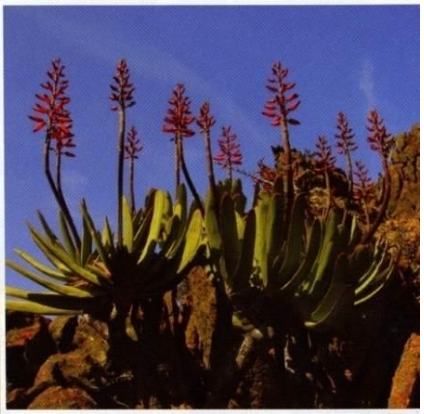
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GET CONNECTED

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BELOW: In early spring the Fan Aloe erupts in a blaze of exuberant colour with its laxly-flowered, delicate inflorescences extending high into the sky, attracting any thirsty would-be pollinators.

MIDDLE RIGHT: A mature, neatly compact adult Fan Aloe adorned with a flush of flowers and stems blackened by occasional wildfires.

MIDDLE LEFT: A tall, slender, weather-beaten Fan Aloe growing in a harsh rocky environment in the Du Toit's Kloof mountains near Worcester.

BOTTOM RIGHT: An attractive Fan Aloe elegantly draped over the rocks on a hilltop in the Wiesenhof Wildpark near Stellenbosch.

BOTTOM LEFT: A fine clump of *Aloe plicatilis* in full bloom, hugging the steeps slopes of the Badsberg Mountains.

Photo: Stephen Cousins.



