



## Review

## African aloe ecology: A review

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## ARTICLE INFO

## Article history:

Received 7 June 2011

Received in revised form

20 February 2012

Accepted 29 March 2012

Available online 23 May 2012

## Keywords:

Conservation

Economic botany

Ecophysiology

Fire

Pollination

Population structure

Resprouting

Seeds

## 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 up to 20 m. 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 the genus, 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. Furthermore, by better understanding the genus, its utility in practical applications such as ecosystem restoration can be explored further. Hence, this review provides a synthesis of a wide range of available information on several aspects of aloe ecology, and highlights important 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.

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## 1. 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 (Fig. 1) (Holland, 1978; Smith and Van Wyk, 2009; Van Jaarsveld, 1987; Van Wyk and Smith, 2008). 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 and Van Wyk, 2009; Smith et al., 2000). 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 *alloe*, 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.

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## 2. Distribution

The genus *Aloe* Linneus, (Asphodelaceae: Alooideae) comprises a total of 548 accepted species (Grace et al., 2009), the majority of which ( $\pm 350$ ) are found in Africa and concentrated in southern and eastern Africa as well as Madagascar (Fig. 1) (Crouch et al., 2009; Klopper and Smith, 2007; Knapp, 2006). 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 (Crouch et al., 2009; Klopper and Smith, 2007; 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 *Aloe 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 2700 m (Holland, 1978; Sachedina and Bodeker, 1999; West, 1974). Individual species, however, tend to be geographically restricted (Holland, 1978; Sachedina and Bodeker, 1999; West, 1974). 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. *Aloe excelsa*) (Jordan, 1996; Kamstra, 1971). Others produce wingless seeds, presumably limiting their dispersal, thus resulting in dense stands of plants in localised areas (e.g. *Aloe aculeata*) (Jordan, 1996; Kamstra, 1971).

## 3. Anatomy and ecophysiology

### 3.1. 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; Smith and Van Wyk, 2009; Van Jaarsveld, 1989). Aloes produce a bitter-tasting exudate just below the surface of the leaves which provides a means of chemical defence against herbivores (Sity, 2009; Van Jaarsveld, 1989). Most aloes also possess spines along their leaf margins and occasionally throughout the leaf surface as mechanical defense (Sity, 2009; Van Jaarsveld, 1989). 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 (Smith and Van Wyk, 2009; Van Jaarsveld, 1989). 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; Klopper et al., 2010; Van Wyk and Smith, 2008). Aloes range in size from dwarf species only a few centimetres high (e.g. *Aloe longistyla*), to giant 20 m tall tree aloes (e.g. *Aloe barberae*) (Crouch et al., 2009; Knapp, 2006; Van Jaarsveld, 1989). (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. *Aloe bullockii*, *Aloe buettneri* and *Aloe kniphofoides*) possess underground bulbous stems consisting of fleshy leaf bases (Bornman and Hardy, 1971; Van Jaarsveld, 1989; Van der Riet, 1977). Morphologies often vary considerably with environmental conditions, and sometimes taxa appear to intergrade (Smith and Van Wyk, 1991).

### 3.2. Ecophysiology

#### 3.2.1. Plant water relations

Water stored in fleshy leaves, stems, or occasionally fleshy, fusiform roots enable aloes to survive dry seasons or cyclical droughts (Newton, 2008; Van Jaarsveld, 1989). 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 wax-coated leaf surfaces that further prevent moisture loss by reflecting excess sunlight and minimizing evaporation from cells on the leaf surfaces (Sity, 2009; Van Jaarsveld, 1987). Adventitious root systems that grow only a few centimetres below the soil surface allow aloes to benefit from relatively low amounts of precipitation (Jack, 2012; Smith and Van Wyk, 2009). Some *Aloe* species are exceedingly drought-resistant, e.g. *Aloe 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 *Aloe 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.

#### 3.2.2. 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).

### 3.2.3. Temperature requirements

**3.2.3.1. Heat tolerance.** Many aloes can tolerate very high temperatures, e.g. *Aloe dichotoma*, *Aloe pillansii*, *Aloe ramosissima* and *Aloe 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 0.5 m 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).

**3.2.3.2. Cold-tolerance.** 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. *Aloe variegata* (Smith and Van Wyk, 2009) and *Aloe 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.

The least cold-tolerant species are those found in subtropical and near-tropical regions, such as *Aloe 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 mountainous habitat in Lesotho, approximately 2400 m above sea level (Abrie and Van Staden, 2001; Smith and Van Wyk, 2009). Some members of the 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).

### 3.2.4. Soil requirements

The soil requirements of *Aloe* species vary – some grow only in very alkaline soils, e.g. *Aloe arenicola*, *Aloe asperifolia*, *Aloe claviflora*, *Aloe hereroensis* and *Aloe littoralis*, while others prefer acidic soils e.g. *Aloe commixta*, *Aloe haemanthifolia*, *Aloe 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; Kimberley, 1996; Wild, 1975). Other species such as *Aloe dewinteri*, *Aloe argenticauda* and *Aloe pachygaster* are restricted to limestone and dolomite soils (Jankowitz, 1975), while *Aloe 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. *Aloe greatheadii* var. *davyana* and *Aloe secundiflora* can act as nurse plants themselves, colonising and ameliorating harsh conditions in sparsely vegetated or completely denuded landscapes (King, 2008; Smith and Correia, 1992). It is therefore reasonable to assume that the same would apply to other widely distributed, hardy *Aloe* species with relatively non-specific soil requirements.

## 4. 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* (Wabuye 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 (Hoffman, 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 (Human and Nicolson, 2008; Tribe and Johannsmeier, 1996). 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 *Aloe 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.). *A. 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 (Duncan et al., 2006; Powell, 2005).

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; Wabuye and Kyalo, 2008). King (2008) showed that in degraded semi-arid Kenyan rangelands, areas within a 2 m 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).

## 5. Population dynamics

### 5.1. 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 (Bolus et al., 2004; Duncan et al., 2005, 2006; Foden et al., 2007; Jack, 2012; Midgley et al., 1996, 1997). 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 (Duncan et al., 2005, 2006; Midgley et al., 1996).

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 2–4 m 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 (*A. dichotoma*, *A. pillansii* and *A. ramosissima*) from the Northern Cape is still a major threat (Duncan et al., 2005, 2006; Powell, 2005). *A. 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* (Foden et al., 2007; Powell, 2005). 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*.

### 5.2. Stemless aloes

Scholes (1988) studied the changes in a population of the slow-growing, stemless *Aloe peglerae* in the Magaliesberg, South Africa, from 1976 to 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–>0.3 m 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 *Aloe petricola*, a stemless aloe in Mpumalanga, South Africa, was characterized by a preponderance of individuals in the intermediate height classes (0.2–<0.5 m), and very few seedlings and juveniles. This height distribution, which mirrors that of *A. peglerae* in Pfab and Scholes (2004), was suggested to be typical of aloes, since they generally reach flowering size relatively quickly ( $\pm 5$  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–<0.1 m) 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).

### 5.3. Single-stemmed aloes

A study by Stokes and Yeaton (1995) showed that the population structure of *Aloe candelabrum* (= *A. ferox*) at Otto's Bluff in KwaZulu-Natal, South Africa, was characterized by large numbers of aloes in the smaller size classes (0.3–1.0 m) occurring in open areas and taller individuals (1.6–>3.0 m) 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<sup>2</sup> (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 to 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<sup>2</sup>/ha in 1992, to 0.19 m<sup>2</sup>/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 also 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).

## 6. Fire ecology

### 6.1. 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 (Pfab and Witkowski, 1999; Thomas and Goodson, 1992). 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 (Craib, 2005; Jordan, 1996; 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 *Aloe perfoliata* and *Aloe*

*brevifolia*, which occur in lowland fynbos (Smith and Van Wyk, 2009).

## 6.2. 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 *Aloe 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 *Aloe 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. *Aloe inconspicua* and *A. kniphofioides* (Craib, 2005; Van Jaarsveld, 1989). 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).

**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 <i>A. plicatilis</i> in the fire-prone fynbos; this species has corky bark that protects against fire	Dichotomous branching species: <i>A. dichotoma</i> , <i>A. pillansii</i> , <i>A. plicatilis</i> and <i>A. ramosissima</i> generally do not resprout (E. Van Jaarsveld, pers. comm.). <i>A. barberae</i> 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. <i>A. petricola</i> in Weisser and Deall (1989))	Generally poor resprouters (except for <i>A. haemanthifolia</i> ), but sometimes multiple heads are produced at the stem apex (Van Wyk and Smith, 2008). 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 rootstocks in spring (Craib, 2005), but probably also resprout due to mechanical injury during the growing season (R.R. Klopper, pers. comm.)

### 6.3. 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. *A. thraskii* is unusual in that it occurs exclusively in fire-free thickets; despite its fully-covered stems (Bond, 1983). *A. 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 (pers. obs.).

### 6.4. 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. *Aloe reitzii*), and occasionally on cliff faces where fires cannot reach (e.g. *Aloe 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).

### 6.5. 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. *Aloe 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*, *Aloe juddii* and *Aloe gracilis* var. *decumbens* are endemic to the Cape fynbos, and all three are fire-tolerant (McDonald, 1994; Van Jaarsveld and Deacon, 2010; Van Jaarsveld and Struck, 1996). The remaining rambling aloes are found predominantly in the Thicket Biome of the Eastern Cape where fires are infrequent (Smith and Van Wyk, 2009; Van Wyk and Smith, 2008); 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).

## 7. Resprouting

### 7.1. Multi-stemmed and tree aloes

While aloes are generally known to respond to damage to plant organs by increasing growth and suckering (Wabuye 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. *A. 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 *Aloe 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. Cernus, 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).

### 7.2. 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 (Parker and Bernard, 2008, 2009; Penzhorn et al., 1974). 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.

### 7.3. 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.). *A. 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*, *Aloe commixta*, *A. gracilis*, *A. juddii*, *Aloe striatula* and *Aloe tenuior*) are generally fast-growing and most appear to be resprouters (Van Jaarsveld, 1989) (Table 1). *A. 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; Smith and Van Wyk, 2009; Van Jaarsveld and Deacon, 2010; Van Jaarsveld and Struck, 1996). 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 (Craib, 2005; Van Jaarsveld, 1989). 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.

## 8. Pollination ecology

### 8.1. 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 therefore dependent on animal floral visitors for pollination and seed set (Botes et al., 2009a; Hoffman, 1988). 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 (Beylerveld, 1973; Botes et al., 2008; Nicolson and Nepi, 2005). Few aloes produce fragrant flowers, and *Aloe 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 exerted 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). *A. 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 (Hoffman, 1988; Oatley, 1964; 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 *Aloe 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).

### 8.2. 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 (Botes et al., 2009a; Hargreaves et al., 2008; Hoffman, 1988) (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. *Aloe suffulta*), and flowers with stamens and style exerted far from the perianth (e.g. *Aloe sessiliflora*). Some small grass aloe species that produce short-tubed, white or cream-coloured flowers such as *A. inconspicua*, *Aloe minima* and *Aloe linearifolia* are exclusively insect (bee) pollinated (Botes et al., 2009b; Hargreaves et al., 2008). However, bees appear to make relatively small contributions to seed production in other 'ornithophilous'

**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).

<i>Aloe</i> species	Distribution <sup>a</sup>	Inflorescence description <sup>a</sup>	Flowering time <sup>a</sup>	Pollinators and visitors	Reference
<b>Tree aloes</b>					
<i>A. barberae</i>	South Africa: EC, MP, KZN; Swaziland; Mozambique	Branched panicle 40–60 cm long; densely-flowered racemes 20–30 cm 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)
<i>A. dichotoma</i>	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 ( <i>Apis mellifera</i> ) Sunbird spp.	Tribe and Johannsmeier (1996); Van Jaarsveld (2010) Van Jaarsveld (2010)
<i>A. emimens</i>	Somalia	Branched 50–60 cm long candelabriform panicle; racemes 16 cm long & subdensely flowered; flowers glossy red <sup>b</sup>	March (southern hemisphere)	Short-billed generalist nectarivores (Weavers, White-eyes & Starlings); Sunbird spp. & honeybees ( <i>Apis mellifera</i> ) Malachite Sunbirds & bees	Tribe and Johannsmeier (1996)
<i>A. pillansii</i>	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 ( <i>Apis mellifera</i> )	Tribe and Johannsmeier (1996)
<i>A. picatilis</i>	South Africa: WC	Single laxly-flowered racemes with up to 30 tubular, scarlet flowers	August–October	Short-billed generalist nectarivores (Weavers, White-eyes & Starlings); Sunbirds & honeybees ( <i>Apis mellifera</i> ) Sunbird spp.	S.R. Cousins (unpublished data) Tribe and Johannsmeier (1996)
<i>A. ramosissima</i> <sup>c</sup>	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 ( <i>Apis mellifera</i> ) Sunbird spp.	Van Jaarsveld (2010)
<i>A. tongaensis</i>	South Africa: KZN; southern Mozambique	Cylindrical, 47–50 cm long; distinctly inward-curved; outer segments fused in lower half; flowers yellowish orange, vertically presented <sup>d</sup>	April & May	Short-billed generalist nectarivores (Weavers, White-eyes & Starlings); Sunbirds & honeybees ( <i>Apis mellifera</i> ) Sunbird spp.	Van Jaarsveld (2010)
<b>Single-stemmed aloes</b>					
<i>A. africana</i>	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 ( <i>Apis mellifera capensis</i> ) & Short-billed Weavers (destructive foragers)	Botes et al. (2009a)
<i>A. ferox</i> [= <i>A. candelabrum</i> ]	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 ( <i>Apis mellifera</i> ). Sweet bee spp., Formicine ants, Chalcid wasps & Hover flies Bees & (Sunbirds & other bird spp.) <sup>*</sup> Pollen-collecting bees, Nectar-collecting bees & Cape honeybees ( <i>Apis mellifera capensis</i> ) Birds <sup>e</sup> : Primarily Malachite Sunbirds, Streaky-headed Seedeaters, Weavers, Karoo Prinia & Red-faced Mousebirds, Insects: Cape honeybees ( <i>Apis mellifera capensis</i> ) & Solitary bees (primarily <i>Lasioglossum</i> sp.)	Hoffman (1988) Stokes and Yeaton (1995) Botes et al. (2009a); Forbes et al. (2009)
<i>A. lineata</i> var. <i>muirii</i>	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 ( <i>Apis mellifera capensis</i> ), solitary bees (Primarily <i>Lasioglossum</i> sp.) & unidentified bird spp.	Botes et al. (2009a)
<i>A. marlothii</i>	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 <sup>f</sup>	Symes et al. (2008)
<i>A. pluridens</i>	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 ( <i>Apis mellifera capensis</i> ) & unidentified bird species	Botes et al. (2009a)
<i>A. vryheidensis</i>	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 exerted stamens	July & August	Dark-capped Bulbuls, Cape White-eyes, Streaky-headed Canaries, Buff-streaked Chats, Cape Rock thrushes, Greater Double-collared Sunbirds <sup>g</sup> , honeybees ( <i>Apis mellifera</i> ) & Halictid bees	Johnson et al. (2006)

<b>Multi-stemmed aloes</b>							
<i>A. divaricata</i>	Madagascar	Laxly flowered, much-branched, pyramidal panicle up to 1 m tall; flowers reddish-scarlet <sup>b</sup>	April	Sunbirds* ( <i>Nectarinia souimanga</i> ; & stingless bees ( <i>Trigona</i> sp.))	Ratsirarson (1995)		
<b>Stemless aloes</b>							
<i>A. peglerae</i>	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 Seedeaters	Arena et al. (submitted for publication)		
<b>Spotted aloes</b>							
<i>A. greebathedii</i> var. <i>danyana</i>	South Africa: LP, MP, NW, GP, KZN & FS	Up to four inflorescences reaching heights of 1.5 m with up to six branches bearing pale pink to red flowers	June & July	Honeybees ( <i>Apis mellifera</i> )* & Sunbirds	Symes et al. (2009); H. Human, (unpubl. data)		
<i>A. pruinosa</i>	South Africa: KZN	Single much-branched inflorescence reaching 2 m, bearing dark pinkish flowers with a constriction in the middle, and a basal swelling	February & March	Amethyst Sunbirds, honeybees ( <i>Apis mellifera</i> ) & membrane bees (Colletidae)	Wilson et al. (2009)		
<b>Grass aloes</b>							
<i>A. inconspicua</i>	South Africa: KZN	Simple, cylindrical, densely-flowered raceme bearing erect, more or less stalkless, green & white flowers	November	Primarily Solitary bees (mainly female <i>Amegilla fallax</i> )* & an unidentified <i>Pseudapis</i> sp. (Halictidae)	Hargreaves et al. (2008)		
<i>A. linearifolia</i>	South Africa: southern & central KZN	Single head-shaped raceme with short greenish-yellow to pure yellow tubular flowers	February & March	Primarily Solitary and Sub-social bees* & <i>Megachile</i> bees (refer to Table 2 in Botes et al. (2009a,b) for full list of species)	Botes et al. (2009b)		
<i>A. minima</i>	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)		
<i>A. modesta</i>	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)		

<sup>a</sup> Van Wyk and Smith (2008).

<sup>b</sup> Reynolds (1966).

<sup>c</sup> 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.).

<sup>d</sup> Van Jaarsveld (2010).

<sup>e</sup> Only the five most commonly observed bird species for *A. ferax* 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).

<sup>f</sup> 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.

<sup>g</sup> Only one Greater Double-collared Sunbird was observed feeding at an *A. vryheidensis* individual in this study (Johnson et al., 2006).

(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).

## 9. Seed biology

### 9.1. Seed production and dispersal

Aloe fruits are typically three-angled oblong capsules which dry and dehisce when ripe (Jordan, 1996; Kamstra, 1971). The capsules generally house a number of two-winged, wind-dispersed seeds (Jordan, 1996; Kamstra, 1971; Van Jaarsveld, 1989). 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 rainfall availability, 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). *A. 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.

### 9.2. 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: *Aloe 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.

## 10. Economic botany

### 10.1. 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; Low et al., 2006; Smith, 1993; Van Wyk and Smith, 2008). The laxative property of the bitter resinous juice in the leaves of the renowned Socotra aloe, *Aloe 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). *A. 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 (Grace, 2011; Grace et al., 2008, 2009; Shackleton and Gambiza, 2007). Other species wild-harvested and/or cultivated in East Africa include *Aloe marsabitensis*, *Aloe ngongensis*, *Aloe rabaiensis* and *Aloe 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 (Dagne et al., 2000; Klein and Penneys, 1988). The gel possesses moisturizing and emollient properties and is used in a range of cosmetic products, shampoos and skincare creams (Dagne et al., 2000; Grace, 2011; Klein and Penneys, 1988). 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 (Dagne et al., 2000; Grace, 2011; Klein and Penneys, 1988). 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 (Grace et al., 2009, 2008; Low et al., 2006). 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 (Campbell-Barker, 2009; Nyika, 2007). 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 (Grace et al., 2009; Lane, 2004; McCoy, 2007; Smith and Van Wyk, 2009; Watt and Breyer-Brandwijk, 1962). 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 (Grace et al., 2009; Watt and Breyer-Brandwijk, 1962). 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 (Human and Nicolson, 2008; Nepi et al., 2006).

### 10.2. Aloes in African traditional medicine

Aloes are also harvested and utilized for traditional medicine in numerous African countries (Hutchings, 1996; Neuwinger, 1996; Von Ahlefeldt et al., 2003; Von Koenen, 2001; Williams et al., 2001), 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 *Aloe aristata* and *Aloe 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). *A. 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).

### 10.3. The horticultural trade in aloes

Aloes have 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, 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; Gildenhuis, 2005; Mofokeng and Jiwen, 2009; Pfab and Scholes, 2004). 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 curbed 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 (Grace, 2011; Newton and Chan, 1998).

#### 10.4. 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 (Wabuye and Kyalo, 2008; Wabuye et al., 2006). 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 (Wabuye and Kyalo, 2008).

The Kenya Aloe Working Group was also initiated to promote the cultivation of key species used for leaf exudate and mesophyll (Grace, 2011; Wabuye and Kyalo, 2008). 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.

## 11. Aloe conservation

### 11.1. 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 *A. 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 (Grace, 2011; Myers et al., 2000). 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.

### 11.2. 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 (Grace et al., 2009; Smith et al., 2000). 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; Mofokeng and Jiwen, 2009; Pfab and Scholes, 2004; Van Wyk and Smith, 2008). Furthermore, the threats faced by many taxa are exacerbated by their naturally restricted distributions (Holland, 1978; Newton and Vaughan, 1996). As is the case with cycads, this situation 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).

### 11.3. 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 (Kew Royal Botanic Gardens (KRBG), Madagascar Aloe Conservation Project (MACP), 2012; Medhanie and Dioli, 2006). 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 *Aloe suzannae* and *Aloe 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.

## 12. 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 is 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. Finally, undertaking ecological research in understudied aloe diversity hotspots such as east and west Africa and Madagascar is essential to the conservation of the aloes in these regions.

## Acknowledgements

The NRF (NRF64704), the South African National Biodiversity Institute (SANBI) and Michèle Pfab (SANBI) are thanked for providing funding. Thanks go to Ronell Klopper, Ernst Van Jaarsveld and Gideon Smith (SANBI) as well as Craig Symes (University of the Witwatersrand, Johannesburg) for providing several references, photographs and valuable correspondence. Jolene Fisher and Kaera Coetzer are thanked for their assistance with producing the distribution map.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.jaridenv.2012.03.022](https://doi.org/10.1016/j.jaridenv.2012.03.022).

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