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Article in *South African Journal of Botany* · April 2013

DOI: 10.1016/j.sajb.2013.02.174

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

S.R. Cousins ^{a,*}, E.T.F. Witkowski ^a, M.F. Pfab ^{a,b}, R.E. Riddles ^c, D.J. Mycock ^a

^a School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa

^b South African National Biodiversity Institute (SANBI), Private Bag X101, Pretoria 0001, South Africa

^c South African National Biodiversity Institute, Karoo Desert National Botanical Garden, P.O. Box 152 Worcester, 6849, South Africa

ARTICLE INFO

Article history:

Received 21 September 2012

Received in revised form 31 January 2013

Accepted 27 February 2013

Available online xxx

Edited by A Pauw

Keywords:

Allee effect

Dispersal

Flowers

Fruit set

Pollination

Seeds

Seed banks

ABSTRACT

While the pollination ecology of many *Aloe* species is well-documented, knowledge on aloe seed ecology, and hence aloe reproductive ecology in its entirety is limited. The aim of this study was to investigate the reproductive ecology of *Aloe plicatilis*, a Cape fynbos tree aloe endemic to the Cape Winelands, South Africa. Results from a pollinator exclusion experiment conducted at an *A. plicatilis* population on Paarl mountain suggests pollination primarily by insects, although bird visitation significantly increased seed set/fruit indicating possible co-pollination with insects. The species' long-tubed flowers and production of concentrated nectar, with observations of malachite sunbirds as the most common avian visitors to *A. plicatilis* flowers indicate the importance of long-billed specialist avian nectarivores as floral visitors. Analysis of the relationship between plant size and inflorescence production for five populations combined revealed a significant, positive linear relationship between plant size and the logarithm of the number of inflorescences/plant. Natural fruit and seed set determined for three populations (1325, 27,930 and 251,616 seeds/population) suggests low reproductive output compared to several other *Aloe* species. The smallest (31 individuals) and least dense (75 plants/ha) *A. plicatilis* population produced the lowest seed set/plant (128 seeds) and per population (1325 seeds), suggesting an Allee effect. Evaluation of seed dispersal potential showed that potential dispersal distances were approximately three times the canopy height; however, the occurrence of *A. plicatilis* on mountains isolated from more continuous mountain ranges on which the species also occurs suggests the possibility of long-distance dispersal by strong, gusty, summer winds. Soil seed bank samples collected from 13 populations yielded close to zero seedling emergence, indicating the absence of persistent seed banks. *A. plicatilis* seeds stored under ambient laboratory conditions for 3, 18 and 24 months were germinated in an environmental control chamber and a laboratory. High percentage germination was recorded for 18- and 24-month-seed (86 and 80%, respectively), while germination of 3-month-old seeds was three times lower, suggesting the need for after-ripening. Germination of fresh and one-year-old seed under ambient nursery conditions at the Karoo Desert National Botanical Garden in Worcester yielded emergence percentages of 67 and 44%, respectively, and were therefore less successful than germination under more controlled conditions. This is the first known study to investigate the reproductive ecology of a tree aloe species and that of a Cape fynbos aloe. The study highlights the importance of further studies on aloe seed ecology, particularly for rare and threatened species.

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1. Introduction

Knowledge of plant reproductive ecology is key to understanding many community processes such as regeneration, establishment, succession and alien species invasion, as well as species survival strategies and causes of rarity (Grubb, 1977; Bazzaz, 1979; D'Antonio, 1990; Guterman, 1994; García-Fayos and Verdú, 1998; Kaye, 1999). Pollination, which is an integral part of plant reproductive ecology, deals with pollination strategies, flowering phenology and patterns of nectar, fruit and seed production (Lovett Doust and Lovett Doust,

1988), while seed ecology covers dispersal, dormancy and germination (Fenner and Thompson, 2006). The persistence of a plant population is a product of its constituent individuals' collective reproductive success which, in turn, is affected by factors such as plant morphology (size, shape and positioning of plant parts), competition, herbivory, population size and density, and the availability of pollen for fertilization and resources for seed production (Lovett Doust and Lovett Doust, 1988; Stephens et al., 1999; Mustajärvi et al., 2001; Wilcock and Neiland, 2002).

Each species possesses a suite (or syndrome) of floral traits that suggests adaptation to a particular mode of pollination, either self- or cross-pollination (Fægri and van der Pijl, 1979; Primack, 1987; Dafni, 1992; Fenster et al., 2004). Descriptions of syndromes emphasize

* Corresponding author. Tel.: +27 735021425 (mobile).
E-mail address: steevyc@gmail.com (S.R. Cousins).

characteristics such as flower colour, odour, size, shape, rewards, and timing of anthesis (Primack, 1987; Dafni, 1992). Flowers pollinated by energy-demanding vertebrates such as birds and bats are generally large and produce copious amounts of food rewards, while flowers visited by small insects tend to be smaller and produce less food rewards (Primack, 1987). Individual plant species are associated with a particular pollination system that occurs along a continuum from generalized (hundreds of pollinator species) to extremely specialized (a single pollinator species) (Johnson and Steiner, 2000). Most animal-pollinated plants exhibit moderate to highly generalized pollination systems (Waser et al., 1996); however, there is a growing body of literature documenting very specialized pollination systems in the tropics and in the species-rich temperate flora of South Africa (see citations in Johnson and Steiner, 2000). Although floral syndromes may provide clues about potential pollinators, they do not necessarily provide a fool-proof means of predicting all a species' floral visitors, and visitors that do not match the species' floral syndrome may still be important and should not be overlooked (De Merxem et al., 2009).

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

Sometimes dispersed seeds germinate immediately, but in most cases there is a delay, which is brought about either by quiescence or dormancy (Fenner and Thompson, 2006). Wild plant populations often form stores of dormant or quiescent seeds in seed banks, which may last for long periods of time, with intermittent germination of part of the seed bank (Murdoch and Ellis, 2000). Dormancy is caused by a block to germination within an imbibed seed (Murdoch and Ellis, 2000). Thus, dormancy is a temporary failure of a viable seed to germinate after a specified period of time under a particular set of environmental conditions (e.g. moisture availability and temperature) that later induce germination when the restricted state has been terminated by either natural or artificial means (Vleeshouwers et al., 1995). Quiescent seeds, on the other hand, are those that remain ungerminated because the environmental conditions favourable for radicle emergence and seedling growth are lacking (Murdoch and Ellis, 2000). Seed banks comprising dormant or quiescent seeds may be transient (persisting in the soil for <1 year), short-term persistent (1–5 years) or long-term persistent (>5 years) (Bakker et al., 1996). Following this inactive state, the successful germination and survival of a proportion of seedlings is crucial for the persistence of plant populations, and underpins the development and sustainability of plant communities (Murdoch and Ellis, 2000; Leck et al., 2008).

The Allee effect is a phenomenon of prime importance when investigating reproductive ecology in plant populations, particularly in studies on species with small, sparse and/or fragmented populations and which rely on animal vectors for pollination (Stephens et al., 1999). The Allee effect refers to a positive relationship between any component of individual fitness (e.g. probability of reproducing

or dying) and either numbers or density of conspecifics (Stephens et al., 1999; Berec et al., 2007). Decreases in the fitness of individuals often occur in small and/or sparse populations as population size and/or density decline (Berec et al., 2007; Kramer et al., 2009). Plants in such populations tend to receive fewer visits from pollinators, which may not only result in lower seed set (e.g. Lamont et al., 1993a), but also inbreeding depression (e.g. Groom, 1998). If populations drop below the Allee threshold – the size or density at which population growth rate becomes negative (Berec et al., 2007) – this can have dire consequences for the persistence of rare and threatened species.

Aloe L., is the largest genus in the Asphodelaceae, a family of succulent-leaved, petaloid monocots (Smith and Van Wyk, 2009), found primarily on the African continent (see distribution map in Cousins and Witkowski, 2012). With ± 140 *Aloe* species, South Africa has the highest aloe diversity of any African country (Klopper et al., 2009). Aloes produce tubular flowers on many-flowered spikes, simple racemes, or compound racemes, which tend to be densely flowered and brightly coloured (Smith and Van Wyk, 2009). Aloes are generally self-incompatible and therefore reliant on animal floral visitors for pollination and seed set (Hoffman, 1988; Botes et al., 2009). Many *Aloe* species attract insect and bird pollinators by supplying abundant nectar primarily during winter, when alternative food sources are scarce (Beyleveld, 1973; Nicolson and Nepi, 2005; Botes et al., 2008; Symes and Nicolson, 2008; Forbes et al., 2009; Symes et al., 2011). Studies on several *Aloe* species have confirmed the existence of extensive bird pollination systems in the genus (e.g. Hoffman, 1988; Ratsirarson, 1995; Johnson et al., 2006; Forbes et al., 2009; Botes et al., 2008; Symes and Nicolson, 2008; Arena et al., 2013). Avian pollinators are either specialist or opportunistic nectarivores, which may be filtered by specific floral traits, especially nectar properties (Johnson and Nicolson, 2008). Botes et al. (2008) showed that aloes that produce long-tubed flowers with small quantities of comparatively concentrated nectar are associated with specialist long-billed sunbirds as pollinators, while those producing short-tubed flowers that yield large volumes of relatively dilute nectar are generally pollinated by short-billed occasional nectarivores.

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

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

Studies on aloe reproductive ecology have focused primarily on pollination and to a much lesser degree on seed ecology (Smith and Correia, 1992; Symes, 2012; Arena et al., 2013). Fewer still, have addressed aloe reproductive ecology in its entirety, from pollination through to germination. Hence, there is a paucity of information on several aspects of aloe seed ecology, including dispersal, dormancy, longevity, seed banks, and germination. The aim of this study was to investigate the reproductive ecology of *Aloe plicatilis* (L.) Mill., a fynbos tree aloe endemic to the Cape Winelands, South Africa. The objectives were to (a) determine the primary pollinator guild of the species, (b) quantify natural fruit and seed set, (c) conduct tests for the presence of seed banks, (d) investigate seed dispersal potential, and (e) conduct germination studies on fresh and stored seeds.

2. Materials and methods

2.1. Study species and area

A. plicatilis (L.) Mill. (Asphodelaceae: Aloioideae) is one of six tree aloes indigenous to South Africa and the only tree aloe that occurs in the Cape fynbos (Van Wyk and Smith, 2008). The species has a restricted distribution in the mountainous parts of the Cape Winelands (also known as the “Boland”) in the south-western Cape (Fig. 1). The region is characterized by a Mediterranean climate with hot, dry summers (average midsummer temperatures = 15–25 °C) and cool, wet winters (average midwinter temperatures = 7–15 °C) (Manning, 2007). *A. plicatilis* grows in well-drained, acidic soils on steep rocky slopes and outcrops that offer protection from fires (Van Jaarsveld, 1989; Carter et al., 2011). The Cape fynbos has a crown fire regime, with fires occurring primarily during summer, at intervals of 10–30 years depending on the vegetation type (Keeley et al., 2012). *A. plicatilis* occurs at altitudes of 200–950 m, with average monthly wind speeds of 4.5–10.4 km/h and average annual rainfall and temperatures of 420–1900 mm/year and 14–18 °C, respectively (Cousins et al., submitted). *A. plicatilis* is relatively long-lived and slow-growing, with dichotomously branching stems, each of which ends in a set of 12–16 alternate, succulent leaves in a fan-like arrangement (Van Wyk and Smith, 2008; Carter et al., 2011) (Fig. 2c,d). Most *A. plicatilis* individuals reach reproductive maturity at ~15 cm stem diameter and ~0.8 m in height (Cousins et al., submitted). Adult plants average ~1.5 m in height, but exceptionally large individuals may reach up to 5 m (Van Wyk and Smith, 2008).

The flowers are simple, cylindrical and slightly acuminate, ± 5 cm long and scarlet in colour, arranged in laxly flowered racemes (25–30 tubular flowers/raceme) that are 15–25 cm long (Reynolds, 1969) (Fig. 2a,f). *A. plicatilis* flowers from August–October (occasionally November) and the fruiting season starts in early November, with fruit capsules dehiscing from December to January (Van Wyk and Smith, 2008). The fruits are longitudinally-dehiscent capsules, approximately 20 mm long and 16 mm in diameter (Killick, 1988) (Fig. 2d). They are green with a pinkish tinge when fresh and pale manila-coloured when dehiscent (Killick, 1988). The winged seeds are dark brown to black (Killick, 1988).

2.2. Pollination ecology

A pollinator exclusion experiment was conducted at an *A. plicatilis* population on Paarl Mountain (W1, Figs. 1 & 2b) in order to determine whether the species is predominantly bird- or insect-pollinated. Three treatments were applied to three different inflorescences on 17 plants: total exclusion, partial exclusion and a control (Fig. 2b). Exclusion of all potential visitors (i.e. birds, insects and mammals) was achieved by placing a fine gauze bag (± 0.25 mm mesh shade cloth) over each inflorescence and the leaf cluster from which it emerged. For the partial exclusion treatment, a cage made of rigid ± 2 cm gauge wire mesh was placed around the inflorescences,

allowing unrestricted access by bees and other insects, but excluding birds and small mammals. The control involved marking one inflorescence with identifying tape on each individual sampled, allowing unrestricted access by all floral visitors. The experiment commenced at the onset of the flowering season in August 2010 when flowers were at the bud stage so as to avoid any temporal bias. The plants were revisited during the fruiting season in December 2010 to collect the fruits and determine fruit and seed set. Fruit set was calculated as the percentage of pedicels on each inflorescence that bore fruit (which included both visible remains of pedicels and evidence of pedicels as scars on the raceme where flowers were attached). Seed set was determined per inflorescence and per fruit by counting the number of seeds per fruit for all fruits present on the inflorescence.

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

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

2.3. Relationship between plant size and inflorescence production

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

2.4. Natural fruit and seed set

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

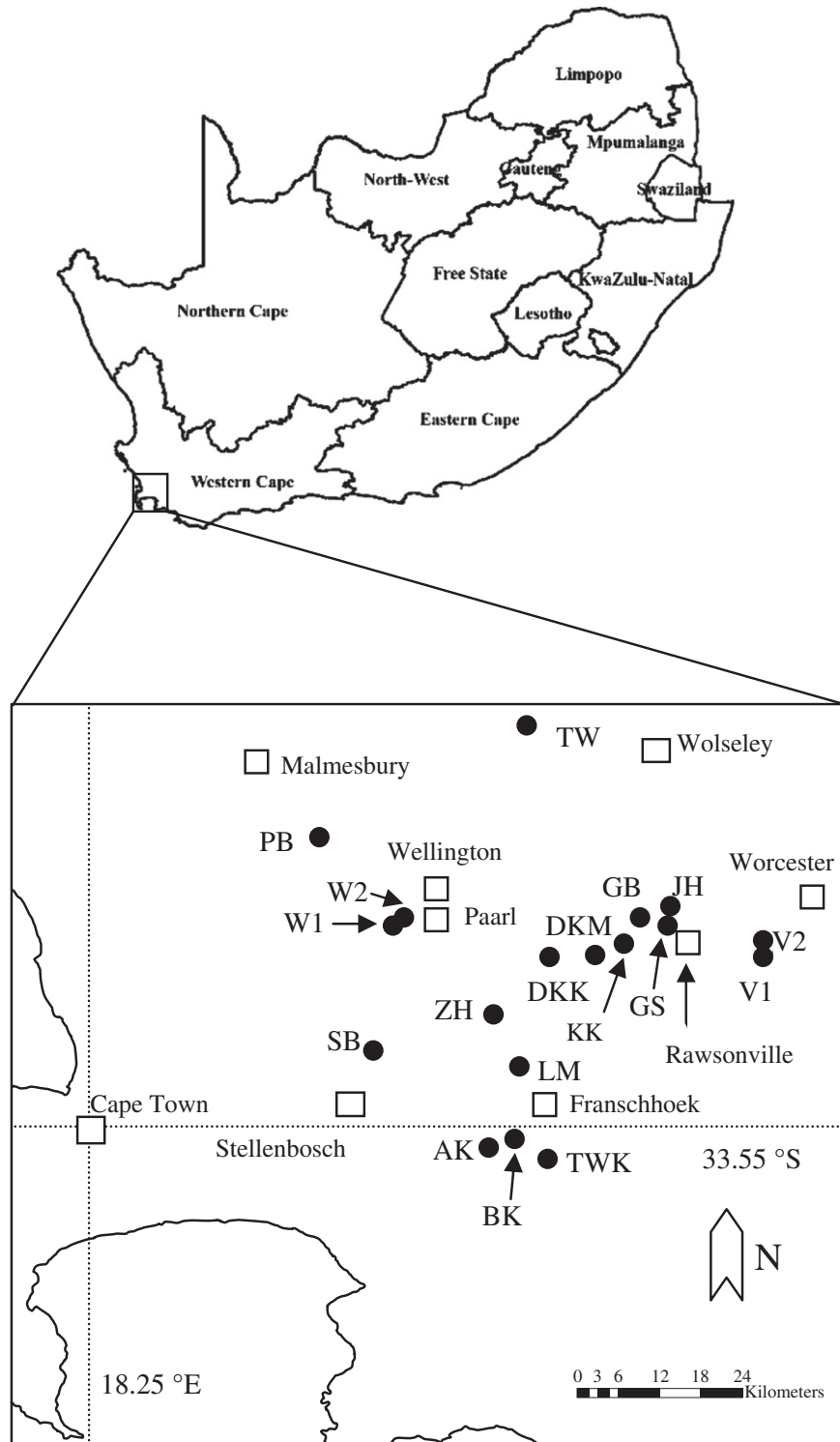


Fig. 1. Distribution map of *Aloe plicatilis* in the south-western Cape, South Africa, showing the populations sampled in this study. Population abbreviations: AK = Assegaaiboskloof, BK = Bosjemanskloof, DKK = Du Toit's Kloof Krom River, DKM = Du Toit's Kloof Molenaar's River, GB = Goudini Badsberg,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

2.5. Seed dispersal potential

Fresh *A. plicatilis* seeds were collected from PB in January 2012 to investigate seed dispersal potential. In May 2012, thirty seeds were weighed and their terminal velocity determined as an index of air lift for ease of dispersal using the method in Lamont et al. (1993b). The seeds were dropped individually from a height of 3 m in still air, while two observers measured the time taken for each seed to

reach the ground using a stopwatch accurate to 0.01 s. Data on wind speed and direction at seven stations within the distribution of *A. plicatilis* were obtained from the Agricultural Research Council of South Africa. Potential dispersal distances were calculated for *A. plicatilis* individuals of three different sizes (a) the mean height at which the onset of reproductive maturity occurs i.e. 0.8 m, (b) the maximum recorded height for *A. plicatilis*, i.e. 4.0 m (Cousins et al., submitted) and (c) the mean height of flowering individuals

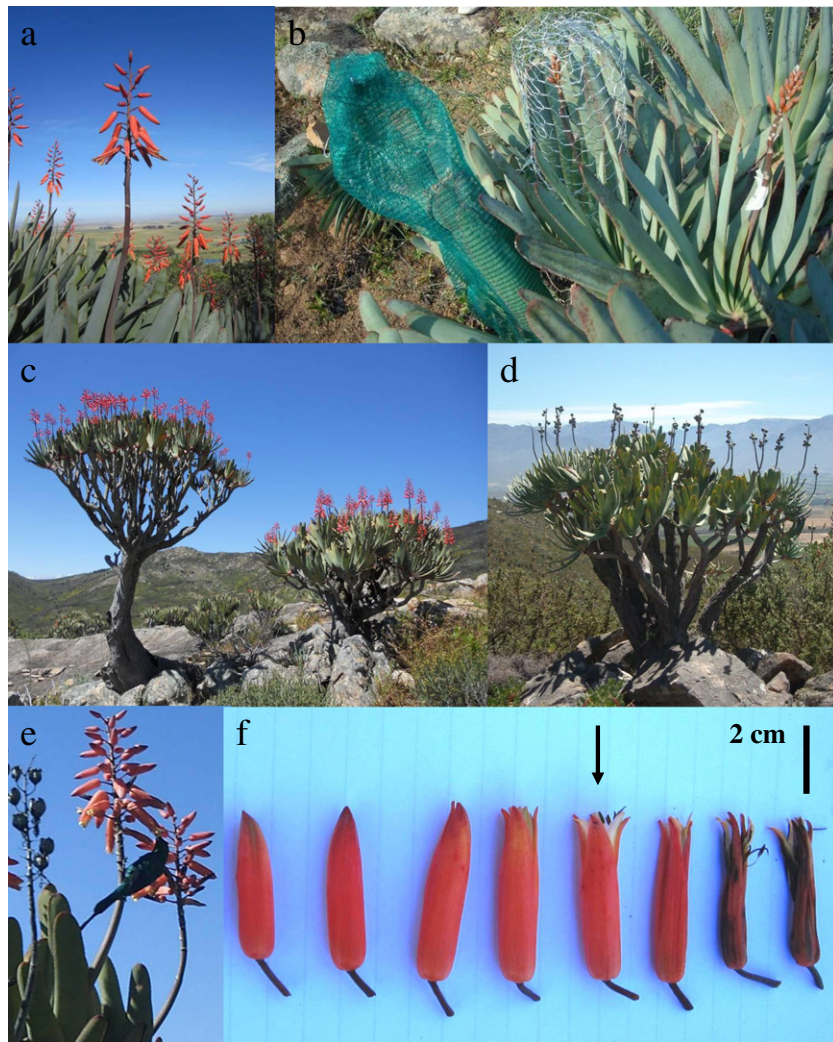


Fig. 2. (a) Close-up of mature *Aloe plicatilis* inflorescences taken at W1 on Paarl Mountain, south-western Cape, South Africa. (b) The three pollinator exclusion treatments applied to an *A. plicatilis* individual at W1. From left to right: 'no visitors' (± 0.25 mm mesh bag), 'insects only' (± 2 cm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

calculated using height measurements and flowering data from V1, DKK, DKM, GS and GB. Dispersal distances were estimated using the following formula from Stokes and Yeaton (1995):

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

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

2.6. Soil seed banks

The presence of soil seed banks was determined on two separate occasions for a total of 13 populations. The first set of soil samples was collected from four populations (DKK, DKM, JH and W2) during the dry season in December 2010 – one year post-dispersal in 2009 and shortly pre-dispersal in 2010. The second set was collected from nine populations (AK, BK, GB, LM, SB, TK, TWK, V2 and ZH) during the rainy season in June 2011 – six months after seed dispersal in 2010. Samples were collected from beneath the canopies of five large

reproductively mature individuals at each population. The soil was placed in seedling trays in the greenhouse at the University of the Witwatersrand, Johannesburg, within two to three weeks of collection. Shade cloth (30%) was placed over the glass roof of the greenhouse and plants were watered to saturation using automatic watering set at approximately 10 min once a day. Emergence of *A. plicatilis* seedlings was observed once a week over a period of six months.

2.7. Germination experiments

2.7.1. Germination under controlled and ambient laboratory conditions

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

The water content of a subset of 100 seeds from KK was determined on a fresh mass basis in the first week of March 2011. Seeds were weighed on a *Precisa 925M-202A* scale correct to four decimal places, and then reweighed after oven-drying at 80 °C for 24 h (a temperature and duration similar to those used for determining the water content of other orthodox seeds e.g. Hay and Probert (1995) and Farrant and Walters (1998)).

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

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

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

Germination rate as mean weeks to germination for each treatment was calculated using the formula:

$$\text{Mean weeks to germination} = \frac{\sum_{i=1}^n (q.i)}{N},$$

where n = total number of weeks, q = number of seeds germinated in the i th week, i = number of weeks and N = total number of seeds tested.

2.7.2. Germination under ambient nursery conditions

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

09 h00 and 14 h00 using a mist irrigation system. Temperatures during the germination period ranged between <20 °C and 38 °C and relative humidity between 25 and 50%. The total number of emerged seedlings was determined on 25 June 2012.

2.8. Statistical analyses

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

3. Results

3.1. Pollination ecology

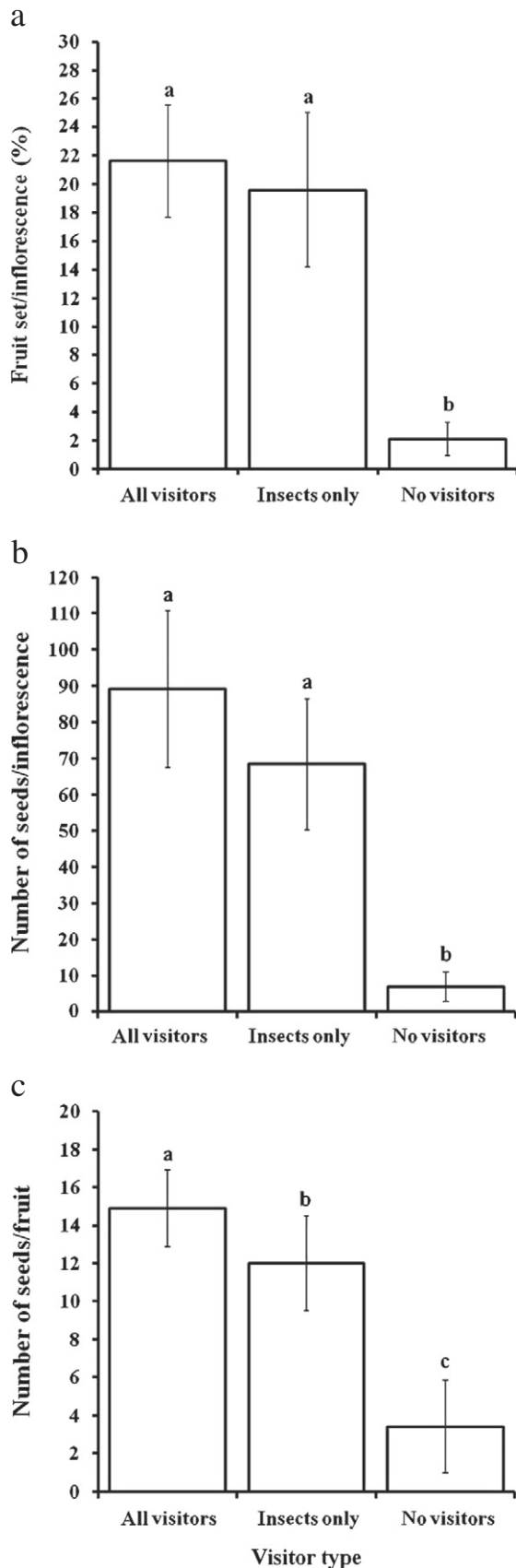
Fruit set/inflorescence differed between treatments ($F_{2,51} = 8.46$, $p = 0.0007$), being significantly lower for inflorescences where all visitors were excluded. Exclusion of birds and mammals did not affect fruit set/inflorescence (Fig. 3a). Seed set/inflorescence followed the same pattern as fruit set ($F_{2,48} = 6.77$, $p = 0.003$), with the 'all visitors' and 'insects only' treatments both being significantly higher than the 'no visitors' treatment (Fig. 3b). Seed set/fruit also differed between treatments ($H_{2,51} = 12.19$; $p = 0.0023$), with 'all visitors' being significantly higher than both 'insects only' and 'no visitors' and 'insects only' significantly higher than 'no visitors' (Fig. 3c). The only bird species observed visiting *A. plicatilis* flowers were three individual malachite sunbirds (*Nectarinia famosa*), one each at GB, PB and W1 (Fig. 2e). Numerous bees were observed entering *A. plicatilis* flowers at GB, one of which was identified as a honeybee (*Apis mellifera*). A single monkey beetle species (Scarabeidae, Tribe Hopliini) and a second unidentified beetle species were observed on two different *A. plicatilis* flowers at W1. Mean standing crop nectar concentration at PB was significantly higher than at W1 (PB: $30.8 \pm 7.91\%$, range = 21.0–46.0%; W1: $15.8 \pm 3.1\%$, range = 9.5–21.5%) ($t_{41} = 7.45$; $p < 0.0001$). Overall nectar concentration for PB and W1 combined was $28.1 \pm 12.0\%$.

3.2. Relationship between plant size and inflorescence production

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

3.3. Natural fruit and seed set

There were no significant differences in fruit set/inflorescence between populations (17% at both W1 and GB and 13% at JH) (Table 1). Mean number of seeds/fruit ranged from 7 to 15. Total seed production/inflorescence ranged from 16 at JH to 50 at GB. Flowering



plants were significantly taller at JH than at GB and W1. Mean number of inflorescences/individual ranged from 4 at GB to 8 at JH. W1 showed the highest calculated seed production/population due to its large estimated population size (3527 plants) and high seed production/individual. Calculated seed production/population at JH was lowest because of its small population size (31 plants) and low seed production/individual despite the larger plants (Table 1).

3.4. Seed dispersal potential

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

3.5. Soil seed banks

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

3.6. Germination

Seed water content prior to storage was $6.91 \pm 1.83\%$. Mean weeks to germination for 3-, 18-, and 24-month-old seeds were 0.8, 2.5 and 2.3 weeks, respectively; hence, 3-month-old seeds germinated approximately three times faster than 18- and 24-month-old seeds. Total germination of 3-month-old seeds after six weeks (28%) was approximately one-third that of the 18- and 24-month-old seeds (86% after three weeks and 80% after seven weeks, respectively) (Fig. 5). Nevertheless, the tetrazolium tests showed that 100% of the ungerminated 3-month-old seeds were viable. The percentage of non-viable, empty seeds was similarly low for all three treatments ($\pm 11\%$).

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

4. Discussion

4.1. Pollination ecology

The pollinator exclusion results suggest that *A. plicatilis* is predominantly pollinated by insects. Differences in fruit and seed set/inflorescence were not significant between the 'all visitors' and 'insects only' treatments, which suggests that the contribution of birds to reproductive success is minimal. The relative abundance of honeybees (*Apis mellifera*) observed at GB and the general scarcity of birds at GB, PB

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

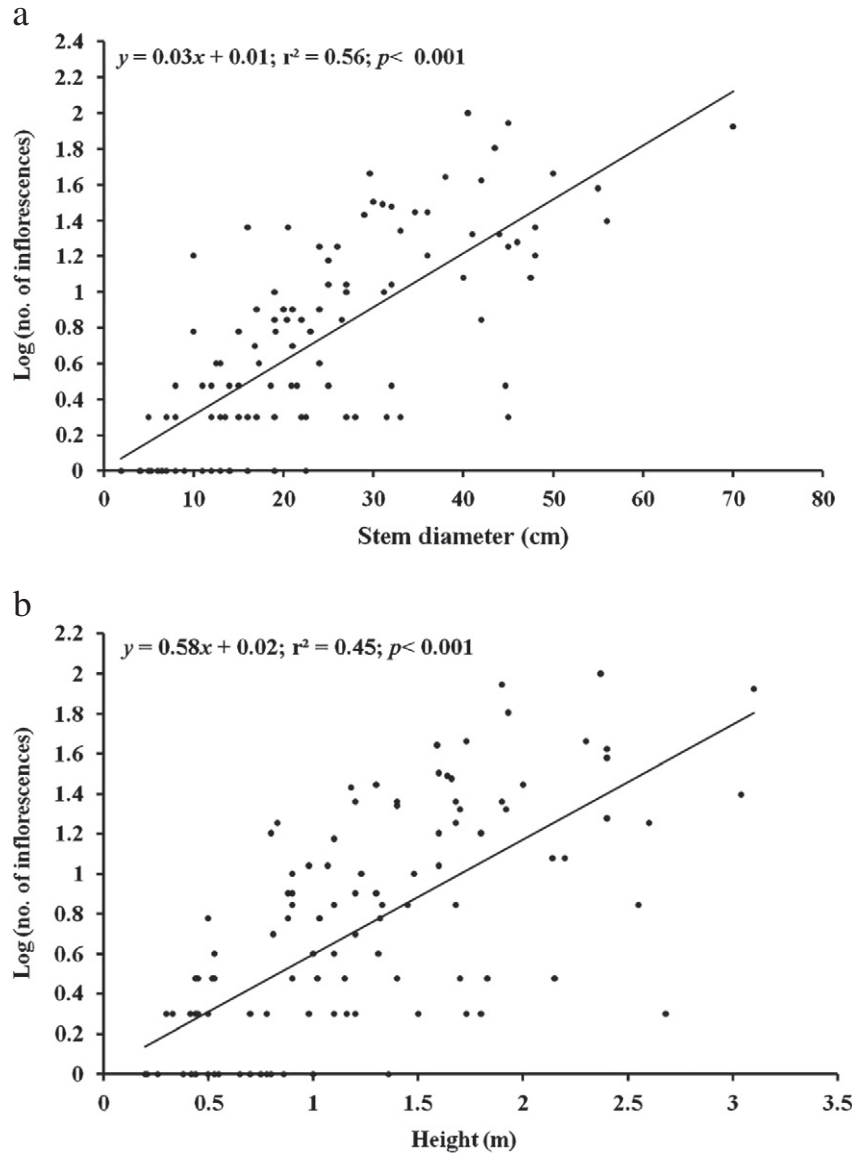


Fig. 4. Relationship between plant size and inflorescences/plant (\log_{10} transformed) for (a) stem diameter and (b) height, from the five *Aloe plicatilis* populations in the south-western Cape, South Africa, where data on flowering were available (DKK, DKM, GB, GS and V1), combined.

and W1 would appear to support this interpretation. Other insects such as the two beetle species observed at W1 may also supplement pollination in *A. plicatilis*. Symes et al. (2009) showed that honeybees were largely responsible for the pollination of *Aloe greatheadii* var. *davyana* Schönland, and Wilson et al. (2009) confirmed the importance of insects

in the pollination of *Aloe pruinoso* Reynolds. *A. greatheadii* var. *davyana* and *A. pruinoso* were also visited by sunbirds, which would be expected due to their low nectar volumes and high sugar concentrations compared to other *Aloe* species (14.8 μ l and 19.7% for *A. pruinoso*, and 15 μ l and 20% for *A. greatheadii* var. *davyana*) (Human and Nicolson, 2008;

Table 1

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

	Windmeul 1 (W1) (3527 plants)	n	Jason's Hill (JH) (31 plants)	n	Goudini Badsberg (GB) (399 plants)	n	df	F	p
Nearest neighbour distance (m)	2.59 \pm 2.14	85	6.88 \pm 7.91	29	2.33 \pm 2.10	26	2, 137	100.25	<0.001
Pedicels bearing fruit/inflorescence (%)	17 \pm 11	15	13 \pm 17	17	17 \pm 16	13	2, 42	0.51	0.606
Number of seeds/fruit	8 \pm 8	15	7 \pm 12	17	15 \pm 7	13	2, 31	1.86	0.173
Height of flowering individuals (m)	1.37 \pm 0.43	23	1.89 \pm 0.51	14	1.33 \pm 0.39	14	2, 48	7.45	0.002
Number of inflorescences/individual = [A]	6 \pm 5 (1–22)	23	8 \pm 9 (1–32)	14	4 \pm 3 (1–13)	14	2, 48	1.69	0.195
Number of seeds/inflorescence = [B]	41 \pm 51 (6–146)	15	16 \pm 27 (4–84)	17	50 \pm 49 (9–146)	13	2, 42	2.60	0.086
Number of seeds/plant = [A] \times [B] = [C]	246 (41–902)	–	128 (16–512)	–	200 (50–650)	–	–	–	–
Seed production/population = [C] \times (population size) \times (percentage of flowering plants in population)	251,616	–	1325	–	27,930	–	–	–	–

Table 2

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

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

Wilson et al., 2009). Human and Nicolson (2008) emphasise that even when floral characteristics are suggestive of specialist nectarivore pollination (e.g. by sunbirds) (as in *A. greateheadii*, var. *davyana*), honeybees can be the primary pollinators and their contribution to pollination in aloes in general should therefore not be discounted.

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

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

(Van Jaarsveld, 2011), although the three quiver tree species are also visited by sunbirds and honeybees (Tribe and Johannsmeier, 1996).

Geerts and Pauw (2009) showed that a large group of Cape plants with long (35–58 mm) tubular flowers are apparently adapted for pollination exclusively by malachite sunbirds, which also appear to be the most common avian visitors to *A. plicatilis*. The long tube lengths of *A. plicatilis* flowers (\pm 50 mm) are consistent with pollination by long-billed nectarivores, since short-billed nectarivores would be unable to reach the nectar at the base of the flower. The Cape sugarbird (*Promerops cafer*) has a bill equally as long as that of the malachite sunbird (Geerts and Pauw, 2009), and has also been observed visiting *A. plicatilis* flowers (Nicolson and Roets, 2012). Other specialist nectarivores that occur within the distribution of *A. plicatilis* and are therefore possible visitors and/or pollinators include *Cinnyris chalybeus* (southern double-collared sunbird) and *Anthobaphes violacea* (orange-breasted sunbird), while *Zosterops pallidus* (Cape white-eye) is a possible opportunistic nectarivore visitor (Rebello, 1987; Sinclair et al., 2011). However, these three species have comparatively short bills that are unlikely to reach the base of *A. plicatilis* flowers, and possibly rob nectar by piercing through the corolla tube as has been observed in other Cape plant species with similarly long corolla tubes (e.g. *Chasmanthe floribunda* (Salisb.) N.E.Br.) (Geerts and Pauw, 2009).

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

In terms of the potential for self-compatibility in *A. plicatilis*, the total exclusion treatment yielded very low fruit and seed set (mean of 2% fruit set and 7 seeds/inflorescence), which suggests a small degree of autonomous self-pollination. However, low reproductive success at JH suggests an inability to self-pollinate, for if isolated flowering plants were self-compatible, greater fruit and seed set in these individuals would be expected. Self-incompatibility is widespread in the genus *Aloe*; though some recent studies suggest this may not be the case for certain species. Autonomous self-pollination has been observed in *Aloe maculata* All., *Aloe kraussii* Baker, (Hargreaves et al., 2012), and *Aloe peglerae* Schönland (Arená et al., 2013). However, seed set/fruit was very low in all three species, especially *A. maculata* and *A. kraussii* (0.02 and 0.11 seeds/fruit, respectively). While self-compatibility

Table 3

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

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

appears to be possible in *A. plicatilis*, detailed supplemental self- and cross-pollination experiments are necessary to confirm its breeding system.

4.2. Relationship between plant size and inflorescence production

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

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

4.3. Natural fruit and seed set

Natural fruit set at GB, JH and W1 was comparable to that measured for *Aloe divaricata* A. Berger, *Aloe linearifolia* A. Berger and *A. marlothii* (15, 19 and 12–18%, respectively) (Ratsirarson, 1995; Botes et al., 2009; Symes et al., 2009), but was less than half that of *A. greatheadii* var. *davyana*, *A. pruinosa* and *A. peglerae* (45–55, 41 and 40%, respectively) (Symes et al., 2009; Wilson et al., 2009; Arena et al., 2013). Number of seeds/fruit, was, however only comparable to that found for certain grass aloe species e.g. *A. inconspicua*, *A. minima* and *A. linearifolia* (ca. 3.5, 10 and 13.5 seeds/fruit, respectively) (Hargreaves et al., 2008; Botes et al., 2009), and was 2–9 times lower than that of *A. peglerae*, *A. greatheadii* var. *davyana*, *A. marlothii* and *A. pruinosa* (all > 34 seeds/fruit) (Symes et al., 2009; Wilson et al., 2009; Arena et al., 2013). Furthermore, estimated seed production/plant in *A. plicatilis* was far lower than that estimated for *A. marlothii* (95,148 for individuals < 2.5 m and 167,549 for individuals > 2.5 m; Symes, 2012) and *A. peglerae* (3869; Arena et al., 2013). However, all the above-mentioned species are variable in terms of growth form, inflorescence size and shape and number of flowers/inflorescence, making comparisons between species difficult. Nonetheless, seed production in *A. plicatilis*, both at the level of individual fruit and whole plant, does appear to be markedly low relative to the size of flowering individuals.

JH exhibited the highest number of flowers/plant, but also the lowest fruit set/inflorescence and the lowest seed set/plant and per population. At GB and W1, almost all inflorescences on flowering individuals observed during population surveys produced at least one fruit, whereas a remarkably large proportion of inflorescences on most flowering individuals at JH died-back after flowering (i.e. functional in

terms of producing pollen, but not fruiting). Post-survey analyses of fruiting plants at JH for which photographs were available ($n = 8$; 57% of all flowering plants in the population) revealed an average of 63% dead inflorescences/plant, and dead inflorescences comprised 77% of the total number of inflorescences of all eight plants combined. Furthermore, inflorescences that did produce fruit were often highly predated by birds (S.R. Cousins pers. obs.). Due to the uncertainty regarding the season in which the dead inflorescences were produced, only inflorescences that bore at least one fruit were sampled in order to determine fruit and seed set. Thus, while measures of reproductive output at JH were not significantly different from those of GB and W1, the results for JH probably overestimate the overall reproductive success at this population due to the unsampled dead inflorescences. Another indicator of reproductive failure at JH is that recruitment appears to be deficient, as surveys of population size structure (Cousins et al. submitted) revealed steep J-shaped stem diameter and height size class distributions indicating a preponderance of large adults and very little recent recruitment. Furthermore, plants at JH were, on average, 7 m apart, which differed significantly from the much shorter nearest neighbour distances of 2.6 m and 2.3 m measured for W1 and GB, respectively, and JH comprised only 31 plants, compared to ~399 at GB and ~3527 at W1 (Table 1).

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

4.4. Seed dispersal potential

Seed terminal velocity of 2.7 m/s for *A. plicatilis* was comparable to the 2.0 m/s calculated for *Aloe candelabrum* A. Berger seed by Stokes and Yeaton (1995). Potential dispersal distances were similar across the study area within plant height categories, and were approximately three times greater than plant height on average. Direct measurements of wind dispersal of the seeds of many plant species in the field show that most are dispersed very short distances, and usually fall near parent plants (Fenner and Thompson, 2006; Howe and Miriti, 2004; Corlett, 2009). Seed shadow patterns for all modes of dispersal are generally described by negative exponential functions (Willson, 1993), with the modal distance of wind-dispersed seeds being approximately equal to canopy height (Nathan et al., 2002). However, the estimated potential dispersal distances for *A. candelabrum* seeds calculated by Stokes and Yeaton (1995) were three-fold the height of seed release — a result that concurs with that calculated for *A. plicatilis*. This difference may possibly be due to aloe seeds generally possessing wings that aid wind dispersal (Jordan, 1999) and are therefore likely to travel further than seeds without any wind dispersal adaptations.

While short-distance seed dispersal influences the local dynamics of plant populations, long-distance dispersal is integral to their large-scale dynamics (Schurr et al., 2009). The “Cape Doctor”, or south-easterly wind, blows over the south-western Cape during summer, when seed dispersal in *A. plicatilis* occurs, and is known to be persistent

and often very gusty, with gusts of up to 35 m/s (128 km/h) recorded in Cape Town (Kruger et al., 2010). Since the geographical distribution of *A. plicatilis* is very patchy, with many populations separated by large distances, it is possible that these isolated populations arose due to long-distance dispersal events caused by strong gusts of wind. Arguably, isolated *A. plicatilis* populations that occur on continuous mountain ranges such as the Du Toit's Kloof and Franschhoek mountains may once have been connected and subsequently become fragmented due to changing climatic conditions over time (see citations in McLachlan and Clark, 2004).

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

Since *A. plicatilis* occurs exclusively on well-drained, rocky mountain slopes that act as fire refugia, it is unlikely that it historically occurred in the less-rocky lowland fynbos between the Paardeberg, Paarl Mountain and the Du Toit's Kloof/Franschhoek mountains. Furthermore, both the Paardeberg and Paarl Mountain occur north-west of several other large *A. plicatilis* populations (e.g. LM, TWK and ZH), from which seed may have been transported by strong south-easterly winds. Testing this hypothesis may prove challenging, as long-distance dispersal events are very rare and difficult to track (Horn et al., 2001; Nathan et al., 2002), although analyses of population genetic variation (e.g. He et al., 2004) may provide a feasible approach.

4.5. Seed banks and seedling recruitment

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

The Cape fynbos is dominated by sclerophyllous evergreen vegetation that dries sufficiently during the summer dry season to produce a predictable and extended wildfire season (Keeley and Bond, 1997). Many fynbos species (e.g. *Protea* and *Erica*) regenerate 1–2 years post-fire, since fire stimulates flowering, seed release from serotinous cones, and breaks seed dormancy through heat or chemicals in charred wood or smoke (Pierce and Moll, 1994; Keeley

and Bond, 1997). Disturbance-dependent fynbos species typically produce strongly dormant seeds with germination triggered by heat or chemicals, while species with 'disturbance-free' recruitment produce non-refractory seeds that lack deep dormancy and therefore have transient seed banks (Keeley and Bond, 1997). Wabuyele and Kyalo (2008) note that although *Aloe* species generally produce an abundance of seeds, recruitment in wild populations is only occasional.

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

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

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

4.6. Germination trials

4.6.1. Controlled and ambient laboratory conditions

Despite the 3-month-old *A. plicatilis* seeds germinating approximately three times faster than both the 18- and 24-month-old seeds, total germination in the former was three-fold less than the latter two (Fig. 5). The tetrazolium tests showed that 100% of the remaining ungerminated 3-month-old seeds that were not empty were viable. These findings suggest that *A. plicatilis* seeds undergo after-ripening –

a progressive loss of primary dormancy in air-dry seeds, which is a function of environmental variables and time (Murdoch and Ellis, 2000). Bairu et al. (2009) suggested the need for an after-ripening period in *A. ferox* seeds, since total germination at various temperatures, light intensities and concentrations of plant growth regulators was <80% after ± 1 month, although 95% of ungerminated seeds were viable. Staggered germination was also observed in *A. greatheadii* var. *davyana* and *A. marlothii* seeds, some of the former still germinating in the second season after sowing (Smith and Correia, 1992; Symes, 2012). Eloff and Liede (1987) reported increased percentage germination in *A. dichotoma*, *A. speciosa*, *Aloe thraskii* Baker and *Aloe vryheidensis* Groenew. seeds stored for ± 16 months under ambient conditions compared to those stored for only four months. However percentage germination in other *Aloe* species studied either decreased or remained fairly consistent over time.

Although the vigour of the 18- and 24-month-old *A. plicatilis* seeds in this study decreased slightly (indicated by slower germination rates), their viability was maintained. This result is, however, in stark contrast to the extremely poor germination of 0.5% Eloff and Liede (1987) obtained for *A. plicatilis* seed stored for 16.5 months under ambient laboratory conditions. However, the initial viability of that particular seed lot was unknown and the reasons for germination failure were therefore unclear. While the potential longevity of seeds stored in an air-dried state in a laboratory may provide clues about their longevity in the field, laboratory-stored seeds are exposed to much smaller variations in temperature, moisture and solar radiation compared to those in habitat (which are also vulnerable to predation). Seeds dispersed in habitat therefore probably survive for much shorter periods. Differences in viability between laboratory-stored seeds and those in the wild have been shown for marula (*Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro), which remain viable for many years in a laboratory, but form small, short-term persistent seed banks in the wild (Helm et al., 2011). In addition, Mbalo and Witkowski (1997) demonstrated the effect of simulated high soil surface temperatures on seeds of *Acacia karroo* Hayne, *Acacia tortilis* (Forssk.) Hayne subsp. *heteracantha* (Burch.) Brenan and *Chromolaena odorata* (L.) K. & R., which all declined in seed viability with increasing duration of exposure at 70 °C. While the viability of *A. plicatilis* seeds in the wild is most likely restricted to <1 year, seed storage and germination experiments *in situ* would help validate this deduction and thus contribute to our understanding of regeneration and establishment not only in *A. plicatilis*, but also aloes in general.

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

5. Conclusion

A. plicatilis appears to be pollinated primarily by insects; however, bird visitation significantly increased seed set/fruit, suggesting co-pollination with insects. Malachite sunbirds appear to be the most common avian visitors to *A. plicatilis* flowers – an observation that is consistent with the species' floral morphology and concentrated

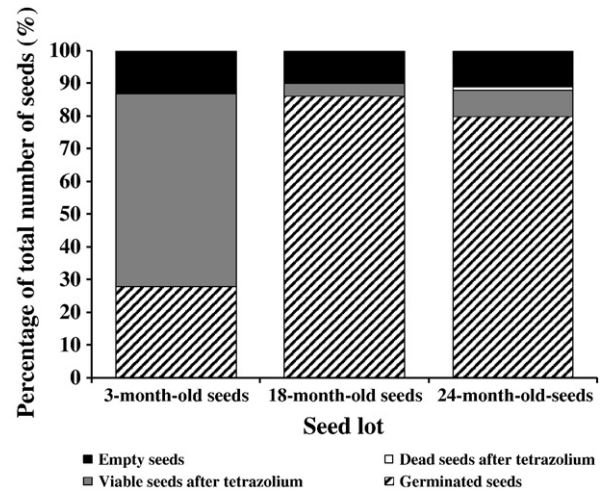


Fig. 5. Total percentage germination, and percentages of dead, empty and viable ungerminated *Aloe plicatilis* seeds after tetrazolium tests following storage under ambient laboratory conditions for three, 18 and 24 months.

nectar which suggest pollination by specialist avian nectarivores. Natural seed set at three populations varied by orders of magnitude, and reproductive success was poorest at the smallest and least dense population. The reproductive failure evident at this population suggests a possible Allee effect, but this requires further investigation. Potential seed dispersal distances in *A. plicatilis* were estimated to be approximately three times canopy height, consistent with a negative exponential seed shadow. However, the species' occurrence on isolated mountains that are disconnected from more continuous mountain ranges where the species also occurs suggests that long-distance dispersal by strong, gusty summer winds is possible. Seed banks in *A. plicatilis* populations appear to be transient, lasting for <1 year, and recruitment is likely erratic and 'disturbance free'. *A. plicatilis* seeds stored under ambient laboratory conditions for 18 and 24 months maintained high viability with total germination at $\geq 80\%$, while that of 3-month-old seed was three times less, suggesting the necessity for after-ripening. Emergence of *A. plicatilis* seeds under nursery conditions was not as successful as germination under controlled conditions in a growth chamber and laboratory. Further pollinator exclusion experiments and floral visitor observations will help verify the species' pollinator guild, and detailed supplemental self- and cross-pollination experiments are required to confirm its breeding system. Very little is known about the germination ecology of *A. plicatilis* (and most other aloes) in habitat. Further studies on germination requirements and recruitment patterns in the genus *in situ* would be especially beneficial for the conservation of rare and threatened *Aloe* species.

Acknowledgements

Thanks go to the National Research Foundation (NRF), the South African National Biodiversity Institute (SANBI), the Centre for Tree Health and Biotechnology (CTHB/FABI) and the University of the Witwatersrand, Johannesburg for funding. Field work was conducted under a permit issued by CapeNature (Permit No. AAA005-00190-0028). Irene Van Gent at the Agricultural Research Council (ARC) of South Africa is thanked for providing wind data. Many thanks go to Hans-Jurie Du Preez, Gerard Lamusse, Matthew Heaven, Matthew Rhoda and Nathan Steyn for field work assistance. Mr Gregory Nicolson is thanked for arranging access to the Paardeberg population. Ms Stephanie Payne is thanked for excellent assistance with the germination experiments. Thanks also go to Dr Craig Symes and Ms Gina Arena for advice on the pollination experiments and two anonymous reviewers are thanked for valuable comments on the manuscript.

References

- Agren, J., 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77, 1779–1790.
- Arena, G., Symes, C.T., Witkowski, E.T.F., 2013. The birds and the seeds: opportunistic avian nectarivores enhance reproduction in an endemic montane aloe. *Plant Ecology* 214 (1), 35–47.
- Bairu, M.W., Kulkarni, M.G., Street, R.A., Mulaudzi, R.B., Van Staden, J., 2009. Studies on seed germination, seedling growth, and in vitro shoot induction of *Aloe ferox* Mill., a commercially important species. *Hortscience* 44 (3), 751–756.
- Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45 (4), 461–490.
- Bazzaz, F.A., 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* 10, 351–371.
- Bazzaz, F.A., Ackerly, D.D., Reekie, E.G., 2000. Reproductive allocation in plants. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*, Second edition. CABI Publishing, Oxon, United Kingdom.
- Berec, L., Angulo, E., Courchamp, F., 2007. Multiple Allee effects and population management. *Trends in Ecology & Evolution* 22 (4), 186–191.
- Beylleveld, G.P., 1973. Transvaal maculate aloes as nectar producers. *Aloe* 11 (2), 29–32.
- Botes, C., Johnson, S.D., Cowling, R.M., 2008. Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology. *Oikos* 117, 875–882.
- Botes, C., Johnson, S.D., Cowling, R.M., 2009. The birds and the bees: using selective exclusion to identify effective pollinators of African tree aloes. *International Journal of Plant Science* 170 (2), 151–156.
- Carter, S., Lavranos, J.J., Newtown, L.E., Walker, C.C., 2011. Aloes: the Definitive Guide. Kew Publishing, Royal Botanic Gardens, Kew.
- Corlett, R.T., 2009. Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica* 41 (5), 592–598.
- Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460.
- Cousins, S.R., Witkowski, E.T.F., 2012. African aloe ecology: a review. *Journal of Arid Environments* 85, 1–17.
- Cousins, S.R., Witkowski, E.T.F., Pfab, M.F., 2013. Elucidating patterns in the population size structure and density of *Aloe plicatilis*, a tree aloe endemic to the Cape fynbos. *South African Journal of Botany* submitted.
- D'Antonio, C.M., 1990. Seed production and dispersal in the non-native invasive succulent *Carpobrotus edulis* (Aizoaceae) in coastal strand communities of central California. *Journal of Applied Ecology* 27, 693–702.
- Dafni, A., 1992. *Pollination Ecology: a Practical Approach*. Oxford University Press, Oxford.
- De Merxem, D.G., Borremans, B., de Jäger, M.L., Johnson, T., Jooste, M., Ros, P., Zenni, R.D., Ellis, A.G., Anderson, B., 2009. The importance of flower visitors not predicted by floral syndromes. *South African Journal of Botany* 75, 660–667.
- Eloff, J.N., Liede, S., 1987. The viability of seed supplied to Botanical Society members by the National Botanic Gardens. *Veld and Flora* 73, 2–9.
- Fægri, K., Van der Pijl, L., 1979. *The Principles of Pollination Ecology*, 3rd ed. Pergamon Press, Oxford.
- Farrant, J.M., Walters, C., 1998. Ultrastructural and biophysical changes in developing embryos of *Aesculus hippocastanum* in relation to the acquisition of tolerance to drying. *Physiologia Plantarum* 104, 513–524.
- Fenner, M., Thompson, K., 2006. *The Ecology of Seeds*. Cambridge University Press, Cambridge.
- Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R., Thomson, J.D., 2004. Pollination syndromes and flora specialization. *Annual Review of Ecology, Evolution, and Systematics* 35, 375–403.
- Forbes, R.W., Craig, A.J.F.K., Hulle, P.E., Parker, D.M., 2009. Seasonal variation in the avian community associated with *Aloe ferox* (Asphodelaceae, Mill.) flowering event in the Eastern Cape, South Africa. In: Harebottle, D.M., Craig, A.J.F.K., Anderson, M.D., Rakotomanana, H., Muchai, M. (Eds.), *Proceedings of the 12th Pan-African Ornithological Congress, Animal Demography Unit*, Cape Town, 2008, pp. 9–17.
- García-Fayos, P., Verdú, M., 1998. Soil seed bank, factors controlling germination and establishment of a Mediterranean shrub: *Pistacia lentiscus* L. *Acta Oecologia* 19 (4), 357–366.
- Geerts, S., Pauw, A., 2009. Hyper-specialization for long-billed bird pollination in a guild of South African plants: the Malachite Sunbird pollination syndrome. *South African Journal of Botany* 75, 699–706.
- Giddy, C., 1973. Aloes from seed. *Journal of the Botanical Society of South Africa* 59, 41–44.
- Groom, M.J., 1998. Allee effects limit population viability of an annual plant. *The American Naturalist* 151 (6), 487–496.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52, 107–145.
- Gutterman, Y., 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *The Botanical Review* 60 (4), 373–425.
- Hargreaves, A.L., Harder, L., Johnson, S.D., 2008. *Aloe inconspicua*: the first record of an exclusively insect-pollinated aloe. *South African Journal of Botany* 74, 606–612.
- Hargreaves, A.L., Harder, L.D., Johnson, S.D., 2010. Native pollen thieves reduce the reproductive success of a hermaphroditic plant, *Aloe maculata*. *Ecology* 91 (6), 1693–1703.
- Hargreaves, A.L., Harder, L., Johnson, S.D., 2012. Floral traits mediate the vulnerability of aloes to pollen theft and inefficient pollination by bees. *Annals of Botany* 109, 761–772.
- Hay, F.R., Probert, R.J., 1995. Seed maturity and the effects of different drying conditions on desiccation tolerance and seed longevity in foxglove (*Digitalis purpurea* L.). *Annals of Botany* 76, 639–647.
- He, T., Krauss, S.L., Lamont, B.B., Miller, B.P., Enright, N.J., 2004. Long-distance seed dispersal in a metapopulation of *Banksia hookeriana* inferred from a population allocation analysis of amplified fragment length polymorphism data. *Molecular Ecology* 13, 1099–1109.
- Helm, C.V., Scott, S.L., Witkowski, E.T.F., 2011. Reproductive potential and seed fate of *Sclerocarya birrea* subsp. *caffra* (marula) in the low altitude savannas of South Africa. *South African Journal of Botany* 77, 650–664.
- Hoffman, M.T., 1988. The pollination ecology of *Aloe ferox* Mill. *South African Journal of Botany* 54 (4), 345–350.
- Horn, H.S., Nathan, R., Kaplan, S.R., 2001. Long-distance dispersal of tree seeds by wind. *Ecological Research* 16, 877–885.
- Howe, H.F., Miriti, M.N., 2004. When seed dispersal matters. *Bioscience* 54 (7), 651–660.
- Human, H., Nicolson, S.W., 2008. Flower structure and nectar availability in *Aloe greatheadii* var. *davyana*: an evaluation of a winter nectar source for honeybees. *International Journal of Plant Sciences* 169 (2), 263–269.
- Johnson, S.D., Hargreaves, A.L., Brown, M., 2006. Dark, bitter-tasting nectar functions as a filter of flower visitors in a bird-pollinated plant. *Ecology* 87 (11), 2709–2716.
- Johnson, S.D., Nicolson, S.W., 2008. Evolutionary associations between nectar properties and specificity in bird pollination systems. *Biology Letters* 4, 49–52.
- Johnson, S.D., Steiner, K.E., 2000. Generalization versus specialization in plant pollination systems. *Trends in Ecology & Evolution* 15 (4), 140–143.
- Jordan, J.D., 1996. The ecology of the aloes of Zimbabwe. *Excelsa* 17, 101–110.
- Jordan, J.D., 1999. Some thoughts on the evolution of *Aloe*. *Excelsa* 19, 61–66.
- Kamstra, M.W., 1971. Aloe seeds. *Excelsa* 1, 19–26.
- Kaye, T.N., 1999. From flowering to dispersal: reproductive ecology of an endemic plant, *Astragalus australis* var. *olympicus* (Fabaceae). *American Journal of Botany* 86 (9), 1248–1256.
- Keeley, J.E., Bond, W.J., 1997. Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecology* 133, 153–167.
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W., 2012. *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. Cambridge University Press, New York.
- Killick, D.J.B., 1988. *Aloe plicatilis* (Liliaceae): Flowering Plants of Africa, 50(1). Botanical Research Institute, Department of Agriculture and Water Supply (Plate 1972).
- Klinkhamer, P.G.L., Meelis, E., de Jong, T.J., Weiner, J., 1992. On the analysis of size-dependent reproductive output in plants. *Functional Ecology* 6, 308–316.
- Klopper, R.R., Retief, E., Smith, G.F., 2009. The genus *Aloe* L. (Asphodelaceae: Aloioideae) in the Free State Province of South Africa. *Haseltonia* 15, 41–52.
- Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnson, M.O., Mitchell, R.J., Ashman, T.-L., 2005. Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution, and Systematics* 36, 467–497.
- Kramer, A.M., Dennis, B., Liebhold, A.M., Drake, J.M., 2009. The evidence for Allee effects. *Population Ecology* 51, 341–354.
- Kruger, A.C., Goliger, A.M., Retief, J.V., Sekele, S., 2010. Strong wind climatic zones in South Africa. *Wind and Structures* 13 (1), 37–55.
- Kunin, W.E., 1992. Density and reproductive success in wild populations of *Diplotaxis erucodes* (Brassicaceae). *Oecologia* 91, 129–133.
- Lamont, B.B., Klinkhamer, P.G.L., Witkowski, E.T.F., 1993a. Population fragmentation may reduce fertility to zero in *Banksia goodii* – a demonstration of the Allee effect. *Oecologia* 94, 446–450.
- Lamont, B.B., Witkowski, E.T.F., Enright, N.J., 1993b. Post-fire litter microsites: safe for seeds, unsafe for seedlings. *Ecology* 74 (2), 501–512.
- Leck, M.A., Parker, V.T., Simpson, R.L., 2008. *Seedling Ecology and Evolution*. Cambridge University Press, New York.
- Lovett Doust, J., Lovett Doust, L. (Eds.), 1988. *Plant Reproductive Ecology: Patterns and Strategies*. Oxford University Press, New York.
- Manning, J., 2007. *Field Guide to Fynbos*. Struik Nature, Cape Town.
- Matlack, G.R., 1987. Diaspore size, shape, and fall behaviour in wind-dispersed plant species. *American Journal of Botany* 74 (8), 1150–1160.
- Mbalu, B., Witkowski, E.T.F., 1997. Tolerance to soil temperatures experienced during and after the passage of fire in seeds of *Acacia karroo*, *A. tortilis* and *Chromolaena odorata*: a laboratory study. *South African Journal of Botany* 63 (6), 421–425.
- McIntosh, M.E., 2002. Plant size, breeding system, and limits to reproductive success in two sister species of *Ferocactus* (Cactaceae). *Plant Ecology* 162, 273–288.
- McLachlan, J.S., Clark, J.S., 2004. Reconstructing historical ranges with fossil data at continental scales. *Forest Ecology and Management* 197, 139–147.
- Murdoch, A.J., Ellis, R.H., 2000. Dormancy, viability and longevity. In: Fenner (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*, Second edition. CABI Publishing, Oxon, United Kingdom.
- Mustajärvi, K., Siikamäki, P., Rytkönen, S., Lammi, A., 2001. Consequences of plant population size and density for plant-pollinator interactions and plant performance. *Journal of Ecology* 89 (1), 80–87.
- Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W., Levin, S.A., 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418, 409–413.
- Nicolson, S.W., Nepi, M., 2005. Dilute nectar in dry atmospheres: nectar secretion patterns in *Aloe castanea* (Asphodelaceae). *International Journal of Plant Sciences* 166 (2), 227–233.
- Nicolson, G., Roets, D., 2012. The Paardeberg: a post-fire botanical assessment. *Veld and Flora* 98 (2), 60–63.
- Ollerton, J., Lack, A., 1998. Relationships between flowering phenology, plant size and reproductive success in *Lotus corniculatus* (Fabaceae). *Plant Ecology* 139, 35–47.
- Peters, E.M., Martorell, C., Ezcurra, E., 2008. Nurse rocks are more important than nurse plants in determining the distribution and establishment of globose cacti (*Mammillaria*) in the Tehuacán Valley, Mexico. *Journal of Arid Environments* 72, 593–601.
- Pfab, M.F., Witkowski, E.T.F., 1999. Contrasting effects of herbivory and reproductive limitation in two populations of the critically endangered species, *Euphorbia clyvicola* R.A. dyer. *Plant Ecology* 145 (2), 317–325.
- Pierce, S.M., Moll, E.J., 1994. Germination ecology of six shrubs in fire-prone Cape fynbos. *Vegetatio* 110, 25–41.

- Primack, R.B., 1987. Relationships among flowers, fruits and seeds. *Annual Review of Ecology and Systematics* 18, 409–430.
- Ratsirarson, J., 1995. Pollination ecology of *Aloe divaricata*, Berger (Liliaceae): an endemic plant species of south-west Madagascar. *South African Journal of Botany* 61 (5), 249–252.
- Rebello, A.G., 1987. In: Rebello, A.G. (Ed.), *A Preliminary Synthesis of Pollination Biology in the Cape Flora: South African National Scientific Programmes Report*, 141.
- Reynolds, G.W., 1969. *The Aloes of Southern Africa*. Balkema, Cape Town.
- Rodríguez-García, R., Jasso de Rodríguez, D., Gil-Marín, J.A., Angulo-Sánchez, J.L., Lira-Saldivar, R.H., 2007. Growth, stomatal resistance transpiration of *Aloe vera* under different soil water potentials. *Industrial Crops and Products* 25, 123–128.
- Savonen, E.-M., 1999. An improvement to the topographic tetrazolium testing of Scots pine (*Pinus sylvestris* L.) seeds. *Seed Science and Technology* 26, 49–57.
- Scholes, M.A., 1988. A population study of *Aloe peglerae* in habitat. *South African Journal of Botany* 54, 137–139.
- Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., Nathan, R., 2009. Long-distance seed dispersal. *Annual Plant Reviews* 38, 204–237.
- Sinclair, I., Hockey, P., Tarboton, W., Ryan, P., 2011. *Birds of Southern Africa*. Struik Nature, Cape Town.
- Smith, G.F., Correia, R.I. de S., 1992. Establishment of *Aloe greatheadii* var. *davyana* from seed for use in reclamation trials. *Landscape and Urban Planning* 23, 47–54.
- Smith, G.F., Van Wyk, B., 2009. *Aloes in Southern Africa*. Struik Nature, Cape Town.
- Steffan-Dewenter, I., Münzenberg, U., Tscharrntke, T., 2012. Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society* 268, 1685–1690.
- Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect? *Oikos* 87 (1), 185–190.
- Stokes, C.J., Yeaton, R.I., 1995. Population dynamics, pollination ecology and the significance of plant height in *Aloe candelabrum*. *African Journal of Ecology* 33, 101–113.
- Symes, C.T., 2012. Seed dispersal and seed banks in *Aloe marlothii* (Asphodelaceae). *South African Journal of Botany* 78, 276–280.
- Symes, C.T., Human, H., Nicolson, S.W., 2009. Appearances can be deceiving: pollination of two sympatric winter-flowering *Aloe* species. *South African Journal of Botany* 75, 668–674.
- Symes, C.T., McKechnie, A.E., Nicolson, S.W., Woodborne, S.M., 2011. The nutritional significance of a winter-flowering succulent for opportunistic avian nectarivores. *The International Journal of Avian Science* 110–121.
- Symes, C.T., Nicolson, S.W., 2008. Production of copious dilute nectar in the bird-pollinated African succulent *Aloe marlothii* (Asphodelaceae). *South African Journal of Botany* 74, 598–605.
- Tribe, G.D., Johannsmeier, M.F., 1996. Bees and quiver trees. *South African Bee Journal* 68, 111–115.
- Van Jaarsveld, E., 1989. The genus *Aloe* in South Africa with special reference to *Aloe hereroensis*. *Veld & Flora* 75 (3), 73–76.
- Van Jaarsveld, E., 2011. The tree aloes of southern and eastern Africa. *Cactus and Succulent Journal* 83 (1), 9–21.
- Van Wyk, B.-E., Smith, G., 2008. *Guide to the Aloes of South Africa*. Briza Publications, Pretoria.
- Vásquez-Yanes, C., Orozco-Segovia, A., 1993. Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics* 24, 69–87.
- Vleeshouwers, L.M., Bouwmeester, H.J., Karssen, C.M., 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology* 83, 1031–1037.
- Wabuyele, E., Kyalo, S., 2008. Sustainable use of east African Aloes: the case of commercial aloes in Kenya. NDF Workshop Case Studies, WG3 — Succulents and Cycads, Case Study 1: *Aloe* spp., East and southern Africa (Mexico).
- Waser, N.M., Chittka, K., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in pollination systems and why it matters. *Ecology* 77, 1043–1060.
- Wiehler, G.D., Thomson, J.D., 1995. Seed dispersal in *Erythronium grandiflorum* (Liliaceae). *Oecologia* 102, 211–219.
- Wiesser, P.J., Deall, G.B., 1989. *Aloe petricola*: ecological notes and effect of fire near Sabie. *Aloe* 26, 27–30.
- Wilcock, C., Neiland, R., 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science* 7 (6), 270–277.
- Willson, M.F., 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107 (108), 260–280.
- Wilson, A.-L., Ward, D., Brown, M., Johnson, S.D., 2009. Seed production in a threatened *Aloe* is not affected by bird exclusion or population size. *Plant Ecology* 203, 173–182.
- Zar, J.H., 1999. *Biostatistical Analysis*, fourth ed. Prentice-Hall, New Jersey.