



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



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ABSTRACT

Studies on plant population size structure provide important baseline information for monitoring and conservation. Traditionally, inverse J-shaped size class distributions (SCD) were considered indicative of 'healthy', stable plant populations; however, this may not hold true for long-lived, slow-growing species. This study assessed the population size structure of 19 populations of *Aloe plicatilis*, a Cape fynbos endemic tree aloe, and quantified population size and density. A strong positive linear relationship between stem diameter (SDr) and height was used to align SDr and height SCD bins, and to harmonize stage and size classes. Onset of reproduction occurs at ~15 cm SDr and ~0.8 m in height. Some *A. plicatilis* individuals appear to display a 'bonsai effect' whereby the growth of individuals in very rocky sites is suppressed. Stunted plants may be non-reproductive 'suppressed juveniles' or 'reproductive dwarfs'. The short, shrub-like growth form of many individuals may also result from height restrictions imposed by persistent strong winds. Population size, extent and density ranged from 31 to >110 000 individuals, 0.05–103 ha and 75–3000 plants/ha respectively. Bell-shaped SCDs were the most common (50% of populations). The SDr and height SCDs for all populations combined were also bell-shaped. Seven populations displayed irregular SCDs, but were similar in structure to the bell-shaped SCDs, both of which were attributed to an adult-persistence population survival strategy. This study challenges the suitability of the inverse J as the only SCD indicative of healthy, stable populations for long-lived, slow-growing species. The study provides baseline demographic data on *A. plicatilis* across its distribution for long-term monitoring, and provides insights useful for examining trends in the demographics of other long-lived, slow-growing species.

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1. Introduction

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

seeds and recruits have been exposed, such as seed predation, disease, harvesting and herbivory (Silvertown, 1987; Bullock et al., 1996; Hutchings, 1997). The spatial structure of plant populations is also a legacy of the spatial arrangement of parent plants, and the historical interactions between them (Hutchings, 1997). Interactions between the factors that shape population structure, may, however result in considerable complexity (Huston and DeAngelis, 1987); hence, inferring mechanisms from known SCDs can be challenging, and necessitates a holistic, integrated approach, with maximal use of available data.

Long-term population monitoring data provide a substantial depth of knowledge about plant population dynamics and their implications for conservation and management. Recent studies on the impact of climate change on plant populations demonstrate the importance of longer-term climatic and demographic processes in shaping the patterns currently observed in plant populations (e.g. Foden et al., 2007; Jack, 2012). However, long-term studies are costly, and in conservation biology it is often not advisable to wait until long-term datasets have accumulated before making management decisions, especially for rapidly declining species (Wiegand et al., 2000). A more feasible way to investigate population dynamics is to use snapshot population assessments distributed over space instead of time. Pérez Farrera and Vovides (2004) emphasise that it is important not to make demographic

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characterisations of a species based on one population only, especially if a snapshot study is used. Demographic studies should be carried out at a metapopulation level to understand the variation and behaviour of the species within and between populations in the range of habitats in which it occurs (Pérez Farrera and Vovides, 2004).

In addition to knowledge of a species' population size structure, information on the distribution of its abundance in both time and space helps elucidate the relationships between the species and its environment (Brown et al., 1995). Furthermore, studies on population size and density add extra weight to baseline population data, which are important for testing hypotheses relevant to conservation and management, as well as species' responses to climate change (Sagarin et al., 2006). Characterisation of population size, size structure and density also helps pinpoint populations that are important for conservation and long-term monitoring (e.g. Knowles and Witkowski, 2000) and therefore provides useful data that are readily available for management (Botha et al., 2002; Mwavu and Witkowski, 2009).

Several short-term studies on plant population structure have quantified differences in structural patterns across populations using size class distribution (SCD) slopes (sensu Condit et al., 1998) combined with indices such as Simpsons index of dominance, Permutation index, evenness, and quotients (e.g. Wiegand et al., 2000; Botha et al., 2002; Mwavu and Witkowski, 2009; Venter and Witkowski, 2010; Helm and Witkowski, 2012). These indices condense large volumes of data contained in SCDs and facilitate analyses of the patterns within and between populations. The next step is to attempt to understand and explain the mechanisms responsible for the patterns that have been revealed using these indices. These mechanisms may be numerous and inter-related, and may operate in concert, for example disturbances such as fire and herbivory (e.g. Helm and Witkowski, 2012), climatic effects such as rainfall, temperature gradients, and frost (e.g. Whitecross et al., 2012), and exploitation e.g. harvesting for traditional medicine (e.g. Botha et al., 2002; Williams et al., 2007).

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

Traditionally, most plant populations were thought to have a 'size hierarchy', i.e. a frequency distribution of plant sizes in which relatively few individuals constitute most of the population's biomass and most individuals are fairly small (Weiner and Solbrig, 1984). In this context, relative proportions of seedlings, juveniles, sub-adults and adults theoretically provide a population health index and offer clues about past and future demographic events (Łomnicki, 1988). Abundant seedlings and juveniles relative to adults result in a classic inverse J-shaped SCD, which is generally interpreted as indicative of a healthy, 'stable' and potentially growing population (Condit et al., 1998). Conversely, a scarcity of seedlings and juveniles (represented by a J-shaped curve) may indicate a declining population (Condit et al., 1998). Thus, deviation from an inverse J SCD (for example by a bell- or J-shaped distribution) may be cause for concern. However, Venter and Witkowski (2010) caution that for slow-growing, long-lived species this may not hold true, since abundant mature individuals can sustain populations despite low or episodic recruitment. Indeed, bell- or J-shaped SCDs have been observed in a number of long-lived, slow-growing species, and were not always considered indicative of

unstable or declining populations (see Scholes, 1988; Witkowski and Liston, 1997; Pfab and Witkowski, 1999; Raimondo and Donaldson, 2003; Méndez et al., 2004).

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

2. Methods

2.1. Study area

Aloe plicatilis is endemic to the Cape fynbos in mountainous areas in the Cape Winelands (also known as the Boland) within the Core Cape Subregion (CCR) of the Greater Cape Floristic Region (GCFR), South Africa. Covering approximately 90 760 km², with an estimated 9383 indigenous vascular plant species, just over 68% of which are endemic, the CCR is one of the richest regions in the world in terms of botanical diversity (Manning and Goldblatt, 2012). The Cape fynbos has a Mediterranean-type climate, with hot, dry, windy summers and cool wet winters (Keeley et al., 2012). Fynbos vegetation is fire-prone and has a crown fire regime, with most fires occurring during summer at intervals of 10–30 years depending on the vegetation type (Keeley et al., 2012). Fire plays a key role in determining major vegetation patterns in the winter rainfall regions of South African perhaps more than any other Mediterranean-type climate region (Keeley et al., 2012).

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

2.2. Study species

Aloe plicatilis, recently segregated from *Aloe* s.s. as *Kumara plicatilis* (L.) G.D. Rowley (Daru et al., 2013; Grace et al., 2013; Rowley, 2013),

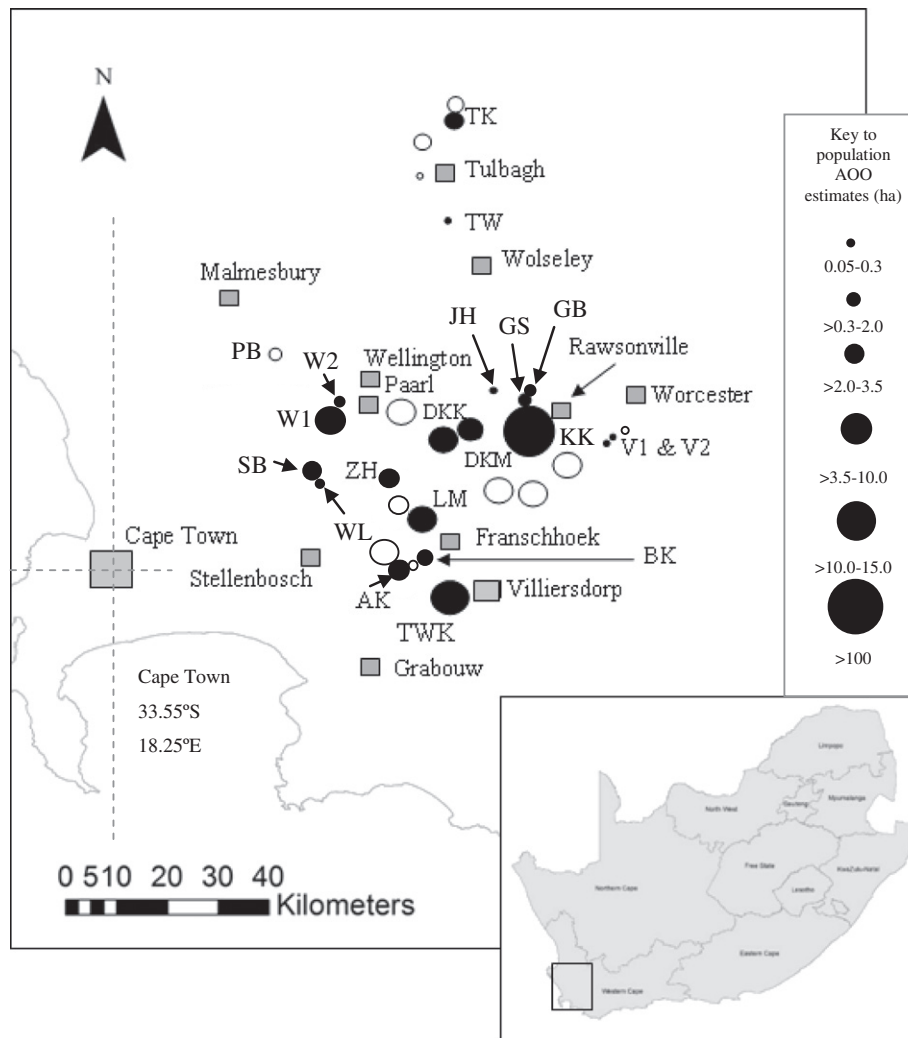


Fig. 1. Distribution of the 31 known populations of *Aloe plicatilis* in the Cape Floristic Region, Western Cape, South Africa. Shaded circles represent the 19 populations that were surveyed for population size structure and density, and open circles represent non-surveyed populations. Grey squares denote major towns or cities. The sizes of the circles correspond with the estimated population Area of Occupancy (AOO) (calculated estimates for surveyed populations (see Table 2) and visual estimates for non-surveyed populations). Population names, abbreviations and localities: AK (Assegaaiboskloof; Berg River, Groot-Drakenstein Mountains, near Franschhoek), BK (Bosjemanskloof, Berg River, near Franschhoek), DKK (Du Toit's Kloof Krom River; Du Toit's Kloof, between Paarl/Wellington & Rawsonville), DKM (Du Toit's Kloof Molenaars River; Du Toit's Kloof, between Paarl/Wellington & Rawsonville), GB (Goudini Badsberg; near Rawsonville), GS (Goudini Spa; near Rawsonville), JH (Jason's Hill; Slanghoek Valley, near Rawsonville), KK (Klipphoutkloof; near Rawsonville), LM (La Motte; bordering Haweqwa Nature Reserve, Franschhoek), PB (Paardeberg; between Wellington & Malmesbury), SB (Skurweberg; Wiesenhof Wildpark, near Stellenbosch), TK (Tulbagh Kleinpoort; Groot-Winterhoek Nature Reserve, near Tulbagh), TW (Tulbagh Waterfall; Waterval Nature Reserve, near Tulbagh), TWK (Theewaterskloof; Hottentots-Holland Nature Reserve, near Yieboom), V1 (Voorsorg 1; Watervalkloof, near Rawsonville), V2 (Voorsorg 2; Grootkloof, near Rawsonville), WL (Wiesenhof Lookout; Wiesenhof Wildpark, near Stellenbosch), W1 (Windmeul 1; Bordering Paarl Mountain Nature Reserve, Windmeul), W2 (Windmeul 2; Rhebokskloof, Windmeul) and ZH (Zachariashoek; Klein-Drakenstein Mountains, Haweqwa Nature Reserve, between Paarl and Franschhoek).

is a relatively slow-growing, well-branched shrub to small tree, with dichotomously branching stems, each of which ends in a set of 12–16 alternate, fleshy leaves in a fan-like arrangement (Carter et al., 2011). Adult plants average 1.5–2 m in height (± 50 –70 years old, based on measurements of the growth rates of plants in cultivation), but exceptionally large individuals may reach 4–5 m (± 130 –160 years old). *Aloe plicatilis* flowers from August to October and the fruiting season starts in early November, with fruit capsules dehiscing from December–January (Van Wyk and Smith, 2008). The relatively small, winged seeds are wind-dispersed. The species grows in well-drained, acidic soils on steep rocky slopes and rocky outcrops that afford it some protection from fires (Van Wyk and Smith, 2008). However, *A. plicatilis* appears to be relatively fire-tolerant, and burnt individuals usually recover by sprouting from apical meristems (Van Jaarsveld, 1989). It is also the only aloe known to have thick, corky bark, which provides further protection against fire damage (Van Jaarsveld, 1989).

2.3. Locating the populations

Initially, a thorough literature survey, consultations with five South African herbaria and exploration of web-based species databases yielded nine known *A. plicatilis* populations, most of which were relatively accessible. There were, however, reports of other lesser-known, more inaccessible populations, and possibly others yet to be discovered, none of which were documented. Extensive networking with researchers, nature conservation officials and landowners was undertaken to locate these undocumented populations. Furthermore, an article on the study was published in Veld & Flora (Cousins, 2010), which included a request to the public to provide information on any lesser-known populations. A total of 22 additional populations were identified through these sources, bringing the total number currently known to 31 (Fig. 1). Triplicate voucher specimens were collected from most of the newly documented populations and lodged in J, PRE and NBG.

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

Population ^a	Land ownership ^b	Vegetation type ^c	Long term average annual rainfall ^d (mm)	Long term average monthly temperature ^d (°C)	Altitudinal range (m)	Topographic position	Predominant aspect	Most recent burn
AK	C	Kogelberg sandstone fynbos	1940	14	387–474	Lower mountain slopes	NE	December 2005
BK	C	Kogelberg sandstone fynbos	1526	15	288–386	Mid to lower slopes mountain slopes	W	February 2010
DKK	C	Hawequas sandstone fynbos	932	15	462–632	Hilltops, mid and lower mountain slopes	NW, SE	2009
DKM	C	Hawequas sandstone fynbos	1062	15	372–501	Lower mountain slopes	S	October 2007
GB	P	Hawequas sandstone fynbos	562	17	481–521	Mid to upper mountain slopes	E	2009
GS	P	Hawequas sandstone fynbos	607	17	236–396	Lower mountain slopes	E	2010
JH	P	Hawequas sandstone fynbos	608	16	337–373	Lower mountain slopes	NE	2005
KK	C/P	Hawequas sandstone fynbos	652	15	213–340	Mid to lower mountain slopes	E	January 2011
LM	C/P	Hawequas sandstone fynbos	771	16	248–445	Mid to lower mountain slopes	W	> 3 years
SB	C	Boland granite fynbos	788	15	414–565	Crests and upper slopes of two ridges	NE, SW	2000
TK	C	Winterhoek sandstone fynbos	921	14	867–944	Mid to lower slopes in high-lying valley	NW	± 10 years
TW	C	Hawequas sandstone fynbos	465	18	192–226	Single rocky outcrop on hillside	Various	± 7 years
TWK	C	Kogelberg sandstone fynbos	1076	16	334–393	Rocky outcrops on lower mountain slopes	Various	2009
V1	P	Hawequas sandstone fynbos	422	15	443–485	Rocky outcrop on lower mountain slopes	N	January 2011
V2	P	Hawequas sandstone fynbos	426	15	458–542	Midslopes	N	January 2011
WL	C	Boland granite fynbos	788	16	203–392	Hilltop	Various	2000
W1	C/P	Boland granite fynbos	580	16	285–338	Mid to lower mountain slopes	NE	≥ 10 years
W2	C	Boland granite fynbos	580	15	579–634	Hilltop and upper slopes	NW	≥ 10 years
ZH	C	Hawequas sandstone fynbos	1013	14	608–830	Rocky outcrops on high-lying plateau	Various	1999 & 2007 ^e

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

2.4. Sampling and measurement

2.4.1. Delineating populations

Before commencing the population surveys, it was important to decide what exactly constituted a population of *A. plicatilis*. Some populations e.g. W1 and W2 (Fig. 1) had clear boundaries, consisted of fairly continuous aggregations of plants and could be circumnavigated in their entirety. Others, e.g. KK and LM were spread out over broad areas and showed dense aggregations of plants in some areas, with more widely scattered plants elsewhere. Due to the difficulty of reaching some individuals in the very steep, mountainous terrain, it was sometimes not feasible to delineate the boundaries of these very large, widely scattered populations. Discrete populations were delineated by taking GPS coordinates of the periphery of the entire population, whereas with very large, more loosely defined populations, only the most accessible and/or most distinct aggregation of individuals that constituted the core of the population was delineated. Attempts were then made to determine the area covered by the rest of these populations using photographs, visual observations with binoculars and topographical maps. Of the 31 known populations, 19 were surveyed (Table 1; shaded circles in Fig. 1). The surveyed populations provided a representative sample over the entire geographical range of the species and a fair representation of high- and low-lying populations, which avoided bias towards easily accessible populations. The eleven unsurveyed populations were discovered subsequent to the major data collection period and hence could not be sampled. However, the location of each of these populations was determined by visiting the population and taking a GPS reading approximately at its core (Open circles, Fig. 1).

2.4.2. Plant-based measurements

Basal SDR 10 cm above the basal swelling was measured using tree callipers and height of the tallest stem was measured with a tape

measure (where the leaf cluster emerges from the stem). Two methods were used to estimate plant density and the total number of individuals: (a) Point centred quarter method (PCQ) and (b) Nearest neighbour method (NN) (Cottam and Curtis, 1956; Marom, 2006). The individuals measured using NN were those closest to the individual measured in each quadrant for the PCQ. A minimum of 40 and a maximum of 90 individuals were sampled for populations with >50 individuals, while every plant was measured in populations with ≤50 individuals. For very inaccessible populations, sample sizes were sometimes <40 due to severe time constraints imposed by long travelling distances and/or inclement weather conditions. For large populations (>50 plants), transects were laid across the population at lengths and distances apart that were appropriate to the spatial extent of the population, with PCQ points spaced at 15–20 m intervals along each transect. Placement of transects in some populations proved challenging due to steep slopes, sheer rock faces, large boulders and dense bush clumps. When laying out the transects, attempts were made to encompass as much topographical variation within each population as possible, so as to avoid any bias towards the gentlest slopes.

2.5. Data and statistical analyses

2.5.1. Delimitation of size and stage class bins

Size class bins were delimited to accommodate more individuals with increasing size, as advised by Condit et al. (1998). This method balances the samples across the size classes, since the number of individuals in successive classes generally declines with increasing size (Condit et al., 1998). Furthermore, stage classes (juveniles, sub-adults and adults) were also taken into account in order to make the size classes biologically meaningful (Helm and Witkowski, 2012). Most studies on the population structure of trees provide little detail on how SDR or height classes relate to stage class. McLaren et al. (2005) and Helm and Witkowski (2012) harmonized stage classes

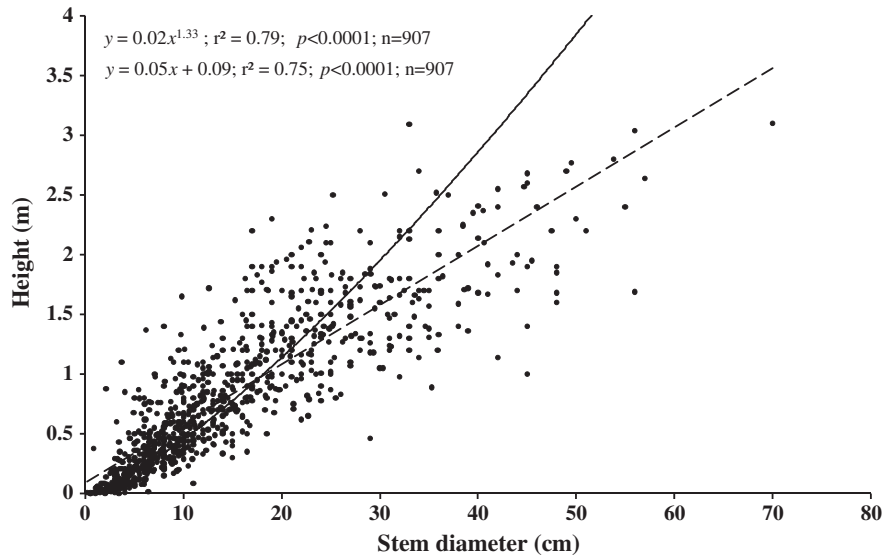


Fig. 2. Regression relationship between stem diameter and height of all plants in the 19 *Aloe plicatilis* populations surveyed. The linear fit (dotted line) was used to synchronise stem diameter size class distributions with height size class distributions. The exponential fit (solid line) was used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

with size classes, but the delineation of boundaries between stage classes was not explicitly defined. Few studies have used a combination of SDr and height to assess population structure, and in this study an

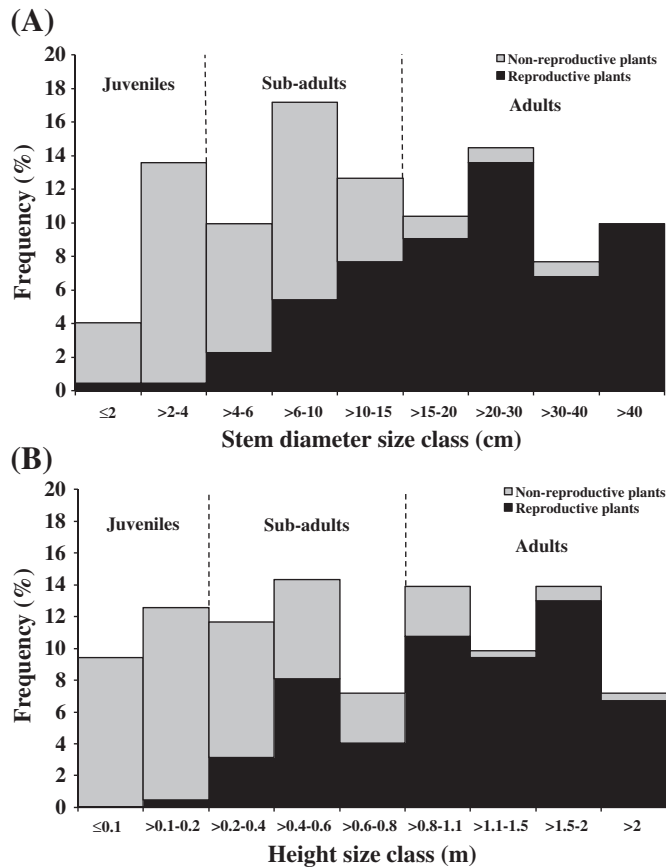


Fig. 3. (A) Stem diameter (SDr) and (B) height size class distributions for plants surveyed in five *Aloe plicatilis* populations for which flowering data was available (DKK, DKM, GB, GS & V1). The percentage of reproductive and non-reproductive individuals in each size class was used to delineate the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

attempt was made to match SDr classes with height classes in order to facilitate easy comparisons between SDr and height SCDs. To this end, a linear regression between height and SDr for individuals from all 19 populations was performed to ascertain the numerical relationship between the two (Fig. 2). This relationship was then used to synchronise SDr and height classes.

To determine the SDr and height classes that correspond with the appropriate stage classes, it was necessary to define the approximate size at which juveniles become sub-adults, and sub-adults become adults. The onset of reproduction provides a relatively clear distinction between juveniles and adults (Donovan and Ehleringer, 1991); however, there is little consensus regarding the point at which a seedling becomes a juvenile (Hanley et al., 2004). For this reason, seedlings were not classified as separate from the juvenile stage class. Juveniles were defined as non-reproductive individuals; sub-adults as plants occupying size classes in which the proportion of non-reproductive individuals outweighed, equalled, or was slightly less than the proportion of reproductive plants (threshold of 40%), and adults were defined as individuals occupying size classes where the large majority of plants were reproductive (>85%). In order to do this, a SCD was constructed for reproductive versus non-reproductive individuals using five populations ($n = 221$ plants) for which flowering data were available (Fig. 3). The stage classes were then defined as: juveniles (SDr ≤ 4 cm; height ≤ 0.2 m), sub-adults ($4 \text{ cm} < \text{SDr} \leq 15 \text{ cm}$; $0.2 \text{ m} < \text{height} \leq 0.8 \text{ m}$) and adults (SDr $> 15 \text{ cm}$; height $> 0.8 \text{ m}$). Following delimitation of size and stage class bins, individuals were assigned to size classes and SCDs were constructed for SDr and height.

2.5.2. Estimates of density and population size

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

$$\text{For NN, } D = \frac{0.3556}{\left(\sum_{i=1}^n \left(\frac{r_i}{\bar{p}} \right)^2 \right)}$$

where 'D' = density (plants/ha), 'n' is the number of individual plants sampled, 'r' is the distance from each sampled individual per quadrant to its nearest neighbour in metres, and 'P' is the total number of random points sampled. For both PCQ and NN: Number of individuals in the population = density × population area. Population area (ha) was calculated using ArcGIS, whereby GPS points of the periphery of each population were used to create Area of Occupancy (AOO) polygons.

2.5.3. Patterns in population size structure

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

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

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

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

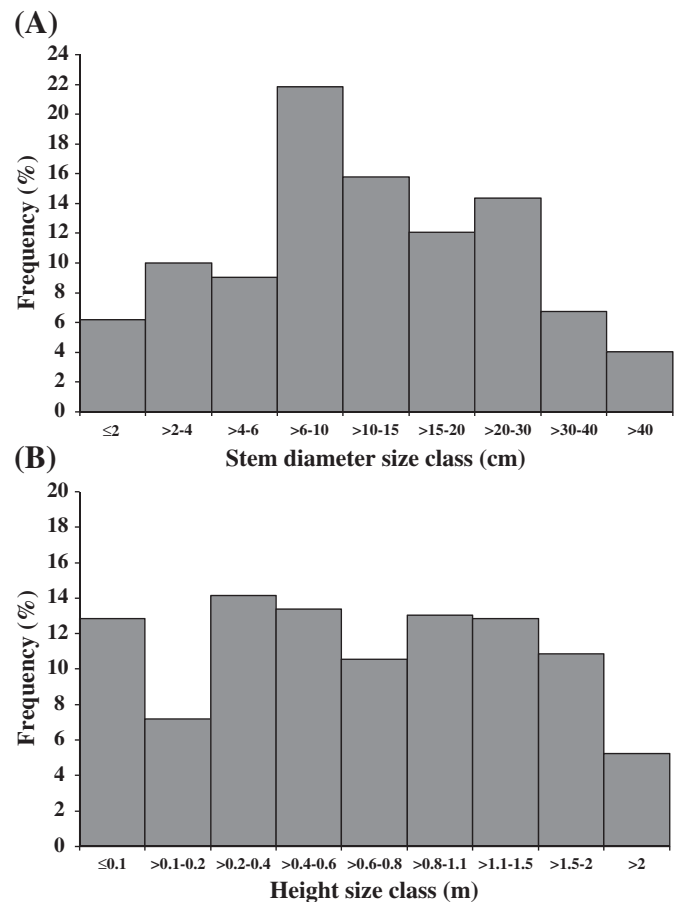


Fig. 4. (A) Stem diameter and (B) height size class distributions for *Aloe plicatilis* individuals from all 19 populations combined. (n = 920 individuals for both (A) and (B)).

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

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

3. Results

3.1. Relationship between stem diameter and height

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

3.2. Stage classes and size at reproductive maturity

The onset of reproduction in *A. plicatilis* at the five populations for which flowering data were available occurred at SDRs >4 cm and heights >0.2 m (sub-adult phase). Flowering was observed in 85% of individuals >15 cm SDR and >0.8 m in height; hence plants exceeding these size thresholds were considered as adults (Figs. 3; 6A). Notwithstanding, reproductively mature individuals were found in even the smallest SDR size classes (<4 cm SDR and <0.2 m height), but such plants were rare.

3.3. Variations in population size and density

Population size varied widely over five orders of magnitude from 31 (JH) to >110 000 individuals (KK) (Table 2). There did not appear to be any relationship between a population's size and its position within the species' distribution, although many of the larger populations tended to be in the core distribution of the species (Fig. 1). Densities were comparable between populations, with only a few being markedly high or low (Table 2; Fig. 6D, E). The PCQ and NN methods often yielded somewhat different density estimates, with PCQ usually higher than NN (10 out of 14 populations). These differences were reflected in the estimated number of individuals per population. There was no relationship between population size and density (linear regression analyses yielded r^2 values of 0.02 and 0.01 ($p > 0.05$) for PCQ and NN respectively). The population with the greatest density (WL) showed high recent recruitment, with large numbers of individuals in the smallest size classes (Group 1, Fig. 5), while the least dense population (JH) showed no recent recruitment (Group 2, Fig. 5).

3.4. Patterns in population structure

The SDR and height SCDs for all populations combined were bell-shaped (Fig. 4A,B). Of the individual populations, one displayed an inverse J-shaped SCD (WL), two were J-shaped (DKM and JH), nine were clearly bell-shaped (AK, KK, LM, SB, TW, V2, W1, W2 and ZH) and seven were irregular or tended towards a 'flatter' shape (BK, DKK, GB, GS, TK, TWK and V1). While the irregular SCDs were visibly different from the bell-shaped SCDs, the two types of SCDs were placed together in Group 3, since the Sør plot indicated a high degree of similarity between them (see Q2, Fig. 7).

3.4.1. Group 1: Inverse J-shaped distributions

High levels of recent recruitment were evident at WL, with large numbers of juveniles and few large adults – a pattern that was reflected in its low P (Table 3) and steep negative SCD slope for SDR and height (Table 4). Evenness was lower for height than SDR due to many individuals ≤ 0.01 m tall (Fig. 5). The SDR and height SCDs exhibited by WL were highly dissimilar to the SCDs of the other populations, thus WL grouped on its own in Q3 in the Sør plot (Fig. 7).

3.4.2. Group 2: J-shaped distributions

The J-shaped SCDs obtained for DKM and JH reflected a preponderance of large adults and few or no juveniles (Fig. 5). Approximately 60% of the individuals at both populations had SDRs ≥ 20 cm. Sixty-eight percent of the plants at DKM and 80% at JH had heights >1.1 m. The J-shaped SCDs were mirrored in the high P obtained for both populations (Table 3). The SCD of JH had a medium-high λ (Table 3), reflecting the dominance of larger plants. Both populations were highly dissimilar to all the other populations, and clustered together in Q4 in the Sør plot (Fig. 7).

3.4.3. Group 3: Bell-shaped and irregular distributions

Nine of the 19 populations had clear bell-shaped SCDs, which were characterised by a dominance of intermediate-sized plants, with few juveniles and few very large adults. However, the bell shape was

sometimes more obvious in the SDR SCDs than height (Fig. 5). The P for bell-shaped SCDs tended to be low-intermediate, with the SCDs of only two populations having medium-high values (W1 and SB) and two with low values for both SDR and height (AK and KK; Table 3), which suggests an intermediate deviation from a monotonic decline for the majority of the populations. This trend is reaffirmed in the SCD slopes, 80% of which were gently negative (Table 4), which usually corresponded with very gentle bell curves. Evenness measures for bell-shaped SCDs were mostly intermediate-high (due to gentle bell-shapes evident in six populations), while SCDs with a pronounced spike at the peak of their bells (KK, LM and ZH) had low evenness. All the populations clustered together in Q2 of the Sør plot (Fig. 7), indicating high similarity between them.

The shapes of the seven populations with irregular SCDs often appeared different from one another and differences were also visible between SDR and height SCDs within populations. However, the Kolmogorov–Smirnov tests revealed that these within-population differences were only significant for BK and TWK (Table 2). P was medium-low across the group, λ was generally low for at least the SDR SCD or the height SCD for all, and E was medium-high (Table 3). The high Sør values within the group were very similar to those of the bell-shaped SCDs, except for TK and GS (Fig. 7).

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

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

4. Discussion

4.1. Variations in population size and density

Variations in population size and density within a species' distribution may result from numerous factors, such as differences in disturbance severity between sites (e.g. Helm and Witkowski, 2012), habitat degradation or fragmentation (e.g. Witkowski and Lamont, 1997), and the extent of available habitats for species with highly specific habitat requirements (e.g. García, 2008). The size and density of individual populations may also vary from year to year depending on spatial and temporal patterns in rainfall and disturbances such as fire and grazing (e.g. *Kniphofia umbrina* Codd, Witkowski et al., 2001). For *A. plicatilis*, possibly one of the most important determinants of population size and density is the extent of rocky areas available as fire refugia. Populations found in areas of low rock cover may be more severely impacted by fires and therefore less dense than those in very rocky sites. A population surveyed shortly after a very intense fire may also be less dense than one in an area that has not burned in many years: populations in older vegetation stands (>7 years) may have had time to recover from mortality in a previous fire. Confinement of populations to fire-safe 'islands' was evident at TW, SB, WL, W2 and ZH, where plants were clearly restricted to discrete rocky outcrops surrounded by areas with comparatively less rock cover. Notwithstanding, other populations (e.g. AK, BK and LM) were found in seemingly continuous rocky landscapes, but were limited to a particular patch or patches therein.

The occurrence of *A. plicatilis* on rocky outcrops in a patchwork of rocky and less-rocky sites means that plants are often clumped. This spatial arrangement of plants may explain the differences in the density estimates provided by the PCQ and NN methods. Marom (2006) also

obtained substantial differences in the density estimates of populations of several *Delosperma* species, a succulent plant genus that also occurs on rocky sites. Overall, PCQ density estimates for *A. plicatilis* ranged from 224 to 1356 plants/ha compared with NN estimates of 206–1331 plants/ha for the same populations, and thus they are quite comparable (Table 3).

Although *A. plicatilis* is a range restricted endemic, it occurs across comparatively wide rainfall and altitude gradients, but variation in temperature is more limited (Table 1). The sizes of the two populations at the easternmost extreme of the distribution (V1 & V2) were amongst the three smallest. Rainfall and temperature may be limiting factors at this range edge, as average annual rainfall diminishes and temperatures increase towards the Little Karoo east of Worcester. Higher temperatures and lower rainfall likely impose physical stress on the species, as plants at V1 and especially V2 displayed relatively depressed vigour and low reproductive output compared with three other populations for which flowering data were available (number of inflorescences per flowering individual = 2 ± 4 at V1, and 2 ± 1 at V2, compared with 4 ± 3 , 8 ± 9 and 6 ± 5 ($\bar{x} \pm$ S.D.) at GB, JH and W1 respectively, Cousins et al., 2013).

The geographical distribution of the species does not appear to show much support for the 'abundant centre hypothesis', which states that populations at the centre of a species' distribution are larger than those at the range edge (see citations in Sagarin and Gaines, 2002). PB, the westernmost population was considerably larger than V1 and V2, although this population was not formally surveyed for number of individuals, and the southernmost population (TWK) was the second largest. Five of the ten largest populations (KK, LM, DKK, ZH and GS) were close to the centre of the distribution, but the remaining five (TWK, W1, WL, SB and TK) were nearer the edges. These findings concur with the review by Sagarin and Gaines (2002), which showed that out of 145 studies that assessed abundance at various populations across species' distributions, only 39% showed support for the formerly widely accepted abundant centre hypothesis.

4.2. Trends in population size structure

4.2.1. Bell-shaped distributions

A cursory scan of most *A. plicatilis* populations may suggest that the species is a multi-stemmed aloe rather than a tree aloe (see classifications in Van Wyk and Smith, 2008), since many individuals appear compact and shrub-like, averaging 1–2 m in height. This generally ubiquitous, visually obvious pattern is reflected in the dominance of individuals in intermediate size classes and the bell-shaped SCDs. Some studies suggest bell-shaped SCDs may result from episodic recruitment (e.g. Witkowski and Liston, 1997; Venter and Witkowski, 2010; Helm and Witkowski, 2012), possibly during high rainfall years or after fire, when seedlings take advantage of increased light, nutrients and space. In most Mediterranean-type climate regions, and especially the Cape fynbos, fire plays a crucial role in determining major vegetation patterns, and is followed by mass recruitment events in many genera such as *Protea* L. and *Leucadendron* R. Br. (Keeley et al., 2012). Such pulsed recruitment typically results from the stimulation of post-fire flowering, seed release from serotinous species, breaking of physical seed dormancy, and smoke-induced germination (Bradshaw et al., 2011). However, a seedling search conducted 22 months post-fire at the *A. plicatilis* population KK yielded no seedlings, which suggests that mass post-fire recruitment is unlikely.

In studies on the population structure of *A. pillansii*, bell-shaped, J-shaped and bimodal SCDs were observed in many populations, and were ascribed to episodic recruitment linked to high rainfall events, although theft and herbivory of individuals in the smaller size classes were also cited as possible causes (Midgley et al., 1997; Bolus et al., 2004; Duncan et al., 2006). In contrast, the *A. plicatilis* fynbos sites are characterised by low inter-annual variation in rainfall (CV of inter-

annual rainfall = <25 to <35%) compared with Succulent Karoo and Nama Karoo sites where *A. pillansii* occurs (>35%) (Schulze, 1997a). Hence, episodic recruitment following unusually high rainfall events may be less likely for *A. plicatilis* than for *A. pillansii*. Rather, recruitment possibly involves the addition of small numbers of seedlings to the population over numerous years. Population persistence may therefore not be as reliant on large-scale recruitment events, but rather on the survival of long-lived adult plants.

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

However, the trend is not so clear-cut, as SCDs obtained for other similar long-lived species such as cacti (e.g. Godínez-Alvarez and Valiente-Banuet, 2004), cycads (e.g. Negrón-Ortiz and Breckon, 1989; Watkinson and Powell, 1997; Raimondo and Donaldson, 2003; Pérez Farrera and Vovides, 2004) and tree succulents (e.g. Midgley et al., 1997; Bolus et al., 2004; Duncan et al., 2006) were a mixture of inverse J, bimodal, bell-shaped and J-shaped, the majority being bimodal. Many species were said to display episodic recruitment, which may account for the dominance of bimodal distributions. Moreover, bell-shaped and bimodal SCDs have also been observed in many forests (e.g. Everard et al., 1995) and savanna trees (e.g. Walker et al., 1986; Helm and Witkowski, 2012).

Based on measurements of six *A. plicatilis* plants planted as seedlings at the Kirstenbosch National Botanical Garden in Cape Town, in 1982, the species has a height growth rate of ± 3 cm/year under garden conditions. A one metre tall individual in the wild would therefore be a minimum of 33 years old, while a very large three metre plant would be ≥ 100 years old. As a result of these slow growth rates and considerable longevity, adult plants, which have a much higher survival probability relative to seedlings and juveniles, would spend many years in the adult size classes before eventually senescing. Thus, if a species employs an adult-persistence survival strategy, whereby populations are consistently dominated by medium-to-large adults with very high survival probabilities, (hence resulting in a bell- or J-shaped SCD) then minimal, intermittent recruitment is not a cause for concern, as long as senescing adults are continually replaced by new recruits.

Besides the hypothesised adult-persistence survival strategy, two other factors may also account for the preponderance of medium-sized *A. plicatilis* plants in many populations. Firstly, some plants may be displaying a 'bonsai effect' whereby restricted rooting space in the rock crevices in which the plants grow limits their size. There is a considerable body of literature on the effects of root restriction on plants, focusing primarily on the growth of plants in small pots (e.g. Tschaplinski and Blake, 1985; Boland et al., 1994). In most of these experiments, plants grown in small pots showed reduced aboveground biomass, belowground biomass and growth rate, thus demonstrating the relationship between root and shoot growth. Thus, individuals

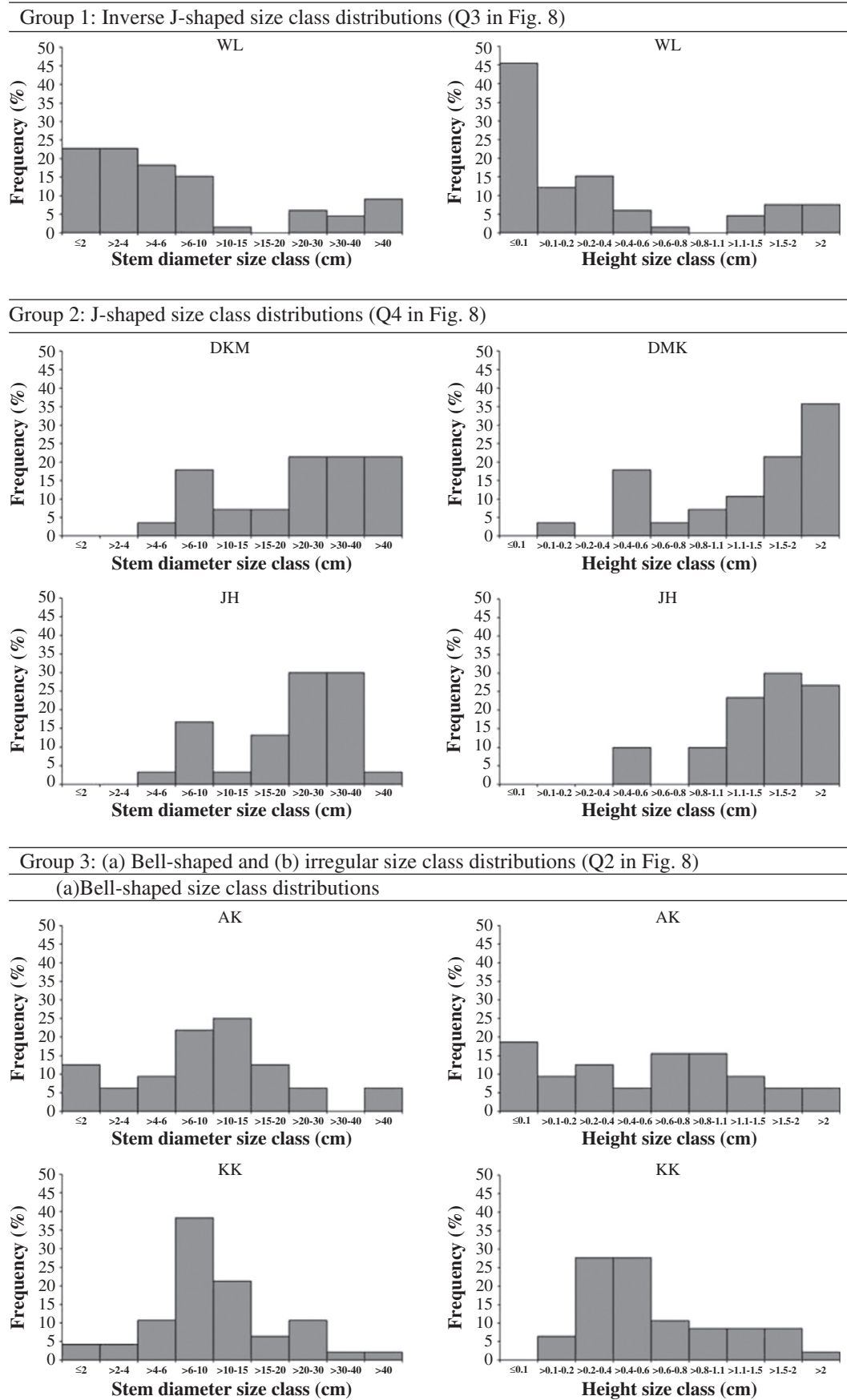


Fig. 5. Stem diameter (SDr) and height size class distributions (SCDs) for 19 surveyed *Aloe plicatilis* populations in the Western Cape, South Africa. Key to population name abbreviations in Fig. 1.

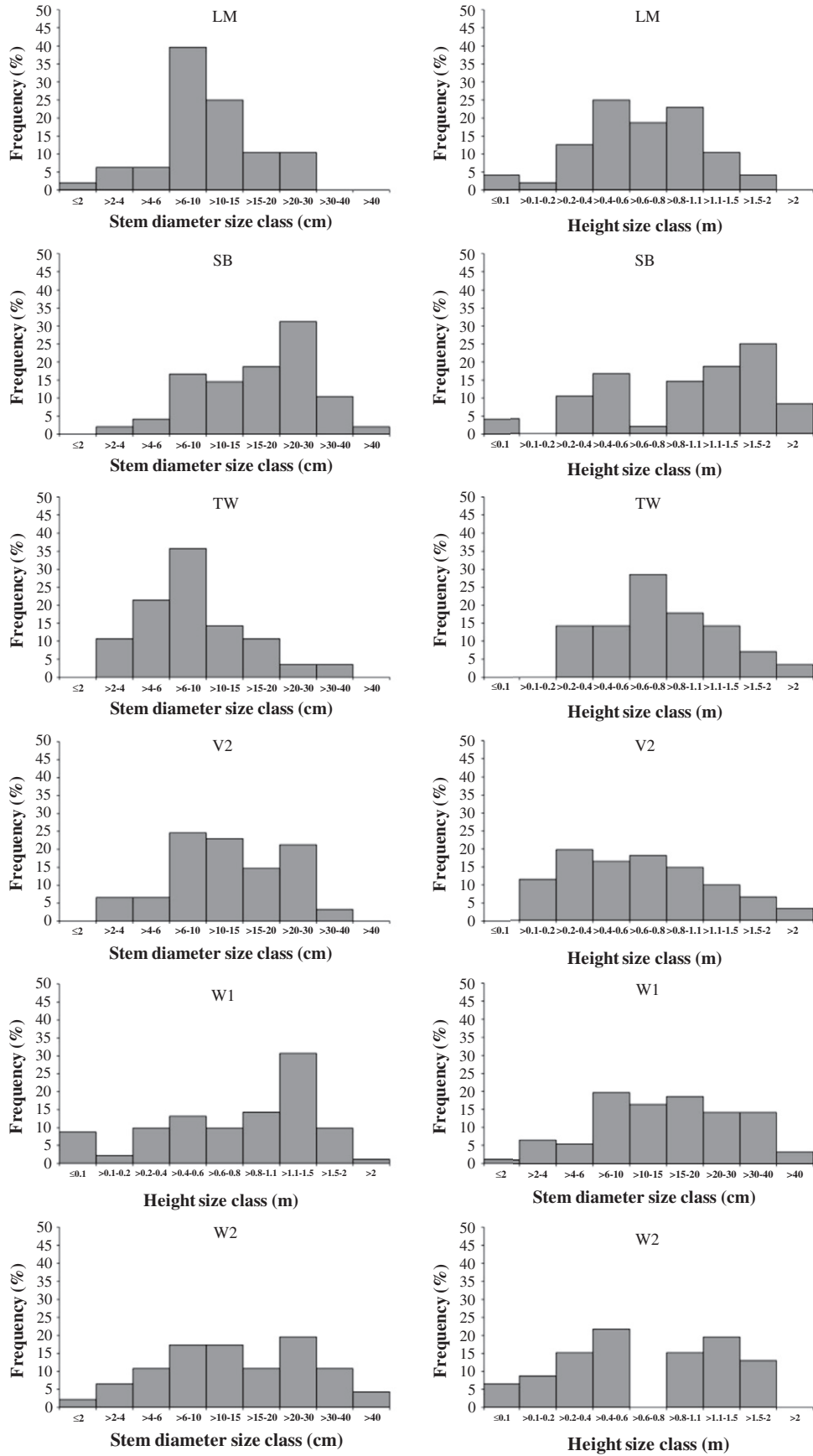
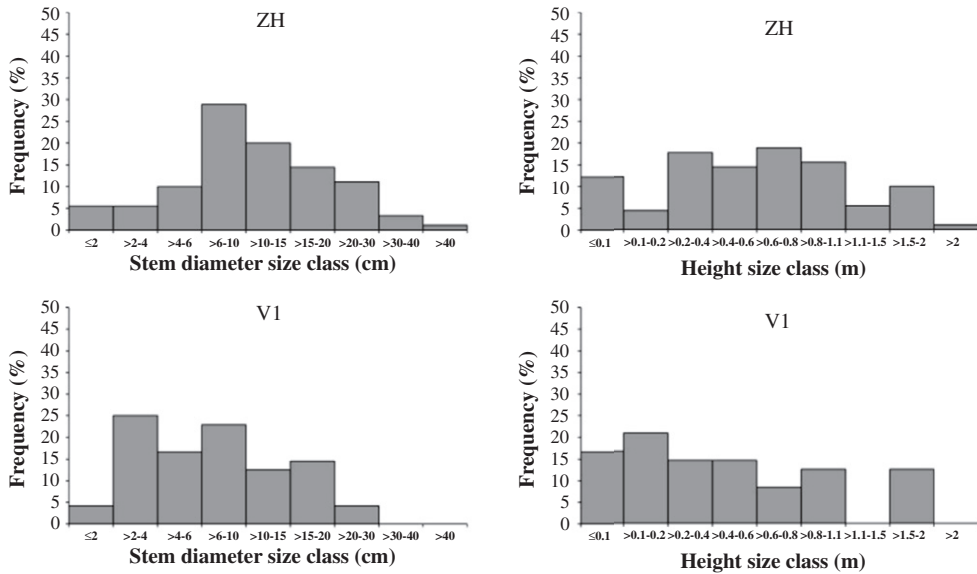


Fig. 5 (continued).



(b) Irregular size class distributions

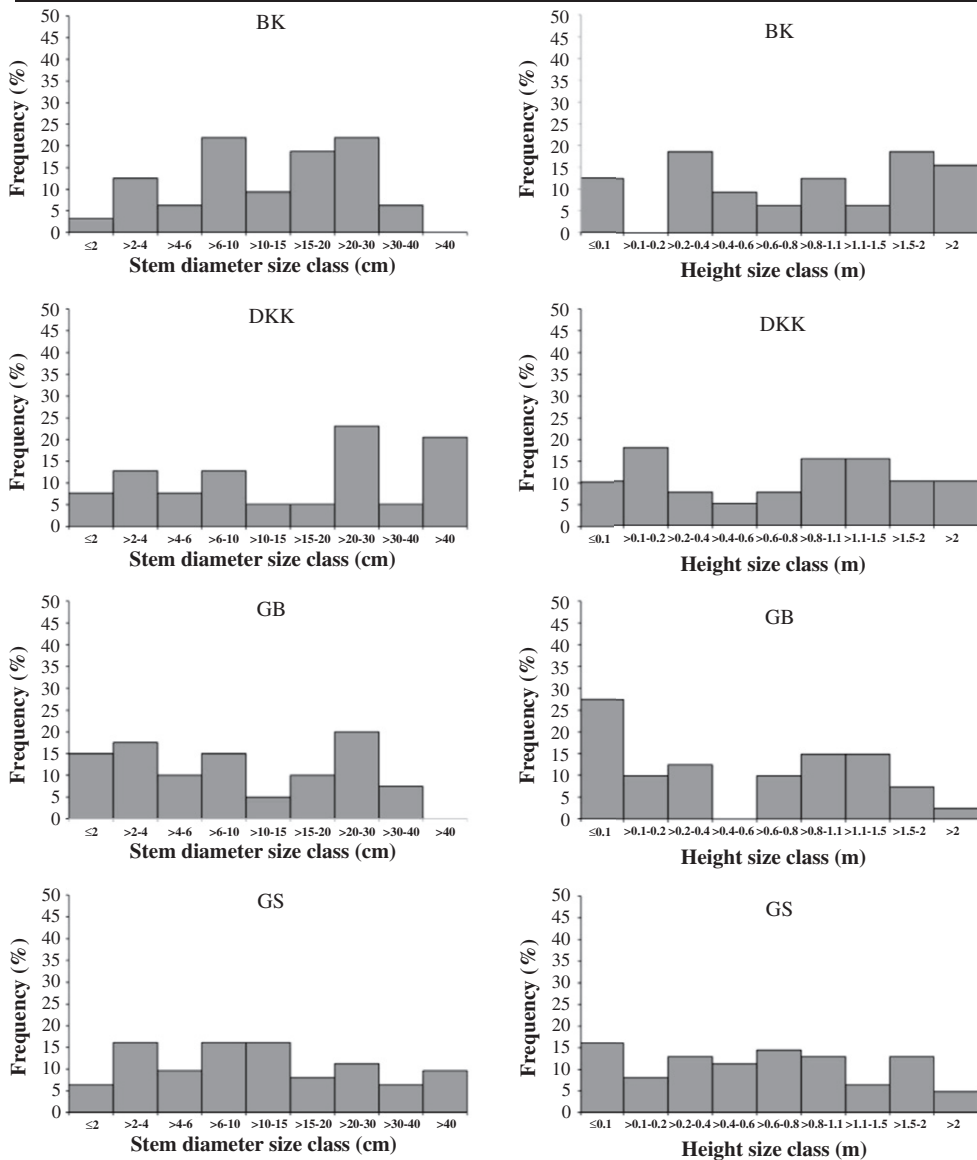


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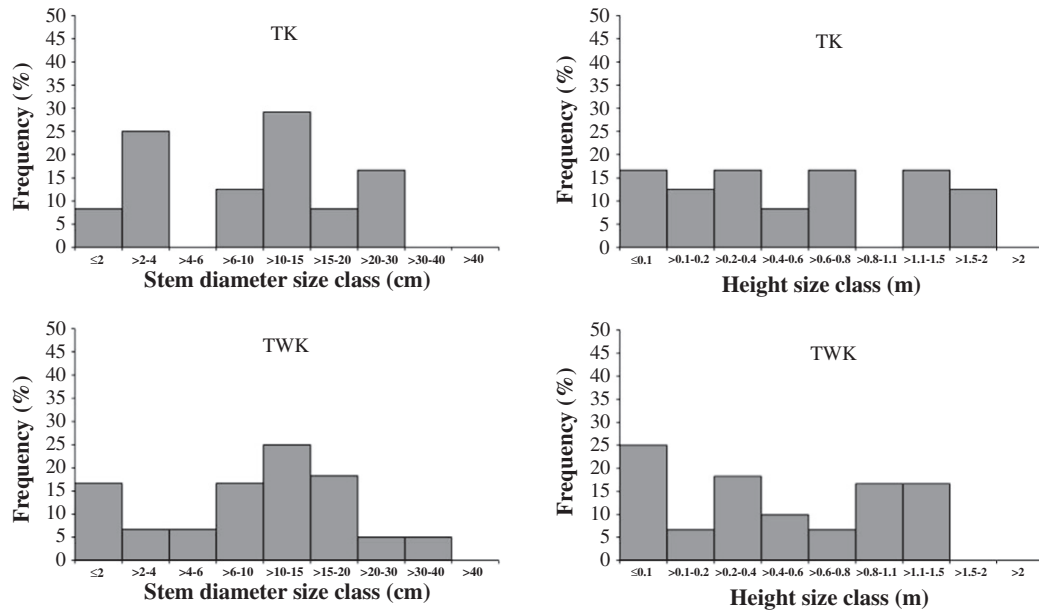


Fig. 5 (continued).

growing in very rocky sites may be smaller than plants of equal age growing in less rocky sites, where greater rooting space has allowed them to grow larger. Bonsai plants may remain as non-reproductive 'suppressed juveniles' (Fig. 6C) for many years during which the onset of flowering is delayed due to growth restrictions and resource limitation, which is considered a key factor in determining the time of first flowering in plants (Lacey, 1986). Upon accumulation of sufficient resources for reproduction, these individuals may become 'reproductive dwarfs', flowering at a size smaller than is typical for the species (Fig. 6B). However, there appears to be a trade-off between the degree of protection from fire and plant size, whereby individuals growing in extremely rocky sites are well-protected, but often stunted (bonsai plants), while plants in less-rocky sites can attain greater sizes, but are less protected from fires.

Secondly, strong, persistent winds may impose height restrictions on the canopy of *A. plicatilis* individuals. The south-western Cape is known for its strong, persistent summer winds, with gusts of up to 128 km/h recorded in Cape Town (Kruger et al., 2010). Large plants growing in exposed sites may be more vulnerable to damage from strong winds. The succulent growth form of *A. plicatilis*, its heavy mass and shallow root system may render this species particularly vulnerable to damage from strong winds. At some populations observations were made of large adult plants that had been toppled over, presumably by wind, but continued to grow if their roots were still partially underground. In general, plants growing in windy places are known to display growth patterns different from plants growing under calm conditions: trees are bent leeward, and/or grow shorter (De Langre, 2008). Mechanically manipulated plant stems grow shorter and, generally speaking, stronger (Watt et al., 2005). Hence, plants are able to adjust their height and slenderness biologically by mechanosensing physical stimuli, including wind (De Langre, 2008). Wind therefore possibly plays a role in limiting the height of *A. plicatilis* individuals growing on very exposed hillsides (Fig. 6F) compared to protected rocky alcoves (Fig. 6G) or amongst shrubs and trees. However, separating this effect from growth restrictions due to limited rooting space/depth is difficult.

4.2.2. Deviations from the bell-shaped distribution

A striking result in this study was that the inverse J-shaped SCD, which has traditionally been thought to be indicative of a healthy, stable and strongly recruiting population (Weiner and Solbrig,

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

Since *A. plicatilis* does not appear to be an episodic recruiter (as suggested by the paucity of inverse J-shaped and bimodal SCDs), the high recruitment observed at WL is unusual. The population last burned 12 years prior to the survey, which supports the hypothesis that recruitment in the species is not strongly linked to fire. WL covered only a single hilltop (0.82 ha), but the size of the population was fairly large and it was also the densest population surveyed (3043 plants/ha). It occurs in close proximity (<1 km) to another reasonably large population (SB), which shares very similar rainfall and temperatures, yet SB exhibits a bell-shaped SCD. It is therefore unclear why WL displays such high levels of recruitment, but it may be that the hilltop offers particularly favourable microsites for seedling establishment. Out of all 19 populations WL had the second highest average rock cover (mean \pm S.D. = $75 \pm 20\%$) around sampled *A. plicatilis* individuals. Furthermore, most of the juveniles at WL were found growing amongst rocks in partially shaded areas under trees and shrubs. These shaded rocky sites possibly provided ideal conditions for seedling establishment, since aloe, and succulents in general, are known to require nurse plants for establishment in wild populations (Godínez-Alvarez et al., 2003; Cousins and Witkowski, 2012).

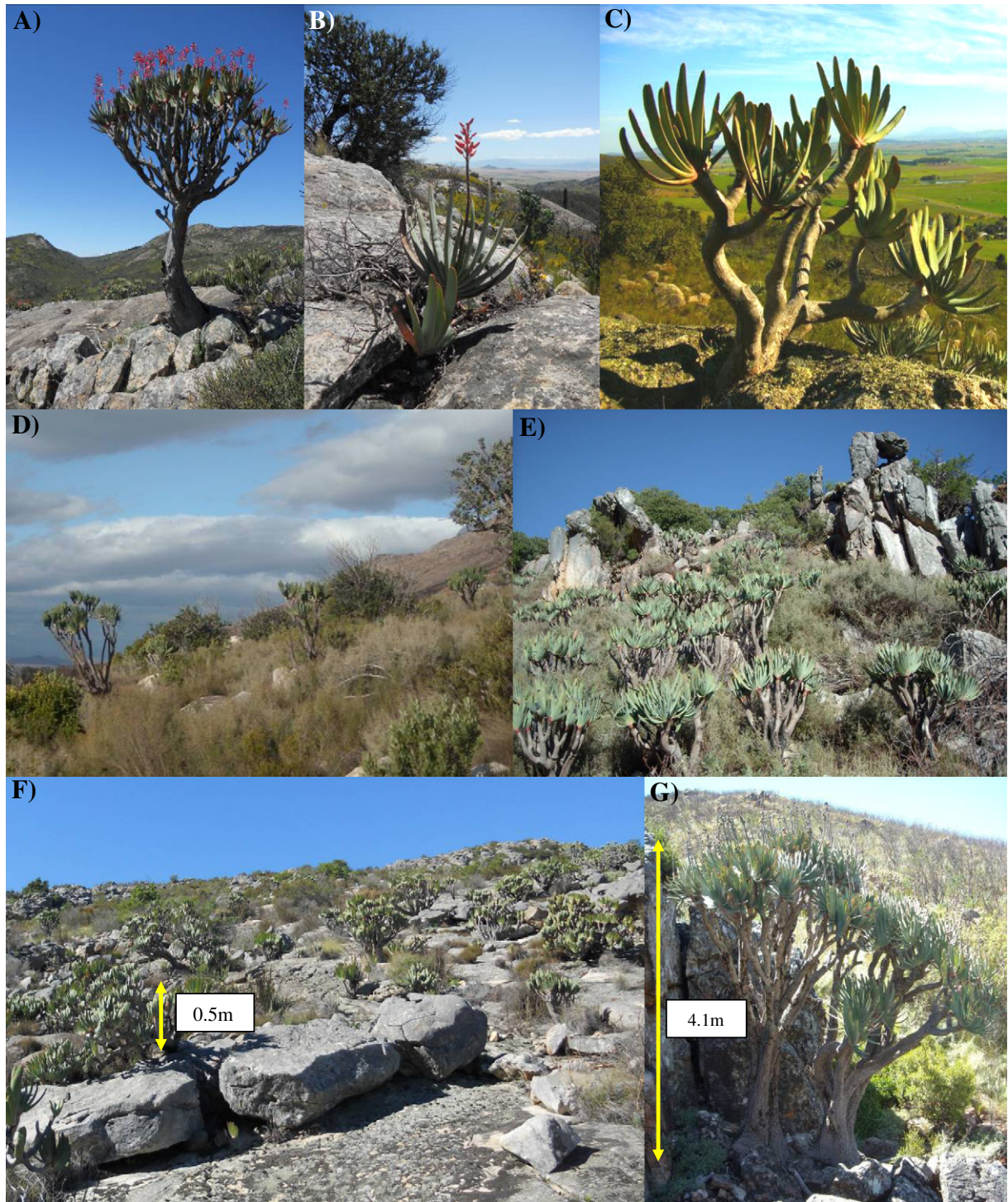


Fig. 6. (A) Reproductive adult *Aloe plicatilis* individual ~2 m high with numerous inflorescences. (B) A juvenile *A. plicatilis* individual in front of a 'reproductive dwarf', which appears to be a juvenile due to its short height (~0.2 m) and small stem diameter (~8 cm), but the presence of an inflorescence indicates reproductive maturity. (C) A 'suppressed juvenile' (~0.4 m) that has possibly remained in the juvenile stage class for many years, yet is of the age at which it could potentially reproduce. (D) *Aloe plicatilis* at Jason's Hill (JH) showing a very sparse distribution of mostly large adults. (E) A stand of *A. plicatilis* at La Motte (LM) showing a very dense aggregation of similar-sized plants. (F) The two largest large *A. plicatilis* individuals observed out of all 19 populations. These plants were growing at Du Toit's Kloof Krom River (DKK) in a rocky alcove that provided shelter from strong winds and fire, thus reducing mechanical stress on the plants and allowing them to attain considerable height. (G) Part of an *A. plicatilis* population on Saronskop near Tulbagh consisting primarily of short, compact individuals (~0.5 m) on an exposed, rocky hillside, where persistent strong summer winds possibly limit plant height.

Only two populations displayed J.-shaped SCDs (DKM and JH), but only JH appears to be in decline. DKM last burned in 2007, three years before the survey, and the presence of a number of standing dead adults suggested a hot fire. The absence of small juveniles suggests that the fire had killed them before they had grown large enough to survive. The adult plants at DKM appeared otherwise healthy, and fruit production

at the time of the survey was high. A section of the population where a rockfall had occurred was missed by the fire, and a number of small *A. plicatilis* individuals were found growing between the rocks, which acted as a fire barrier. However, the sampling transect placed across the population also missed this section and hence these juveniles were not reflected in the SCD. Due to this observed recruitment, and

Table 2

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

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

^a Key to population abbreviations in Fig. 1.

^b Estimated maximum AOO including inaccessible parts of population not included in the population periphery GPS coordinate dataset.

^c Estimated maximum population size using maximum AOO.

^d Minimum AOO and estimated population size for LM, since the population extended beyond the bounds of the surveyed area.

the presence of many large, reproductive adults, DKM is not considered to be in decline. Furthermore, the presence of juveniles in unburned sites and their absence in the burned patches further supports the hypothesis that *A. plicatilis* is not a post-fire recruiter.

JH was the smallest population (31 plants), by far the least dense (75 plants/ha) and had the steepest positive SCD slope. Cousins et al. (2013) showed that of the populations GB, JH and W1, plants at JH

exhibited the lowest seed set/plant and per population. Several plants had inflorescence abortion rates of 75–100% and inflorescences that did produce fruits were often highly predated by birds. Hence, JH appears to be displaying the Allee effect whereby the fitness of individual plants in a small and/or sparse population declines as population size or density decreases (Stephens et al., 1999). *Aloe plicatilis* individuals at JH may be too few and too far apart to attract sufficient pollinators, resulting

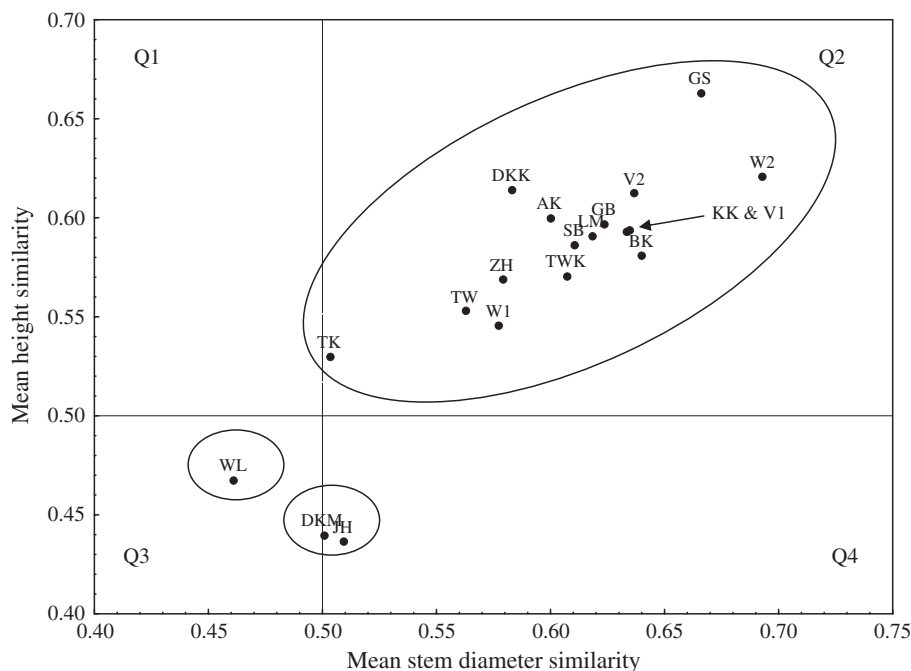


Fig. 7. Regression relationship between mean Sørensen similarity index for height and stem diameter between populations. Mean similarity values indicate the degree to which the structure of each population is similar to that of all the other populations combined. Q1: High height similarity, but low stem diameter (SDr) similarity; Q2: High height and high SDR similarity; Q3: Low height and low SDR similarity; Q4: Low height and high SDR similarity. See Fig. 1 for key to population abbreviations.

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

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

in pollen and/or pollination limitation. The lack of recruitment and the preponderance of large adult plants suggest that the population may undergo local extirpation if reproductive failure persists.

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

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

This is the first study we know of to align SDR and height SCDs for a single species and draw comparisons between them to test levels of agreement within populations. The few significant differences between SDR and height SCDs within populations (five out of 19) suggest that SDR and height size class bins were well aligned using the regression relationship between SDR and height. Furthermore, few differences between SDR and height SCDs also suggest that for *A. plicatilis*, SDR and height measurements portray population structure equally well. Hence, if repeat surveys were to be conducted, one could measure either one or the other, which would limit the time and costs involved.

5. Conclusion

Aloe plicatilis populations showed wide variation in population size and density, but there was no relationship between the size or density of a population and its position within the species' geographical distribution. Frequent bell-shaped size class distributions (SCD) and the occurrence of only one population with an inverse J-shaped SCD suggest that *A. plicatilis* adopts an adult-persistence population survival strategy, whereby populations consist mainly of medium-to-large adults, with low recruitment rates, but are nonetheless stable. This

Table 4
Size class distribution (SCD) slope of the regression between size class midpoint and the number of plants per size class for stem diameter and height SCDs of 19 populations of *Aloe plicatilis* in the south-western Cape, South Africa. Significant relationships are indicated in bold. Key to population abbreviations in Fig. 1.

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

finding challenges the suitability of the inverse J-shaped SCD as the only indicator of a stable, 'healthy' population for slow-growing, long-lived species. The dominance of medium-sized shrub-like adults in many populations may result from growth restrictions imposed by limited rooting space and strong persistent winds that might otherwise topple tall individuals growing in exposed sites. This study provides important baseline data on the demographics of *A. plicatilis* populations for monitoring, and offers useful insights into trends in the demographics of slow-growing, long-lived plant species in general.

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