

Vachellia erioloba dynamics over 38 years in the Kalahari Gemsbok National Park, South Africa



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Vachellia erioloba is a keystone tree species in the southern Kalahari. This long-term study over nearly four decades tracks two populations in different landscapes (the interior sandy duneveld versus the clayey Nossob riverbed) of a large conservation area and offers valuable data on this species under natural soil moisture conditions and with limited anthropogenic influences. In 1978, 18 trees were permanently marked in a 1 ha plot in the interior duneveld of the Kalahari Gemsbok National Park (Dankbaar site). In the Nossob riverbed all trees in a 1 ha plot were surveyed in 1979 (Grootkolk site). At both sites, tree height and stem circumference were subsequently measured at irregular intervals until 2016 in order to investigate growth rates and population structure. Of the 18 marked trees at Dankbaar, six died and three showed coppice regrowth following substantial dieback after a fire. A mean height increase of 60 mm/year was recorded and the mean height of the remaining uncoppiced trees was 6.8 m in 2016. Stem diameter growth rate per year varied widely between trees and between years with a mean value of 2.5 mm/year over the 38-year period. Growth rate calculated for three 10-year intervals varied. Using the mean growth rate derived in the current study and stem size of the dead trees, the mean age of the trees when they died was estimated. At the Grootkolk site, the position of the centroid in relation to the midpoint of the diameter class range suggests that this population is gradually becoming a mature to old population with limited recruitment. This was supported by the size class distribution curves. However, no differences between slopes or intercepts of the stem diameter size class distributions were found.

Conservation implications: This study was conducted in a large conservation area, that is, a natural ecosystem excluding most of the anthropogenic threats that are present outside of the park. The study illustrated that in the duneveld the population studied was self-sustaining, with recruitment occurring and large individuals presumably dying of old age. Although fire caused a few individuals to coppice, no fire-related deaths were reported. In the Nossob riverbed, surveys started in a stand of predominantly young trees and the size class distribution at that stage already showed a lack of recruitment. This stand is ageing and will likely disappear at this site; however, new young stands are appearing at other sites in the Nossob riverbed. Under the current conditions with negligible anthropogenic influences, it therefore appears that some *V. erioloba* populations in the park are increasing in size while others are decreasing, but that overall the species will persist. The impact of global climate change on this species is, however, unknown.

Keywords: conservation area; growth rate; Kgalagadi Transfrontier Park; long-term study; size class distribution; tree age.

Introduction

Ecological patterns generated from a single snapshot in time should be used carefully when trying to identify the underlying processes driving the system (Jeltsch, Moloney & Milton 1999), and long-term data can be very useful to assist with the interpretation of ecosystem patterns and processes. However, appropriate long-term data are difficult to find in the case of long-lived organisms such as trees, whose lifetimes are usually considerably longer than those of researchers (Menges 2000). In arid systems, this is further exacerbated by low rates of biotic change (Cody 2000; Lawley et al. 2013; Van Rooyen et al. 2015). In such systems, to accommodate climatic fluctuations, the monitoring of woody species should take place over a timespan in excess of 20 years (O'Connor 1985).

In arid savannas, the tree component may seem to be constituted by even-aged cohorts (Midgley & Bond 2001; Wiegand, Ward & Saltz 2005); however, what appear to be cohorts among adult trees may not be even-aged individuals (Seymour 2008). Even-aged stands are interpreted

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as evidence of the importance of abiotic factors, particularly rainfall, to produce pulsed recruitment. Apparent even-aged stands signify the release from fire or herbivory whereby different-aged saplings are allowed to recruit simultaneously into larger height classes, thus appearing of equal age (Midgley & Bond 2001).

In the southern Kalahari, *Vachellia erioloba* is regarded as a keystone species because it provides food, shelter, perches, nests and roost sites to many types of animals and harbours a distinct assemblage of plant species below its canopy (Barnes 2001; Leistner 1967; Milton & Dean 1995; Seymour 2008; Steenkamp et al. 2008). It is listed as a protected tree species in South Africa (Government Notice no. 1602, 2016). There are, however, growing concerns over increased mortality in mature *V. erioloba* in the southwestern Kalahari (Schachtschneider & February 2013). The reasons proposed for the increase in mortality include an increase in fire frequency (Seymour & Huyser 2008), increasing groundwater abstraction (Powell 2005; Shadwell & February 2017), harvesting (Seymour 2008), diseases (Slippers et al. 2014), arboricides (Powell 2005) and competition for resources from alien invasive species such as *Prosopis* (Robertson & Woodborne 2002; Schachtschneider & February 2013; Zachariades, Hoffman & Roberts 2011). These threats are especially relevant outside of conservation areas, emphasising the importance of protected environments in which *V. erioloba* individuals, exposed only to natural threats such as fire, can be studied.

Vachellia erioloba is a long-lived tree with a lifespan in excess of 240 years (Steenkamp et al. 2008). Mature individuals of this species are reportedly not easily affected by short-term climatic variations (Barnes 2001), possibly because individuals have some of the deepest roots of any known species (the maximum recorded is 68 m), allowing them access to deep groundwater sources (Jennings 1974 in Moustakas et al. 2006). Quantitative information on growth rates and lifespan of the species are, however, still inadequate (Steenkamp et al. 2008).

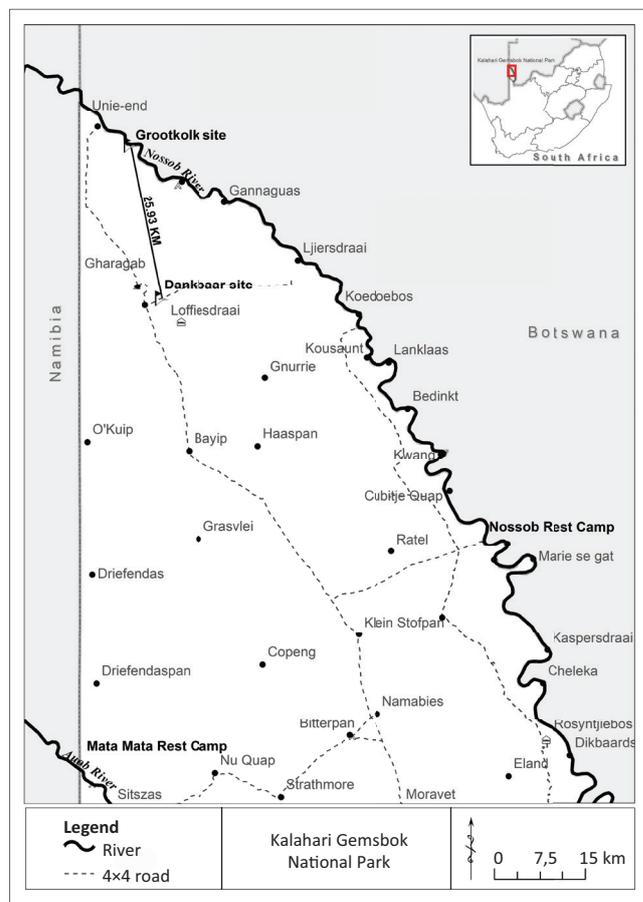
From 1978, surveys were initiated in the Kalahari Gemsbok National Park (KGNP) to gather information on the growth rate, lifespan and population dynamics of *V. erioloba* in the interior duneveld (Dankbaar) and in the Nossob riverbed habitats (Grootkolk). The objectives of this paper were (1) to report on the mean annual increase in stem diameter and tree height of the 18 marked *V. erioloba* trees at the Dankbaar site; and (2) to document the mean age of those trees that died in the interior duneveld of the park; and (3) at the Grootkolk site to describe changes in the size class distribution of a *V. erioloba* population in the Nossob riverbed. The publication of these findings contributes to our understanding of *V. erioloba* population dynamics within large conservation areas without many of the anthropogenic factors proposed to increase mortality in this species.

Study area

The KGNP is situated in the southern Kalahari (24°15'S–26°30'S and 20°00'E–20°45'E) and covers approximately 9600 km² (Figure 1). It forms part of the Kgalagadi Transfrontier Park, together with the Gemsbok National Park in Botswana.

The mean annual rainfall recorded from 1976 to 2015 at Nossob Rest Camp in the park is 194 mm (Figure 2), with most rain falling between January and April. The annual rainfall has a high coefficient of variation and the rain often falls as short-duration, high-intensity thunderstorms. Temperatures show a large range, with winter lows reaching -10.3 °C and summer highs reaching 45.4 °C (Van Rooyen & Van Rooyen 1998).

Sampling was conducted at two sites (Figure 1). The first site is situated 2.7 km east of Dankbaar (1040 m above sea level) in the interior duneveld in the *Acacia* (*Vachellia*) *erioloba* – *Schmidtia kalahariensis* low duneveld landscape (Van Rooyen et al. 2008). This open tree savanna, dominated by *V. erioloba* (tree) and *S. kalahariensis* (grass), occurs in the interior duneveld in the northern part of the park. The aeolian sands of the Low Duneveld landscape are piled into a gently undulating landscape. Beneath the sand lies a vast sheet of calcareous or silicified sand or sandstone that contains grits



km, kilometres.

FIGURE 1: Location of the two *Vachellia erioloba* study sites, Dankbaar situated in the interior duneveld and Grootkolk located in the Nossob riverbed, within the Kalahari Gemsbok National Park.

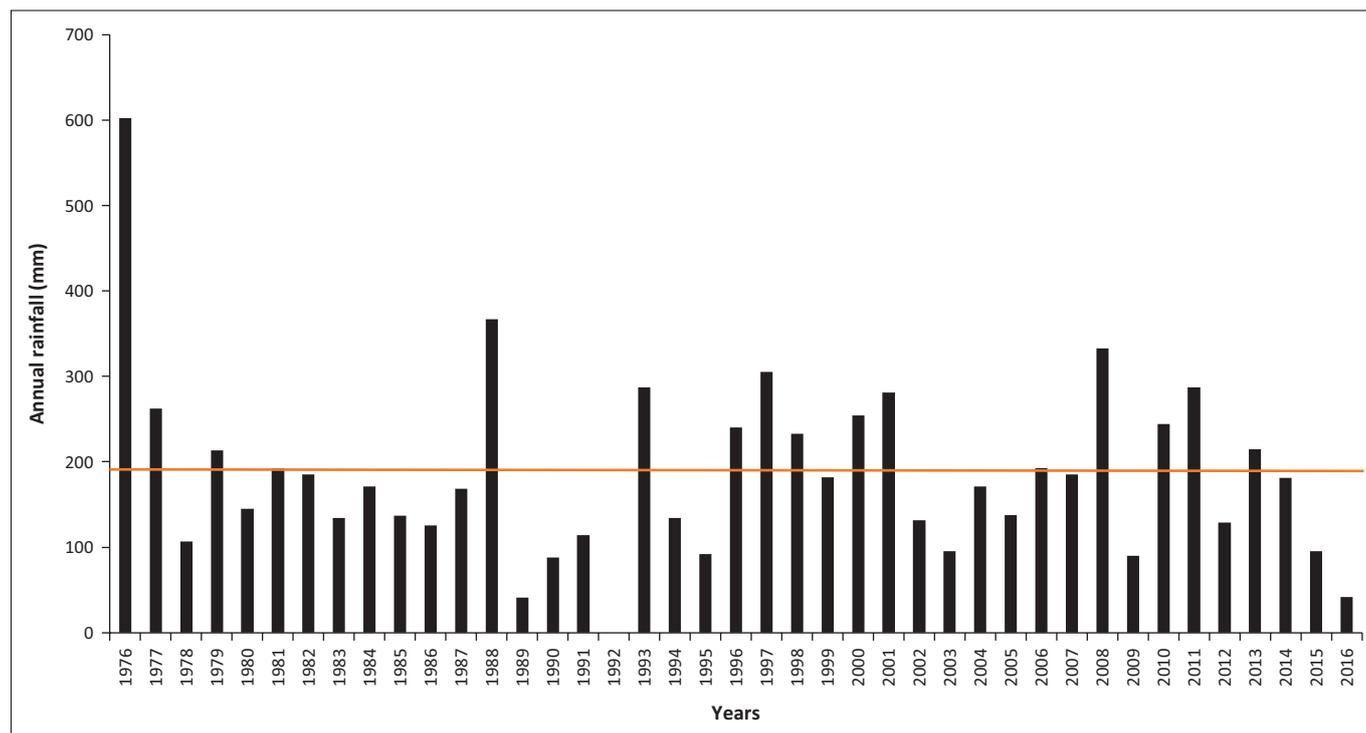


FIGURE 2: Total annual rainfall (January to December) at Nossob Rest Camp from 1976 until 2016. The orange line represents the mean annual rainfall of 194 mm.

and minor conglomerates (Malherbe 1984). Van Rooyen (1984) describes the duneveld soils as deep, red, eutrophic, fine and medium sandy soils of the Hutton soil form, or yellow-brown, eutrophic and calcareous, fine to medium sandy soils of the Clovelly soil form (Soil Classification Working Group 1991). The second site, at Grootkolk (1041 m above sea level), is situated in the Nossob riverbed in the *Acacia (Vachellia) erioloba* – *Acacia (Vachellia) haematoxylon* riverbeds landscape (Van Rooyen et al. 2008). This landscape is characterised by large scattered *V. erioloba* trees with a dense grass stratum dominated by *Panicum coloratum*. Van Rooyen (1984) described the Nossob riverbed's soil as deep, calcareous, reddish-brown and grey-brown loam with clay soils of the Oakleaf, Dundee and Valsrivier soil forms. Upstream from the Grootkolk site, shallow, brown and yellow-brown calcareous sands and loams of the Mispah soil form occur (Soil Classification Working Group 1991). Fine-grained soils in arid areas show the so-called inverse texture effect (Noy-Meir 1973), with the result that there is less available soil water and consequently lower production on fine-textured soils than on coarse-textured soils (Van Rooyen et al. 1984).

Methods

Field surveys

Two study sites (Dankbaar site and Grootkolk site) were surveyed on numerous occasions; however, survey methods used at these two sites differed. In 1978, all *V. erioloba* trees were marked in a 1 ha plot at the Dankbaar site. Tree height and stem circumference were recorded for each of the 18 permanently marked trees at irregular intervals from 1978 to 2016 (survey years 1978, 1980, 1983, 1985, 1988, 1989, 1991, 1994, 1998, 1999, 2008 and 2016). In 2016, for the first time

since the original survey in 1978, all additional trees within the plot were measured and permanently marked.

At the 1 hectare (ha) Grootkolk site, height and stem circumference of all *V. erioloba* individuals were measured at irregular intervals from 1979 to 2016 (survey years 1979, 1984, 1986, 1989, 1994, 1996, 1999, 2008 and 2016). The stem circumferences of all dead trees were also recorded at Grootkolk in the year of the survey when the tree was found to have died.

Analysis

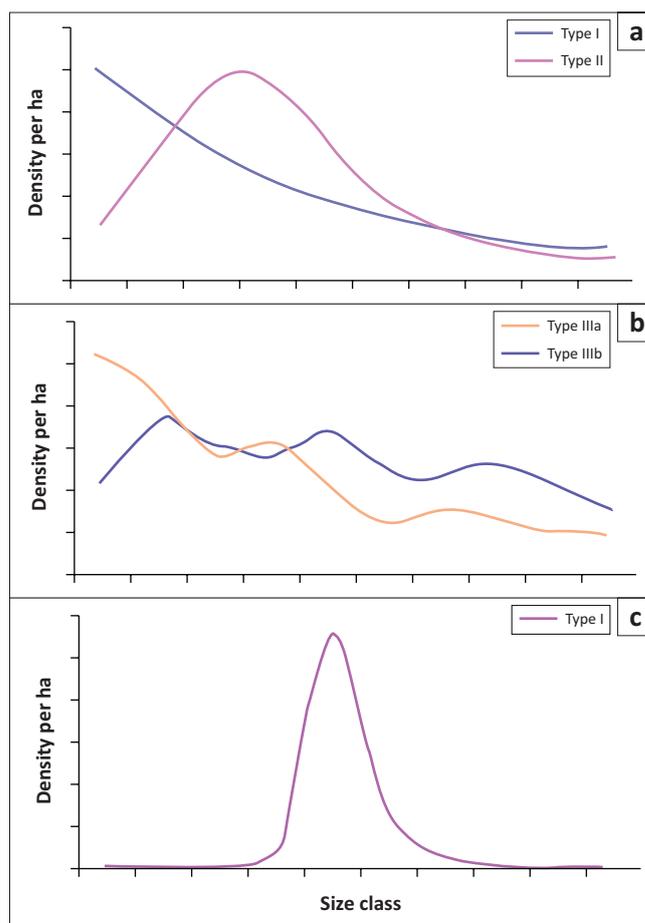
Because of the different survey methods used at the two sites; the data collected could not be analysed in the same manner for both the sites. For example, only the 18 marked trees at Dankbaar were surveyed throughout the 38-year period; thus an analysis of the population structure is inappropriate as the entire population in the 1 ha plot was not surveyed.

An estimate of the growth rate per year over the entire study period (38 years) was calculated for each marked tree at the Dankbaar site by subtracting the first measured stem diameter (1978 survey) from the last live measured stem diameter and dividing by the number of years between these two measurements. Similarly, this method was used to calculate changes in height of a tree. A linear regression using GraphPad 7.02 (GraphPad Software, www.graphpad.com) of stem diameter versus annual growth rate was used to investigate the relationship between these two variables. Additionally, stem diameter growth rates over the first 10-year period (1978–1988), second 10-year period (1988–1998) and third 10-year period (1988–2008) were calculated for each marked individual. This was calculated in the same

way as for the entire period, but using the first and last measured diameters for the appropriate periods and calculating a mean across all the individuals. Dead and coppiced individuals were excluded from the calculations from the survey year in which the death or coppicing was recorded for the first time.

The mean stem diameter in 1978 and 2016 of all marked trees was used to estimate the average age using the growth rate determined in the current study. The average age of all the marked trees in 1978 and in 2016 were calculated by dividing the mean stem diameter for the particular year by the growth rate determined in the current study. For comparative purposes the mean age of the trees was also calculated by the same method using the mean diameter growth rate for only the interior duneveld (3.2 mm/year) and for the interior duneveld and riverbed combined (3.6 mm/year) reported by Steenkamp et al. (2008). Age was also determined using the growth rate for the interior duneveld and riverbed combined (5.1 mm/year) based on the equation derived for the relationship between radiocarbon age and stem circumference (Steenkamp et al. 2008). These calculations were made using the mean stem diameter of the live trees in 2016 as well as the last 'alive' measured stem diameter for the dead trees. These calculations were also performed for the Grootkolk population using the mean stem diameter of the stem circumference classes.

The stem circumferences for trees at the Grootkolk 1 ha plot were classified into 12 equal stem circumference classes (0–20, > 20–40, > 40–60, > 60–80, > 80–100, > 100–120, > 120–140, > 140–160, > 160–180, > 180–200, > 200–220, > 220–240 starting with class 1 and ending with class 12) for each of the survey years. The size class distribution was examined visually to classify the population into one of four population structure types (Gaugris & Van Rooyen 2007; Figure 3). In this model, Type I size class distribution represents a growing population and follows an inverse J-shaped curve, which represents the ideal curve shape for a growing population in a natural environment. There is a constant decrease in the number of individuals as the size classes increase, and the curve spans the whole range of size classes described for the species. Populations with a Type II curve have a near ideal population structure that differs from a Type I only by having a lower abundance of smaller size classes. Populations with Type III size class distributions are typically associated with disturbance. The Type IIIa curve broadly resembles a Type I size class distribution but applies to populations where a section of the curve spanning one or several size classes is missing or where abundance is lower than expected. The typical large pool of small individuals is generally missing in Type IIIb and the size class distribution shows a succession of minor peaks, even with some gaps where one or several size classes may be missing altogether. In the Type IV curve, one or two peaks are observed over a restricted range of size classes, and this curve thus represents an abnormal size class distribution. The curve is either bell-shaped with a peak more or less in the middle of the size



Source: Adapted from Gaugris, J.Y. & Van Rooyen, M.W., 2007, 'The structure and harvesting potential of the sand forest in Tshanini Game Reserve, South Africa', *South African Journal of Botany* 73, 611–622. <https://doi.org/10.1016/j.sajb.2007.06.004>

FIGURE 3: Idealised shapes of the four different population curve types.

class range, or it shows a high frequency of large size classes, with little or no representation of smaller classes.

For the 1 ha Grootkolk site the number of individuals recorded per stem circumference size class was calculated in order to obtain the density of trees per size class. Regressions were performed on the density (D_i) of individuals against size class (M_i) (Gaugris & Van Rooyen 2007). The diameter class midpoint (M_i) was calculated as the mean of the upper and lower limit of each size class (Condit et al. 1998). Logarithmic transformations, $\ln(D_i + 1)$ and $\ln(M_i)$, were used to standardise the data (Lykke 1998; Niklas, Midgley & Rand 2003) before performing least square linear regressions, that is, $\ln(D_i + 1)$ for the y -axis and $\ln(M_i)$ for the x -axis. The value of +1 was added because some size class bins were empty (Lykke 1998). The linear regressions were evaluated in terms of their slopes and y -axis intercepts (Gaugris, Vasicek & Van Rooyen 2012; Van der Merwe & Geldenhuys 2017). Strongly negative slopes typically represent regenerating populations (Condit et al. 1998), and a high y -axis intercept indicates many small individuals in the population. A y -axis intercept near to zero indicates that few small individuals are present (Everard, Midgley & Van Wyk 1994). Both slopes and y -axis intercepts of regressions were compared statistically across

years by means of an analysis of covariance using GraphPad 7.02 (GraphPad Software, www.graphpad.com).

Two additional mean values were calculated for the stem diameter distribution for each survey year: (1) the 'centroid' was calculated as the arithmetic mean of all stem diameters recorded; and (2) the 'midpoint of stem diameter range' was calculated as the mean of the upper and lower limits of the diameter range included in the size class distribution. Niklas et al. (2003) found a relationship between the position of the centroid and the diameter class range midpoint for a species. If a centroid value is smaller than the midpoint value, the population is young and growing. When the centroid value is larger than the midpoint value, the population is mature to old. In general, as the mean stem diameter increases in a population, self-thinning occurs and the density decreases, in such a way that an increasing part of the biomass is found in fewer individuals (Niklas et al. 2003; Silvertown & Charlesworth 2001). As self-thinning occurs the centroid of a population shifts towards the right within the size class distribution.

Results

Growth rate

Over the period of 38 years, 6 of the 18 originally marked trees at the Dankbaar site died (33%) and three showed coppice regrowth following substantial dieback because of a fire (Table 1-A1). In 1978 the mean height of the 18 trees was 5.1 m and mean stem diameter 235.85 mm. In 2016 the mean height of the remaining nine originally marked trees that had not experienced dieback was 6.8 m and mean stem diameter 282.7 mm. The mean height for the six dead individuals at the onset of the study was 6.1 m and at the time of last measurement before death 6.8 m. A mean height increase of 60 mm/year was calculated. The 2016 survey measured the remaining 12 originally marked trees as well as 12 additional trees now present; thus, after 38 years, the population increased by six trees in the 1 ha plot.

A linear regression of growth rate against stem diameter (Figure 4) indicated that growth rate decreases significantly as stem diameter increases, that is, as the individuals age

TABLE 1: Age calculations for *Vachellia erioloba* trees in the interior duneveld at the Dankbaar site using mean stem diameter of the 18 originally marked trees in 1978, the nine remaining live trees recorded in 2016 and the six dead trees last measured stem diameter when last surveyed as alive, derived by different methods.

Method	Mean age (years)		
	Eighteen trees (1978)	Nine live trees (2016)	Six dead trees
Mean diameter growth rate of 2.5 mm/year (current study)	94	113	142
Mean diameter growth rate of 3.6 mm/year: interior dunes and riverbed combined (Steenkamp et al. 2008)	66	78	99
Mean diameter growth rate of 3.2 mm/year: only interior dunes (derived from Steenkamp et al. 2008)	74	88	111
Relationship between stem circumference, converted to diameter, and radiocarbon age: interior duneveld and riverbed combined (Steenkamp et al. 2008); that is, 5.1 mm/year	47	56	71

($p = 0.022$). The mean growth rate for the first 10-year period (1978–1988) was 2.99 mm/year, the second 10-year period (1988–1998) 1.01 mm/year and the third 10-year period (1998–2008) 2.84 mm/year, indicating a variable growth rate over time. Stem diameter growth rate per year varied widely between the nine remaining trees (0.91 mm – 4.86 mm/year), with a mean value of 2.5 mm/year. Depending on the choice of mean annual growth rate or application of the regression between stem circumference and age, the mean age of the six dead trees could be estimated at between 71 and 142 years (Table 1).

Population structure

At the Grootkolk site, 61 live and 14 dead individuals were recorded in the initial survey in 1979. The number of live individuals at Grootkolk in the Nossob riverbed gradually decreased over the survey period (Figure 5). Initially the size class distribution of the trees from 1979 to 1999 could visually be classified as Type IIIb curves; however, there was a gradual transition to a Type IV curve from 2008 to 2016 (Figures 3 and 5). In spite of the decreasing tree numbers and the change of curve shape, linear regressions on the density of individuals against the diameter class midpoint (Figure 1-A1) revealed no significant differences between the slopes (Table 2-A1) or intercepts (Table 3-A1) of the fitted lines.

Using calculations from Steenkamp et al. (2008) for the interior duneveld and riverbed, the largest live tree at Grootkolk was aged between 195 and 212 years, while the relationship between stem circumference and radiocarbon age for the interior duneveld and riverbed combined aged the tree between 136 and 148 years (Table 2). When using the same two methods of calculation, most of the dead trees fell in the age categories 25–53, 37–71 and 49–89 years.

In all survey years the position of the centroid (arithmetic mean of all stem diameters recorded per site) was to the left of the midpoint of the size class distribution. However, the difference between these two values decreased over time and in 2016 the two values were nearly the same (Table 4-A1),

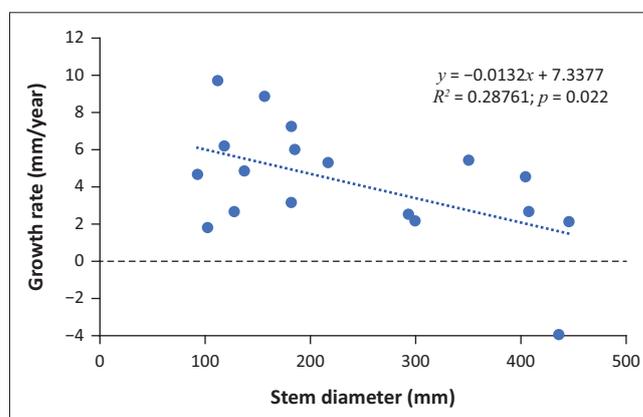


FIGURE 4: Linear regression of stem diameter versus annual stem diameter growth rate for the 18 marked *Vachellia erioloba* trees at the Dankbaar site in the Kalahari Gemsbok National Park.

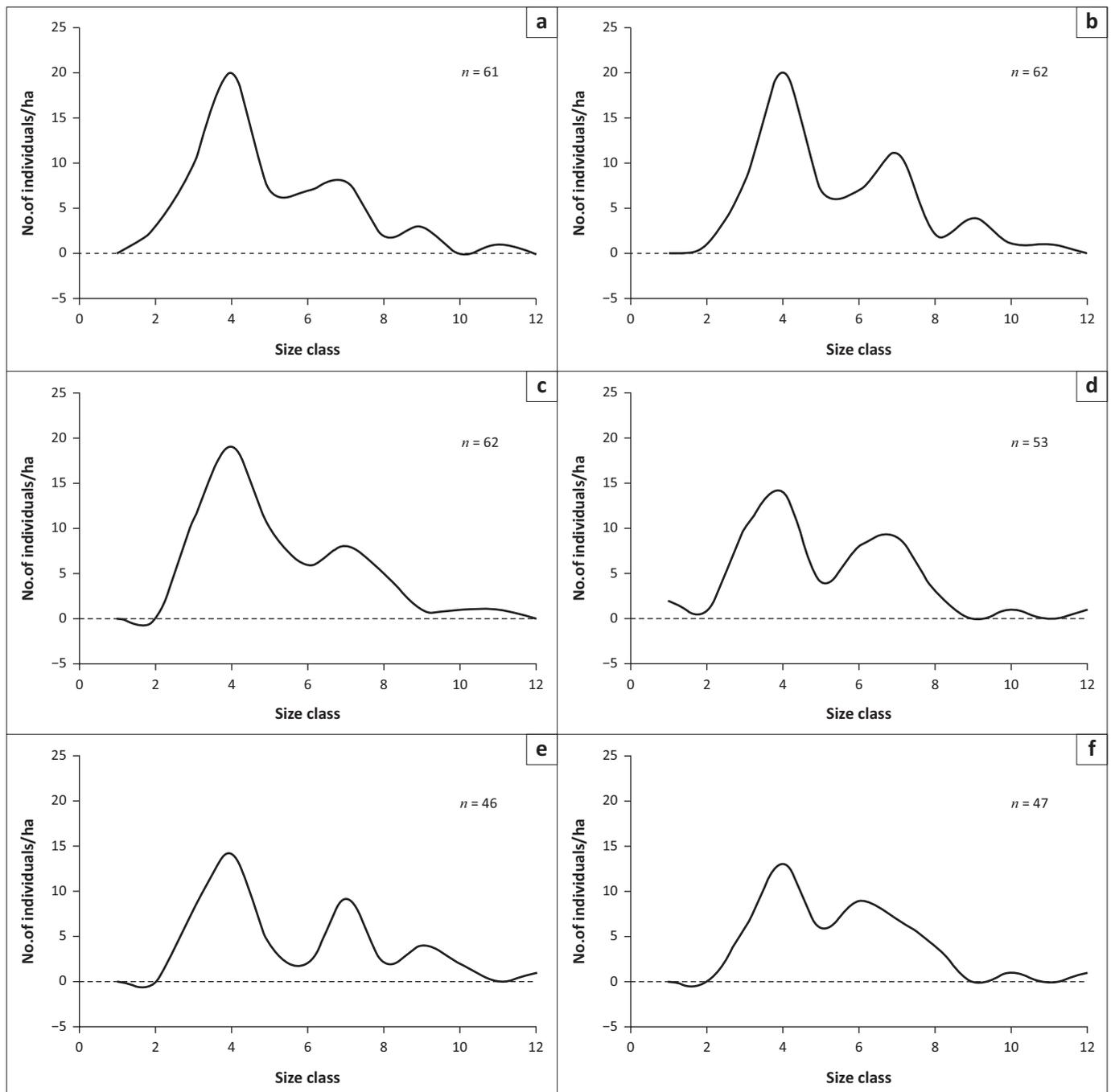
indicating that the population was changing from a young and growing population to a mature to old population.

Discussion

Growth rate

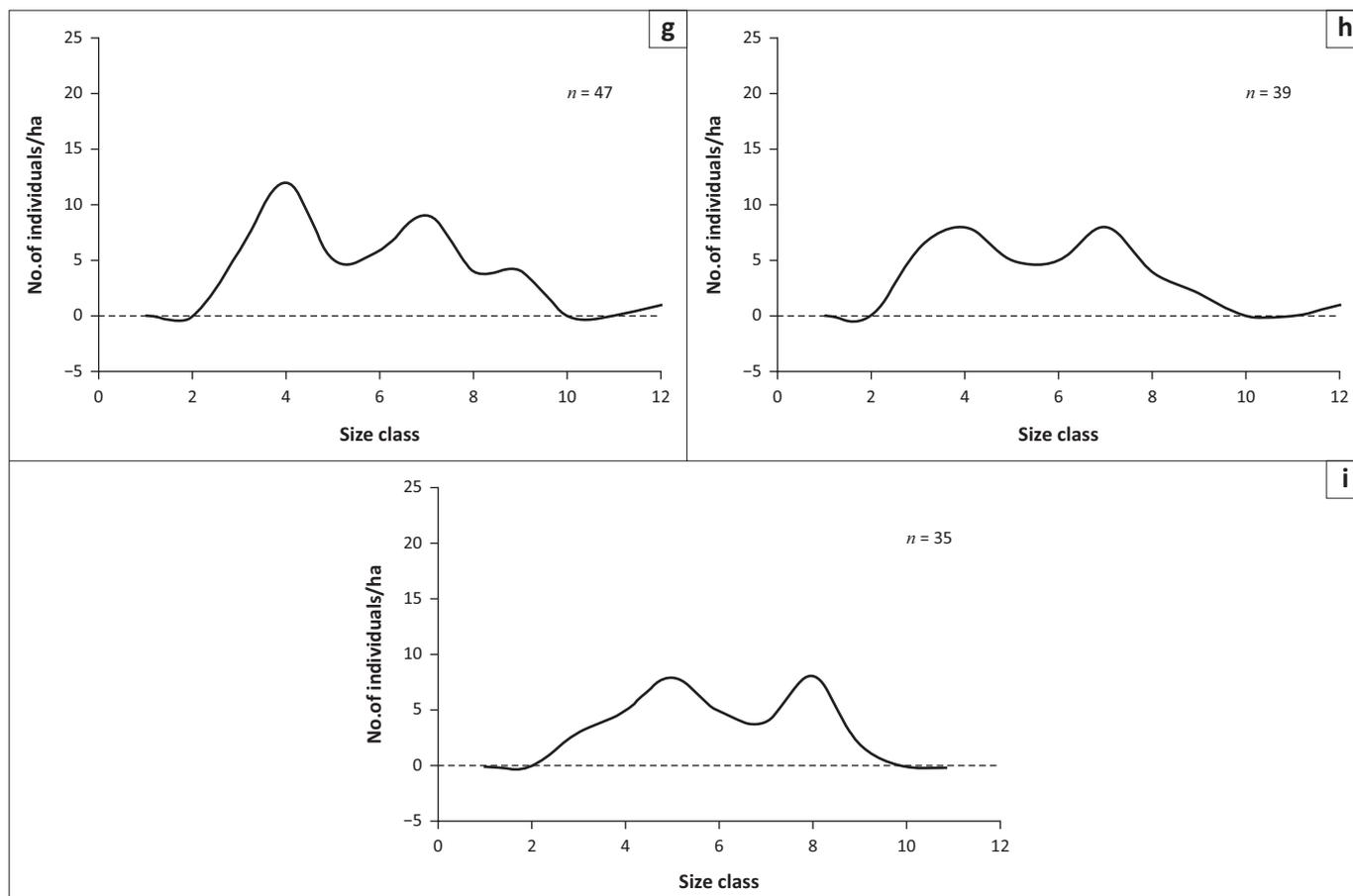
Marked *V. erioloba* tree stem diameters at Dankbaar in the interior duneveld increased at a mean rate of 2.50 mm/year (range 0.91 mm – 4.86 mm/year) over the monitored period. This mean annual diameter increase is less than the 3.6 mm/year established by Steenkamp et al. (2008) and substantially lower than the 12 mm – 14 mm/year previously

reported for *Acacia* species growing in arid and semi-arid environments (Gourlay 1992). The Steenkamp et al. (2008) study used annual growth ring and radiocarbon ageing to determine growth rates. A mean growth rate was derived from individuals in the interior duneveld as well as in the Nossob riverbed. If only the individuals in the interior duneveld in the Steenkamp et al. (2008) study are considered, then the mean annual diameter increment is 3.2 mm/year. Although Steenkamp et al. (2008) concluded that the growth rate did not differ significantly between trees growing in the dry Nossob riverbed and those growing in the interior duneveld, growth rate varied substantially



n, number of trees surveyed at the site in each survey year; ha, hectare.

FIGURE 5: Size class distribution curves of *Vachellia erioloba* individuals at the Grootkolk site in the various survey years. (a) 1986; (b) 1984; (c) 1986; (d) 1989; (e) 1994; (f) 1996; (g) 1999; (g) 2008; (i) 2016.



n, number of trees surveyed at the site in each survey year; ha, hectare.

FIGURE 5 (Continues...): Size class distribution curves of *Vachellia erioloba* individuals at the Grootkolk site in the various survey years. (a) 1986; (b) 1984; (c) 1986; (d) 1989; (e) 1994; (f) 1996; (g) 1999; (g) 2008; (i) 2016.

TABLE 2: Age calculations, derived by different methods, for *Vachellia erioloba* trees at the Grootkolk site in the Nossob riverbed using mean stem diameter of the circumference class for the largest live tree; and for circumference size classes that recorded the majority of the dead trees.

Method	Mean age (years)			
	Largest live tree class (> 220 cm – 240 cm)	Dead tree class (> 40 cm – 60 cm)	Dead tree class (> 60 cm – 80 cm)	Dead tree class (> 80 cm – 100 cm)
Mean diameter growth rate of 2.5 mm/year (current study)	280–307	51–76	76–102	102–127
Mean diameter growth rate of 3.6 mm/year: interior dunes and riverbed combined (Steenkamp et al. 2008)	195–212	35–53	53–71	71–89
Mean diameter growth rate of 5.2 mm/year: only the riverbed (Steenkamp et al. 2008)	134–147	25–37	37–49	49–61
Relationship between stem circumference, converted to diameter, and radiocarbon age: interior duneveld and riverbed combined (Steenkamp et al. 2008), that is, 5.1 mm/year	136–148	25–37	37–49	49–62

between individual trees. Variability in the growth rates of other tree species has been reported and the suggested underlying causes for this phenomenon include microsite conditions and/or genetic potential of individual trees (Stahle et al. 1996).

Depending on the equation used to determine the age of the dead trees there could be a twofold or greater difference in calculated age at both the Dankbaar (Table 1) (71 years as opposed to 142 years) and Grootkolk (Table 2) (25 years as opposed to 127 years) sites. The high variability in estimated age at which 6 of the 18 marked trees died (48, 103, 163, 178, 181 and 191 years, using the mean annual diameter increase of 2.5 mm/year calculated for this current study) was unexpected. Moustakas et al. (2008), using a combination

of aerial photographs and satellite images covering a period of 61 years to provide spatial data on mortality, found that *V. erioloba* mortality risk was greatest for trees of intermediate size. This does not seem to be the case for the Dankbaar population, where mortality was found to be predominantly among the large trees. At Grootkolk, the data seem to indicate that mortality was highest in smaller size classes and gradually declined for larger size classes. The density of trees at Grootkolk was low, and consequently self-thinning (Silvertown & Charlesworth 2001) is unlikely to have occurred.

Population structure

On the basis of the position of the centroid in relation to the midpoint of the stem diameter class range, the Grootkolk

population could be considered as a population gradually changing from young and growing to mature to old. This is supported by a visual assessment of the size class distribution, which showed a gradual transition from a Type IIIb to a Type IV curve shape over the 38 years. The large peak of young individuals in size class 4 that was evident at the first survey gradually became smaller and shifted to size class 5, and a prominent second peak emerged at size class 8 at the last survey.

At Grootkolk, few seedlings were recorded and few individuals appeared to be recruiting into the population. The low survival of size class 2, 3 and 4 individuals over the monitored period could possibly be ascribed to individuals progressing to larger size classes over the monitored period without being replenished. This is supported by the fact that size classes 5 and 8 had more individuals at the end of the monitoring period than when monitoring commenced. Overall, the survival of individuals in the larger size classes (e.g. size classes 6, 7 and 9) exceeded that in the smaller size classes (e.g. size classes 1, 2 and 3). In spite of the fact that the Grootkolk population was almost halved over the 38-year period, the slopes and intercepts of the size class distribution regressions showed no differences between years (Figure 1-A1).

In their study, Steenkamp et al. (2008) reported an ageing size class distribution with poor recruitment at some sites in the Nossob riverbed. At other sites, many young individuals were found with only a few mature or dying trees in these populations. The Grootkolk site situated in the same riverbed illustrated an ageing population with few young individuals. It has been suggested that flooding of the Nossob River and/or consecutive years of above-average rainfall were necessary for regeneration of *V. erioloba*. Steenkamp et al. (2008) were, however, unable to find support to substantiate the need for flooding.

Seed germination of *V. erioloba* is best after good rain events, and seedling survival depends on the availability of moisture during the next few seasons. Mortality rates during seedling establishment are generally higher than during the adult stages (Silvertown & Charlesworth 2001). Seedlings and saplings suffer high mortality in dry years (Barnes 2001; Theron, Van Rooyen & Van Rooyen 1985; Van Rooyen & Van Rooyen 1998; Van Rooyen et al. 1984). The high density of wildlife in the Nossob riverbed could also have contributed to the ageing of the Grootkolk population, with losses in young individuals because of trampling and browsing by herbivores and occasional toppling and breaking of larger trees by wind. Likewise, insects and rodents that impact on the seed pool may be more numerous in the riverbed habitat (Steenkamp et al. 2008). Furthermore, competition from a well-established grass layer may inhibit tree seedling establishment and growth in the riverbed (Steenkamp et al. 2008); however, this was not evident at the Grootkolk site. Fire also significantly impacts *V. erioloba* populations. After good rainfall, sufficient fuel accumulates and enables fire to

spread through the landscape. In general, up to one-third of individuals in an area that experiences a fire are killed by the fire, with most of the individuals subsequently resprouting from the base (Van der Walt & Le Riche 1984). Large old trees, especially those with hollow stems, are most sensitive to fire (Milton & Dean 1995). During the study period, fire only occurred at the Dankbaar study site (large fires in 1995 and 2012). No tree mortality resulting from the fire was evident at the site; however, three of the individuals displayed coppiced growth subsequent to fire. *Vachellia erioloba* population dynamics differed at the two study sites over the last 38 years. Considering all tree mortalities and recruitments, the Dankbaar population can be considered a self-sustaining population with an increase of 12 new individuals (net increase of six trees) at the site over the 38-year period. The density (number of individuals per the 1 ha plot) of the Grootkolk population is declining and the size classes of the remaining individuals increasing as the population ages.

Conclusions and management implications

There is growing concern that mortality rates in *V. erioloba*, a keystone species of the Kalahari, are increasing as a result of threats such as increasing fire frequency, groundwater abstraction, competition from alien invasive species, diseases, harvesting and the effect of arboricides. This study in the KGNP provided an ideal opportunity to investigate *V. erioloba* dynamics in a natural environment, under different soil types and consequently water availability, where threats were negligible or absent. The different survey methods used at the two sites and alternative data analysis techniques have provided findings on the growth of individual trees as well as on population dynamics. Additionally, the study provided evidence that the population studied in the interior duneveld was self-sustaining and although the population in the Nossob riverbed was declining, new young populations were being established elsewhere in the riverbed (Steenkamp et al. 2008).

The continued monitoring of the population at the two sites, where baseline data are already available, is highly recommended. However, monitoring sites should also be established at additional sites outside of park borders to incorporate sites in which various threats to this species can be investigated. It would also be imperative to determine growth rates in the riverbeds. Rainfall stations should be erected at all sites to enable the investigation of the influence of significant rainfall events and drought on seed germination, seedling survival and adult mortality.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

N.v.R. donated the data set to South African Environmental Observation Network. The authors provided financial and/or institutional support and conducted numerous field surveys over the years. H.v.d.M. and M.W.v.R. compiled the manuscript with valuable input from the remaining co-authors.

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Appendix starts on the next page →

Appendix 1

TABLE 1-A1: Changes in stem diameter (mm) from 1978 to 2016 of 18 marked *Vachellia erioloba* trees at the Dankbaar site in the interior duneveld of the Kalahari Gemsbok National Park.

Number	1978	1980	1983	1985	1988	1989	1991	1994	1998	1999	2008	2016	Growth rate (mm/year)
1	299.36	308.92	309.87	318.47	337.58	339.17	315.29	340.76	331.21	340.76	334.39	340.76	1.090
2	127.39	149.68	175.16	162.42	178.34	184.71	178.34	210.19	175.16	200.64	232.48	178.34	1.341
3	181.53	197.45	200.64	186.31	229.30	232.48	226.11	254.78	254.78	257.96	Dead	Dead	3.640
4	136.94	140.13	138.54	141.72	146.50	175.16	159.24	200.64	159.24	175.16	197.45	229.30	2.430
5	111.46	117.83	118.79	125.80	124.20	151.27	149.68	178.34	159.24	168.79	191.08	296.18	4.861
6	404.46	426.75	429.94	426.75	445.86	436.31	439.49	442.68	445.86	452.23	Dead	Dead	2.227
7	292.99	324.84	328.03	369.43	308.92	334.39	328.03	340.76	337.58	334.39	331.21	76.43†	-
8	92.36	92.36	105.10	98.726	117.83	117.83	124.20	136.94	130.57	133.76	143.31	181.53	2.347
9	156.05	187.90	187.90	200.64	200.64	221.34	222.93	238.85	242.04	254.78	273.89	324.84	4.442
10	101.91	117.83	117.83	111.46	111.46	125.80	111.46	124.20	121.02	121.02	Dead	Dead	0.910
11	181.53	203.82	211.78	213.38	213.38	213.38	203.82	222.93	219.75	226.11	229.30	251.60†	-
12	117.83	140.13	136.94	149.68	146.50	160.83	146.50	159.24	162.42	159.24	203.82	235.67	3.101
13	350.32	372.61	369.43	369.43	394.90	396.50	394.90	404.46	407.64	407.64	Dead	Dead	2.730
14	184.71	197.45	203.82	210.19	207.01	234.08	213.38	248.41	222.93	222.93	261.15	299.36	3.017
15	407.64	452.23	429.94	417.20	439.49	426.75	417.20	436.31	420.38	423.57	477.71	458.60	1.341
16	436.31	487.26	512.74	452.23	445.86	444.27	410.83	Dead	Dead	Dead	Dead	Dead	0.723
17	445.86	468.15	484.08	468.15	471.34	480.89	442.68	474.52	452.23	474.52	477.71	Dead	1.062
18	216.56	229.30	245.22	257.96	264.33	269.11	254.78	283.44	267.52	273.89	296.18	254.78†	-

†, Coppice.

TABLE 2-A1: Statistical comparison of slope values for linear regressions fitted on the density of individuals against the diameter class midpoint of live trees at Grootkolk in the Kalahari Gemsbok National Park using an analysis of covariance.

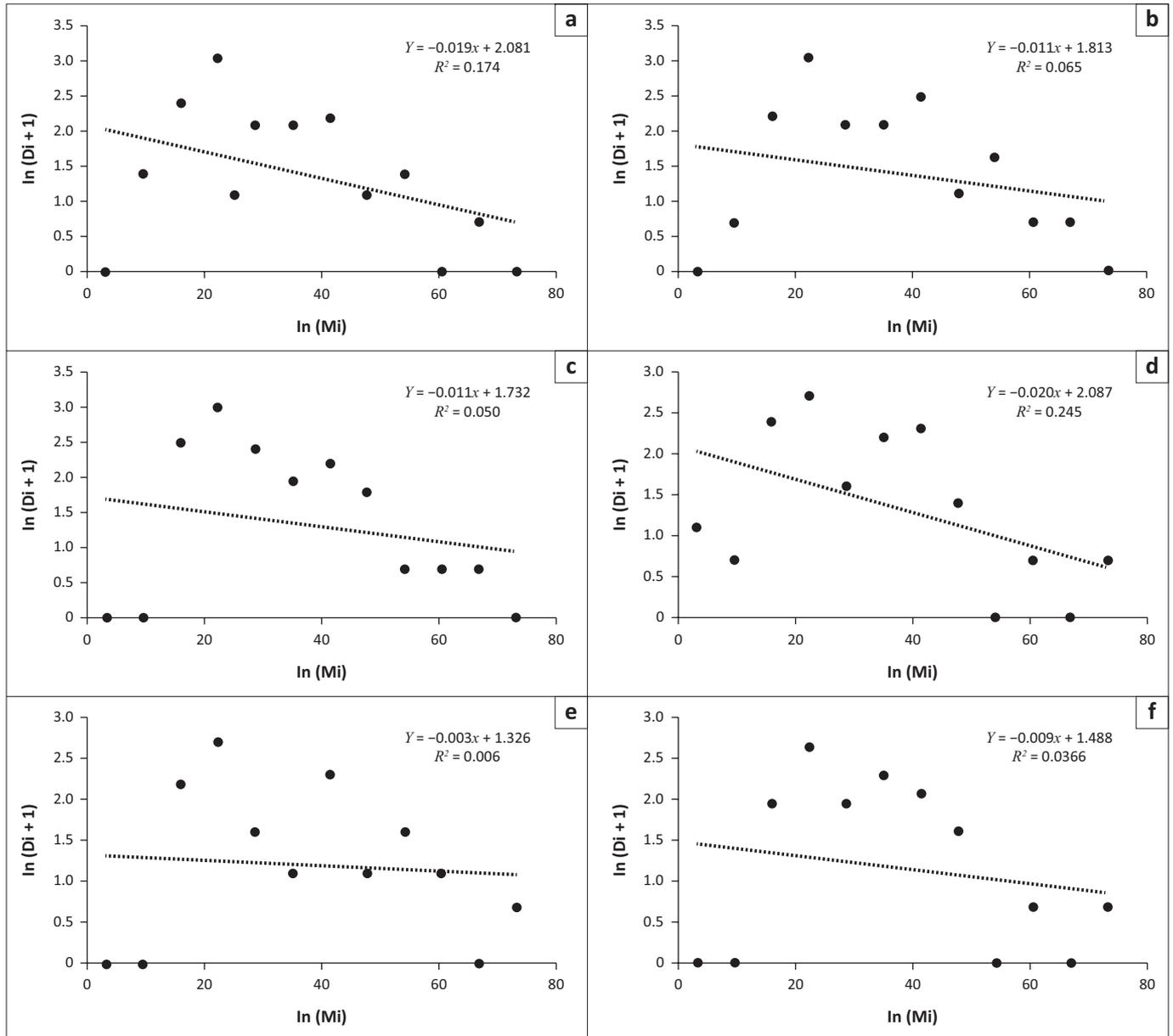
Survey year	1979	1984	1986	1989	1994	1996	1999	2008	2016
Equation	$y = -0.019x + 2.081$	$y = -0.011x + 1.813$	$y = -0.011x + 1.732$	$y = 0.020x + 2.087$	$y = -0.003x + 1.326$	$y = -0.009x + 1.488$	$y = -0.006x + 1.436$	$y = -0.006x + 1.356$	$y = -0.007x + 1.287$
1979	-	$f = 0.170$; $p = 0.685$	$f = 0.171$; $p = 0.684$	$f = 0.007$; $p = 0.9335$	$f = 0.732$; $p = 0.403$	$f = 0.287$; $p = 0.598$	$f = 0.462$; $p = 0.505$	$f = 0.470$; $p = 0.501$	$f = 0.398$; $p = 0.535$
1984	-	-	$f = 0.0005$; $p = 0.982$	$f = 0.273$; $p = 0.607$	$f = 0.183$; $p = 0.674$	$f = 0.072$; $p = 0.897$	$f = 0.072$; $p = 0.792$	$f = 0.066$; $p = 0.800$	$f = 0.042$; $p = 0.839$
1986	-	-	-	$f = 0.266$; $p = 0.612$	$f = 0.146$; $p = 0.701$	$f = 0.011$; $p = 0.919$	$f = 0.054$; $p = 0.819$	$f = 0.049$; $p = 0.827$	$f = 0.030$; $p = 0.865$
1989	-	-	-	-	$f = 1.000$; $p = 0.329$	$f = 0.423$; $p = 0.523$	$f = 0.648$; $p = 0.430$	$f = 0.672$; $p = 0.422$	$f = 0.578$; $p = 0.456$
1994	-	-	-	-	-	$f = 0.081$; $p = 0.780$	$f = 0.022$; $p = 0.883$	$f = 0.0313$; $p = 0.862$	$f = 0.051$; $p = 0.823$
1996	-	-	-	-	-	-	$f = 0.017$; $p = 0.896$	$f = 0.014$; $p = 0.908$	$f = 0.005$; $p = 0.947$
1999	-	-	-	-	-	-	-	$f = 0.0004$; $p = 0.984$	$f = 0.005$; $p = 0.945$
2008	-	-	-	-	-	-	-	-	$f = 0.003$; $p = 0.960$
2016	-	-	-	-	-	-	-	-	-

TABLE 3-A1: Statistical comparison of intercept values for linear regressions fitted on the density of individuals against the diameter class midpoint of live trees at Grootkolk in the Kalahari Gemsbok National Park using an analysis of covariance.

Survey year	1979	1984	1986	1989	1994	1996	1999	2008	2016
Equation	$y = -0.019x + 2.081$	$y = -0.011x + 1.813$	$y = -0.011x + 1.732$	$y = -0.020x + 2.087$	$y = -0.003x + 1.326$	$y = -0.009x + 1.488$	$y = -0.006x + 1.436$	$y = -0.006x + 1.356$	$y = -0.007x + 1.287$
1979	-	$f = 0.004$; $p = 0.952$	$f = 0.009$; $p = 0.925$	$f = 0.018$; $p = 0.895$	$f = 0.169$; $p = 0.686$	$f = 0.250$; $p = 0.622$	$f = 0.153$; $p = 0.699$	$f = 0.420$; $p = 0.524$	$f = 0.830$; $p = 0.373$
1984	-	-	$f = 0.023$; $p = 0.881$	$f = 0.038$; $p = 0.847$	$f = 0.222$; $p = 0.643$	$f = 0.308$; $p = 0.585$	$f = 0.202$; $p = 0.658$	$f = 0.500$; $p = 0.487$	$f = 0.934$; $p = 0.345$
1986	-	-	-	$f = 0.001$; $p = 0.982$	$f = 0.086$; $p = 0.772$	$f = 0.145$; $p = 0.707$	$f = 0.077$; $p = 0.784$	$f = 0.265$; $p = 0.612$	$f = 0.581$; $p = 0.454$
1989	-	-	-	-	$f = 0.093$; $p = 0.764$	$f = 0.162$; $p = 0.691$	$f = 0.082$; $p = 0.778$	$f = 0.310$; $p = 0.584$	$f = 0.700$; $p = 0.412$
1994	-	-	-	-	-	$f = 0.011$; $p = 0.917$	$f = 0.0001$; $p = 0.993$	$f = 0.056$; $p = 0.815$	$f = 0.255$; $p = 0.619$
1996	-	-	-	-	-	-	$f = 0.012$; $p = 0.914$	$f = 0.015$; $p = 0.905$	$f = 0.143$; $p = 0.709$
1999	-	-	-	-	-	-	-	$f = 0.056$; $p = 0.815$	$f = 0.247$; $p = 0.624$
2008	-	-	-	-	-	-	-	-	$f = 0.074$; $p = 0.788$
2016	-	-	-	-	-	-	-	-	-

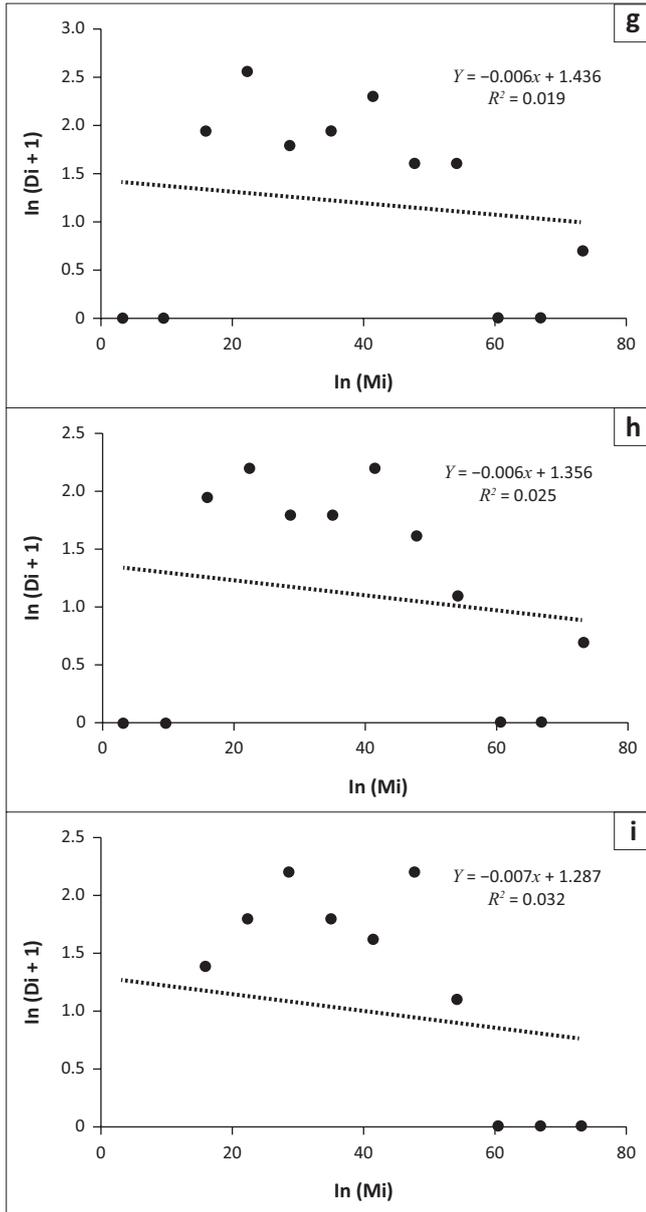
TABLE 4-A1: Calculated centroid (arithmetic mean of all stem diameters recorded per site in mm) and the midpoint (mm) of the size class distribution for each year surveyed at the Grootkolk site in the Nossob riverbed.

Year	1979	1984	1986	1989	1994	1996	1999	2008	2016
Centroid (mm)	2.85	3.10	2.98	2.89	3.27	3.16	3.34	3.32	3.48
Median (mm)	3.82	3.82	3.50	3.18	4.46	4.46	4.46	4.46	3.50



Mi, size class; Di, density of individual.

FIGURE 1-A1: Linear regressions fitted on the $\ln(Mi)$ against $\ln(Di + 1)$ of live trees at Grootkolk in the Kalahari Gemsbok National Park in (a) 1979, (b) 1984, (c) 1986, (d) 1989, (e) 1994, (f) 1996, (g) 1999, (h) 2008 and (i) 2016, where Mi, midpoint of the size class and Di, density of individuals.



Mi, size class; Di, density of individual.

FIGURE 1-A1 (Continues...): Linear regressions fitted on the $\ln(M_i)$ against $\ln(D_i + 1)$ of live trees at Grootkolk in the Kalahari Gemsbok National Park in (a) 1979, (b) 1984, (c) 1986, (d) 1989, (e) 1994, (f) 1996, (g) 1999, (h) 2008 and (i) 2016, where M_i , midpoint of the size class and D_i , density of individuals.