ALOE PILLANSII ON CORNELL'S KOP:

ARE POPULATION CHANGES A RESULT OF INTRINSIC LIFE HISTORY PATTERNS OR CLIMATE CHANGE?

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ABSTRACT

Aloe pillansii populations in the biodiversity hotspot of the Succulent Karoo in Southern Africa are thought to be under threat of extinction. This study investigated the population at the type locality; Cornell's Kop in the Richtersveld, South Africa. It has been suggested that theft, animal damage and more recently climate change have caused a decline in the population by over 50% in the last decade, however very little is known about this rare species. Repeat photography and surveys were used to analyse life history patterns and dynamics of the population and thus establish what the potential threats to this keystone species actually are. Repeat photography indicates that there have been high rates of adult mortality over the last fifty years (1.8% of the population dies annually), which results in an average predicted lifespan of 39 years for the remaining adult population on Cornell's Kop. However a recent survey reported that over 40% of the population recorded were seedlings, which weren't found in a 1995 survey, which is indicative of a recent recruitment pulse on Cornell's Kop and that conditions on the hill are still habitable for *A. pillansii.* Growth analyses suggest that *A. pillansii* has an average annual growth rate of 20 $mm.yr^{-1}$, which in turn means that 8 m individuals may be up to 453 years old. This long-lived strategy would require *A. pillansii* to only recruit infrequently, during periods of high rainfall, in order to sustain a viable population, which is consistent with findings on other large desert succulents. Seedling ages were estimated from their heights and it was found that 50% of the seedlings appear to have germinated five to ten years ago; this is consistent with rainfall records from the area which indicate that rainfall was consistently above the annual average for this same period. The findings indicate that although the adult *A. pillansii* population is declining, the presence of 30 seedlings suggest that the population is entering a recruitment phase after just coming out of a lengthy senescent phase. Although *A. pillansii's* extensive lifespan makes it a potentially useful indicator species of climate change, the evidence presented in this study does not suggest that climate change has affected the dynamics of this population.

KEYWORDS

Aloe pillansii; climate change; population dynamics; repeat photography; Succulent Karoo

INTRODUCTION

Internationally, South Africa is well known for the high diversity of its unique ecosystems. Its floral and faunal richness make it one of the most biologically diverse countries in the world, which includes within its borders two of the world's 25 biodiversity hot spots, the Cape Floral Kingdom and the Succulent Karoo (Myers *et al.* 2000). The lesser known of these two hot spots is the Succulent Karoo region in the Northern Cape province. It is in fact the only arid land biodiversity hot spot in the world (Myers *et al.* 2000), and contains roughly three times more species than the next most diverse desert, the Sonoran Desert in North America, in just under three times the area (Cowling & Hilton-Taylor 1999). In terms of succulent richness, the Succulent Karoo contains approximately 10% of all known succulent species in the world (Van Jaarsveld 1987) and covers an area of approximately 100 000km^2, containing over 5 000 species, of which 40% are endemic, in 730 genera of which 9% are endemic (Cowling & Hilton-Taylor 1999).

As with many other biologically diverse ecosystems, the Succulent Karoo is threatened by a number of anthropogenic activities, such as mining, agriculture and overgrazing (Myers *et al.* 2000). However, as atmospheric CO^2 concentrations continue to rise at increasing rates, these concerns have to assume lower priority status as the threat of global warming is rapidly becoming the most prominent concern for conservationists everywhere. Global climate change threatens to alter the functioning of most of the world's ecosystems and global circulation models (GCM's) predict broad-scale habitat loss for many species (Midgley *et al.* 2002). To provide evidence of global climate change, scientists use indicator species of both plants and animals to show that species are dying or shifting their ranges because of climatic changes in their native environments. These expected shifts are likely to take the form of increases in elevation and polewards shifts of species distributions (Hughes 2000). A number of studies in the northern hemisphere have already found possible climate-related range shifts for a wide array of animal species such as butterflies (Parmesan *et al.* 1999), bats (La Val 2004), frogs, birds and lizards (Pounds *et al.* 1999). Studies on plant species have also found range expansions of Arctic (Sturm *et al.* 2001), and Antarctic shrubs (Smith 1994), as well as increases in growth of number of species due to increased CO^2 levels (Myneni & Keeling 1997).

Studies in Southern Africa looking for similar climate indicator species have focused mainly on the tree succulent *Aloe dichotoma*. Results from repeat photography (Kaleme 2003) and bioclimatic modeling (Foden 2002) of this species suggest that it may already be shifting its range southwards as climate changes have begun to affect their central populations detrimentally. Both studies found that *A. dichotoma* populations in the southern winter rainfall areas were consistently in better health, i.e. exhibited less mortality and more recruitment, than the more northerly populations in summer rainfall areas. These results agree with predicted climate change models of the area (Midgley *et al.* 2002). In light of these findings, it is important that other potential indicator species are researched to provide a more comprehensive understanding of how climate change might affect Southern Africa's ecosystems in the future.

One such species is *Aloe pillansii* (L. Guthrie), a rare and endemic tree succulent very similar to, and often mistaken for, *A. dichotoma* (Reynolds 1950). Commonly known as the 'Bastard quiver tree' or 'Basterkokerboom', *Aloe pillansii,* is far less common than it close relative *A. dichotoma*, and is only found only in a few restricted locations in southern Namibia and in the Richtersveld in the extreme northwestern parts of South Africa. Their limited distribution in these areas makes *A. pillansii* a potentially good indicator of climate change in Southern Africa, since these are the areas that Foden (2002) and Kaleme (2003) suggest are already showing the first signs of changing climatic variables. Its potential value as an early warning mechanism for climate change has brought this distinctive succulent species to the public and academic world's attention over the last decade. Recent literature has reported that *A. pillansii* populations are under threat and rapidly approaching extinction unless conservation programs are immediately instituted (Midgley 1997, Midgley *et al.* 1997, Wiliamson 1998, Powell *et al.* 2000, Rogers 2004). As a result of these reports and its restricted range and small population size, estimated at just over 1200 individuals in South Africa (Bolus *et al* 2004), it has been placed on the IUCN red data list as a critically endangered species, likely to have lost over 80% of the population in the last decade (Golding 2002).

A number of explanations for the declining populations have been offered by previous researchers. The leading theories suggest that theft, animal damage (Midgley 1997, Midgley *et al.* 1997, Wiliamson 1998) and more importantly, climate change (Foden 2002, Rogers 2004) are among the most likely causes of *A. pillansii 's* decline. However, existing theories are speculative, as few quantitative studies have been undertaken on this enigmatic species. *A. pillansii* 's affinity for hot and dry areas, often in inaccessible locations in the inhospitable Richtersveld, has made it very difficult to study its life history patterns. The literature surrounding *A. pillansii* indicates just how little is known about this species, with some studies reporting the total population size at less than

200 (Midgley *et al.* 1997) while more recent studies suggest that are over 1500 individuals in Namibia (Loots & Mannheimer 2003) and at least 920 individuals in South Africa (Powell *et al.* 2000). Similarly very little is known of the lifespan of these succulent tree aloes which makes it very difficult to understand their life history strategies, and thus predict population changes over time.

While theft, animal damage and climate change are important concerns for *A. pillansii,* it is also vitally important that its life history patterns are better understood before any conclusive statements can be made about the state of the *A. pillansii* population in Southern Africa. Studies of similar types of desert plants in America, namely *Agave deserti* (Jordan & Nobel 1979) and *Carnegiea gigantea* (Jordan & Nobel 1982), indicate that these large arid zone succulents tend to be relatively long-lived species and rely on pulsed recruitment events in good rainfall years. Such long-lived strategies allow plant populations to survive for a number of decades without recruitment occurring before the population is actually threatened with extinction. Anecdotal evidence suggests that *A. pillansii* is also a fairly long-lived species. Studies on the closely related, *A. dichotoma,* suggest that it may well live for over 250 years (Kaleme 2003), although carbon dating of a small adult *A. dichotoma* aged the tree at 100 (± 45) years (Vogel 1974)

Questions addressed in this study

This study aims to illuminate *A. pillansi* 's life history patterns as well as to identify what the main threat to *A. pillansii* populations in Southern Africa are. The study was conducted on Cornell's Kop in the western Richtersveld in South Africa, which is the type locality for *A. pillansii.* Previous studies on the *A. pillansii* population on Cornell's Kop (Midgley 1997, Midgley *et al* 1997, Williamson 1998) have been limited by a lack of quantitative data. Using repeat photography and surveys, this study forms the most comprehensive analysis of the *A. pillansii* population on Cornell's Kop to date. This study addresses the following issues:

- The status of the *A. pillansii* population on Cornell's Kop;
- The life history patterns of *A. pillansii,* in terms of recruitment strategies, lifespan, annual growth increment and mortality;
- Causes of mortality of the *A. pillansii* population on Cornell's Kop;
- The effects of climate change on the *A. pillansii* population on Cornell's Kop;
- Potential conservation measures that could be adopted.

METHODS

Study Site

Cornell's Kop is situated just outside the eastern border of the Richtersveld National Park in the Northern Cape province of South Africa between 28.41 S and 16.88 E. and 15km east of the Orange River border between South Africa and Namibia. Cornell's Kop is longitudinally orientated for about 0,75 km in an east-west direction (Williamson 1998). The hill lies above the 120 m contour with its summit recorded at 195 m.

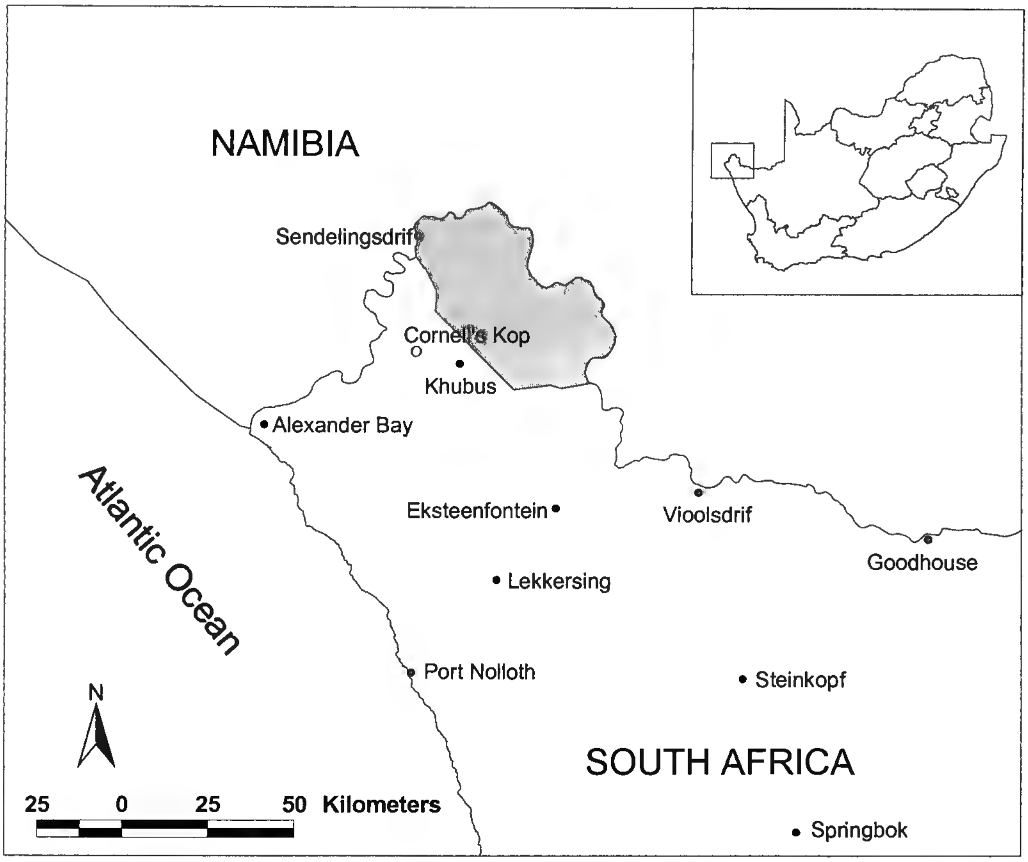

Figure 1: The location of Cornell's Kop in relation to the Richtersveld National Park (shaded area) and major towns

Many studies have incorrectly cited Cornell's Kop as the southern-most distribution of *Aloe pillansii* (Powell *et al.* 2000) and while it is the most westerly-situated population of *Aloe pillansii*, there are known populations found near Eksteenfontein 50 km further south than Cornell's Kop.

Cornell's Kop experiences extremes of climatic conditions. In winter temperatures can drop to almost zero while summer temperatures are known to reach over 40 °C. The hill receives periodic winter rainfall with an annual average of about 60 mm, but this precipitation is highly variable (Williamson 1998) and some years are known to have received no rain at all. Other than precipitation, the hill experiences cool Atlantic fogs, which generally occur in winter. Cornell's Kop experiences violent winter and summer gales which blow from opposite directions, leaving every slope on the hill exposed to destructive sand storms at some time during the year (Williamson 1998).

Surveys

Cornell's Kop has long been a prominent location for research on *A. pillansii* and its potential decline. In September of 2000, a group of researchers (see Powell *et al.* 2000) completed a survey of the Richtersveld for South African National Parks (SANParks) of 920 *Aloe pillansii* individuals in 19 sub-populations, one of which was Cornell's Kop. All living *Aloe pillansii* plants on Cornell's Kop were marked and given a number and the following variables were recorded: GPS position and altitude, estimates of plant height, number of living heads on the plant, slope and aspect. Other variables were also recorded but these were not used in this study's analysis.

Over the period from the 30th of March to the 1st of April 2004, the *A. pillansii* population on Cornell's Kop was resurveyed. All marked plants were photographed, their heights were remeasured using a ranging rod and their basal circumference recorded using a tape measure. Any unmarked plants, including seedlings, were also recorded, their GPS positions taken using a Garmin 765 instrument and their basal circumference and heights measured. The basal circumference and GPS positions of all the skeletons of dead *A. pillansii* individuals on the hill were also recorded.

These two surveys provided the basis for an analysis of changes to the *A. pillansii* population over time. Unfortunately because only the seedling's heights (<1m) seem to have been measured accurately in the 2000 survey, the estimated heights for the juveniles and adults from this survey were too rough and therefore could not be used for this study. Thus only the annual growth rates for the seedlings could be used. In 1995 Midgley *et al.* (1997) also surveyed the Cornell's Kop population, measuring only the heights of both living and dead individuals. His results are also used for a comparative study of size class distributions.

Repeat Photography

Using material from archives and previous studies of Cornell's Kop, a number of old photographs of *A. pillansii* plants on Cornell's Kop were located. These photographs span a period of 67 years, with the oldest of these photographs dating back to 1937 and then at regular intervals during the intervening years with the most recent photographs being taken in 2001.

Using prominent features, both in the fore- and background, of the original photograph of the landscape, such as rocks, trees and the skyline, the camera position on Cornell's Kop of each of the original photographs was triangulated and then recorded with a Garmin 765 GPS instrument. By looking through the viewfinder of the camera and adjusting the camera's focal length and the position of the tripod, the parameters of the original photograph could be fairly accurately replicated. Two repeat photographs were then taken with a Canon EOS 300 camera, one with a person of known height standing in it for scaling purposes and the other an exact match of the original photograph. These photographs, along with the original photographs, were digitised and used to analyse both the mortality rate within the population as well as the growth rate of individual trees.

Firstly to assess mortality, matched photographs were used to trace the presence/absence of certain *A. pillansii* individuals in the population over time. Identifiable individuals present in the original photograph but absent from the more recent repeat photograph were considered to have died. In theory, any individuals present in the repeat but not in the original photograph should be considered as recruits (Bowers *et al.* 1995). However, due to the small size of the *A. pillansii* seedlings, no recruits were visible in any of the repeat photographs.

Any original photograph, in which five or more living trees occurred, was analysed to measure the extent of mortality over time. Many of the trees also occurred in more than one original photograph and could thus be used to determine an estimate of when tree death occurred. In this way, estimates of mortality dates for 23 trees were calculated by assessing the subset of the population present in Landscape Match 1, Landscape Match 4, Landscape Match 7 and Landscape Match 11 (see Appendices 1 & 2). The total number of trees present in the original photograph was counted and deaths were noted as they occurred over the period covered by the photographs and expressed as an annual mortality rate.

Secondly, to assess growth rates in individual trees, the original and repeat photographs were rescaled in Adobe Photoshop 6. 0 until the permanent features of the photographs (generally, a rock in the foreground of the picture) had exactly the same dimensions. This was necessary because although the original position of the camera fairly accurately located, the focal length was difficult to match exactly. The rescaling process was done by adding an invisible layer on top of the original photograph and drawing a line along the length of one of the permanent features of the photograph; generally a rock in the foreground of the picture. The invisible layer with the measuring line was then superimposed on the repeat photograph. The repeat photograph could then be proportionately scaled up or down until the line covered the same feature in the repeat that it had in the original.

Once the two photographs had taken on equal dimensions, the repeat image was superimposed on the original. By reducing the opacity of the repeat image, it was possible to align the permanent features of the two images on top of each other and thereby check the scaling of the two images. When the two images were properly matched, measurements of each tree in both photographs were taken using the ruler function in Adobe Photoshop 6. 0.

Using the height measurements from the survey of the marked trees, the measurement of the trees in the repeat photograph could be related to their actual heights. By using ratios, the heights of the trees in the original image could be found and the changes in height calculated. Although a total of 38 photographs were matched in this study, only 21 photographs, in which the tree(s) was close enough to the camera to make accurate measurements of its height, could be used for the growth analysis.

Using growth rates for the seedlings calculated from the survey, and with the growth rates for adults from matched photographs, possible ages of individual plants were calculated. Predicted ages of adults were calculated using only growth rates from photographs taken in or before 1985. This was done in order to reduce variability in growth rates, which can vary from year to year depending on stochastic environmental events. Thus an average worked out over this longer time span is likely to be more accurate than one which may only cover a particularly good period of growth. Finally individual growth rates were also plotted against slope and aspect to establish whether growth was related to the microhabitat of each individual.

RESULTS

The distribution of *Aloe pillansii* plants on Cornell's Kop is displayed in terms of their position on the mountain (Figure 2) and in terms of their aspect and altitude (Figure 3). Individuals were mostly north facing with the majority lying between 130 m and 180 m. The adults and seedlings in the population, both alive and dead, appear to be randomly dispersed across their preferred range on Cornell's Kop. This is an isolated population as there are no other *Aloe pillansii* plants within a 2 km radius of the Cornell's Kop population.

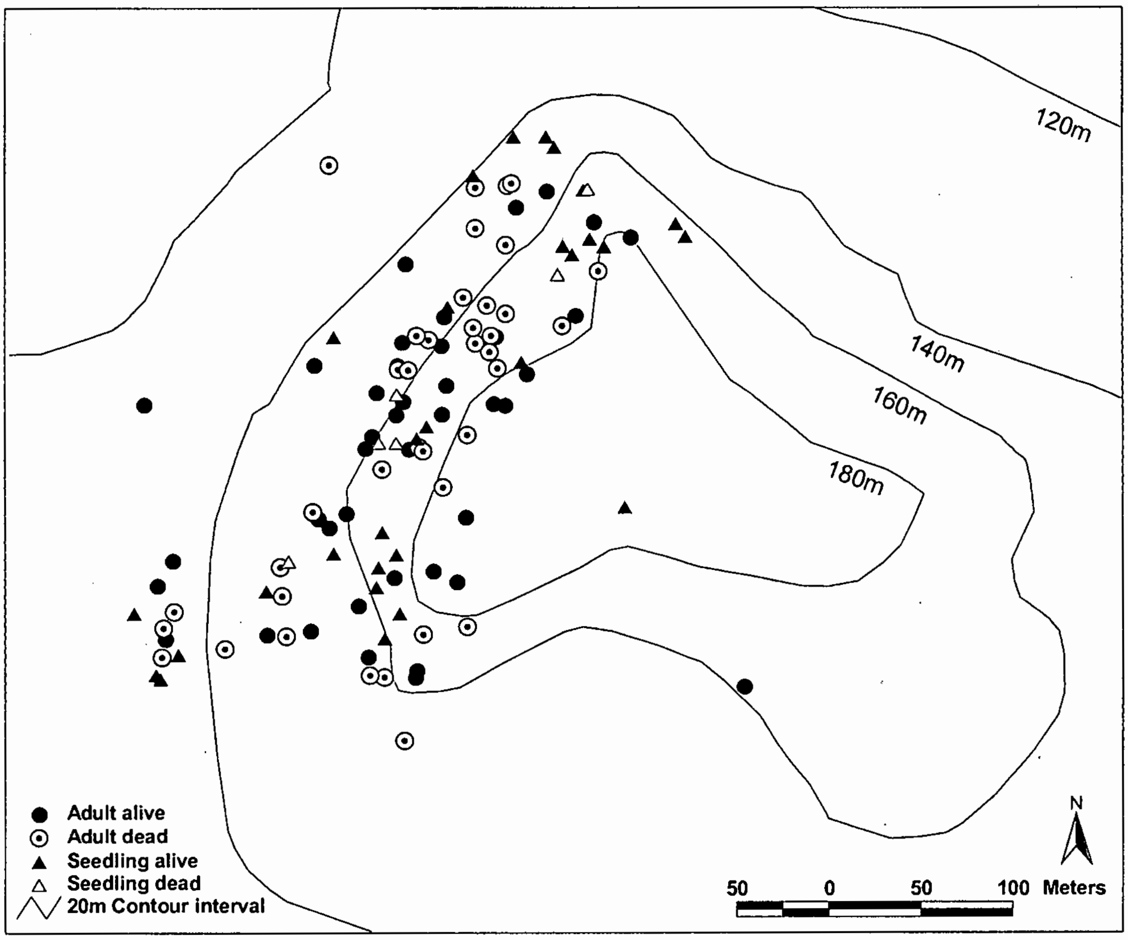

Figure 2: Distribution of living and dead adults and seedlings of *Aloe pillansii* on Cornell's Kop. Adult alive (38), adult dead (37), seedling alive (30), seedling dead (6)

The correlation between the basal circumference of each tree and its height (Figure 3) was used to extrapolate the height at death for dead tree skeletons whose bases were still intact and their basal circumference could still be measured. These heights could then be used to construct a more accurate size class distribution for the dead *A. pillansii* plants on Cornell's Kop.

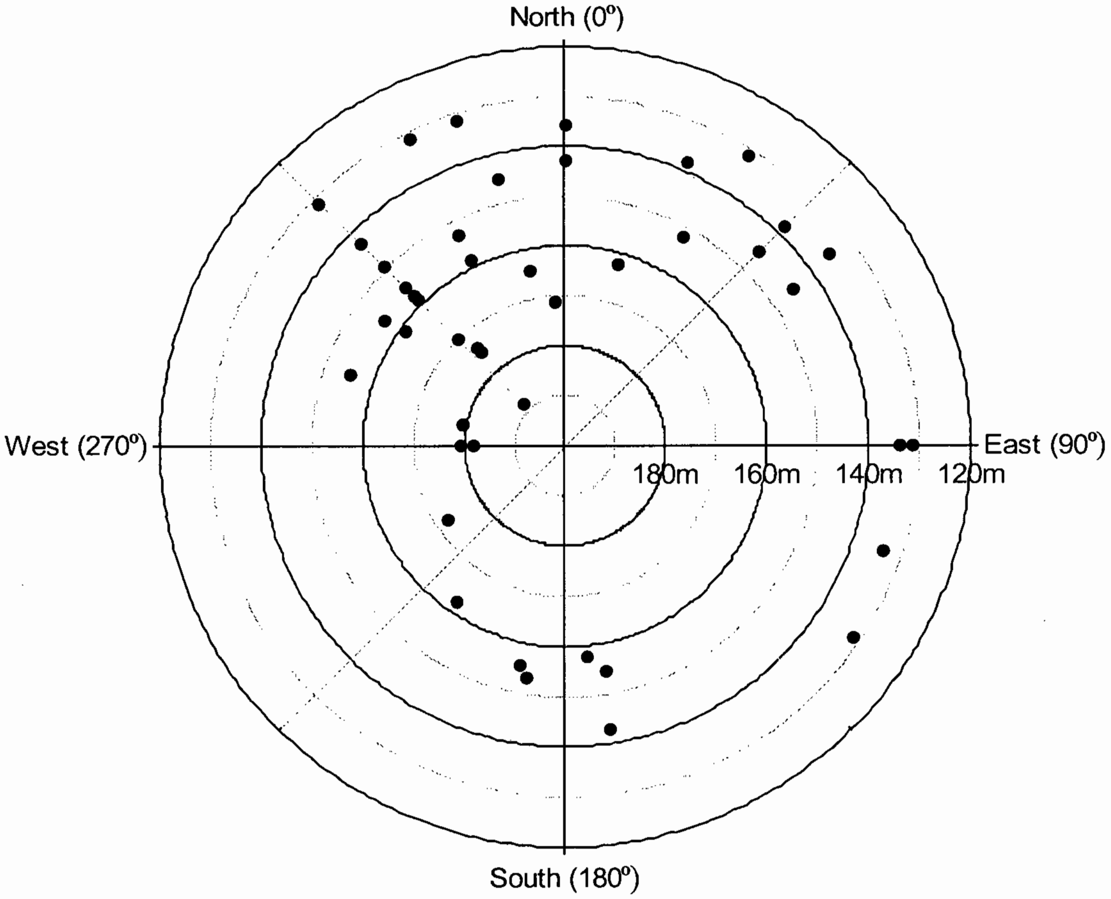

Figure 3: The distribution of *Aloe pillansii* plants numbered by SANParks (n =55) with respect to altitude (concentric rings) and aspect (quadrants) on Cornell's Kop.

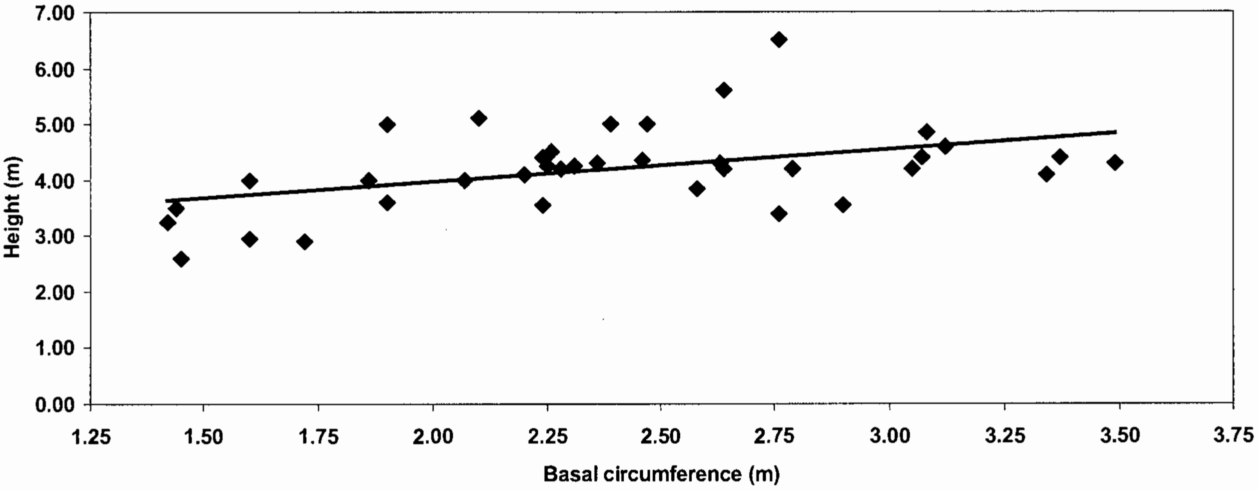

Figure 4: The relationship between basal circumference and height for 38 living *Aloe pillansii* individuals on Cornell's Kop ($y = 0.5785x + 2.8164$, $R^2 = 0.1896$, $p < 0.01$). Only living adult plants were included in the analysis as seedling heights skew the data significantly, two plants taller than 8 m were excluded, as they appeared to be significant outliers.

Figure 5a was constructed using data from the Midgley *et al.* (1997) survey of the *Aloe pillansii* population on Cornell's Kop. However, in their analysis the heights of dead individuals were measured from tree skeletons found on the mountain and do not account for any degradation in size of the tree skeletons since their death. Figure 5b was constructed from data from the 2004 survey, using the same size classes but the height at death of the dead trees was more accurately assessed from their basal circumferences and the equation in Figure 4. Figure 5a indicates that most of the population was adult (>2. 5 m) with very few seedlings (< 1 m) present in 1995 while the more recent study found that the population had over ten times as many seedlings in 2004 than it did in 1995. Figure 5b also shows that most of the dead trees only died when they were over four m tall. Both figures indicate that there were very few juvenile plants (1-3 m) found in either survey.

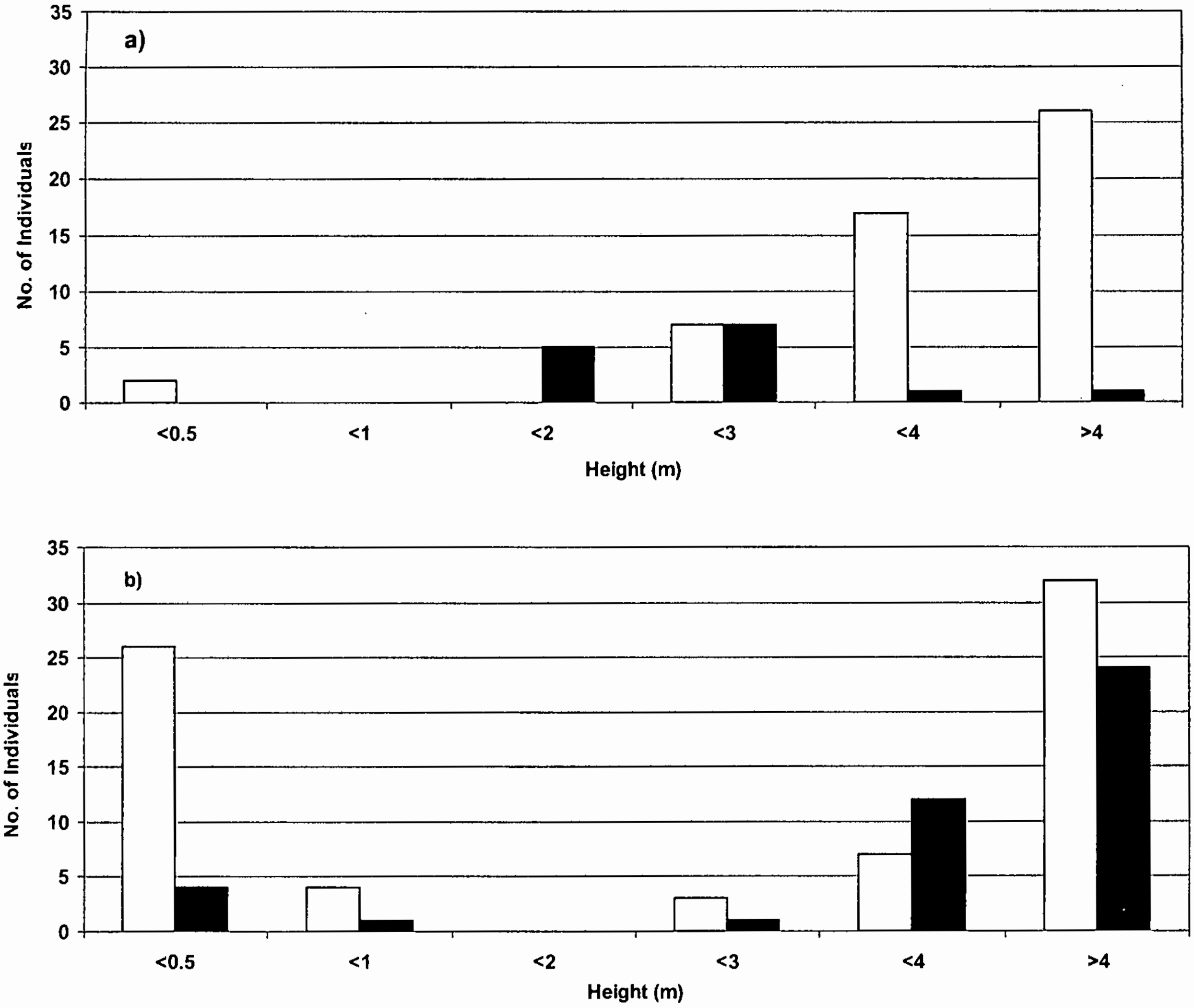

Figure 5a & b: Size class distributions of all *Aloe pillansii* trees on Cornell's Kop, both living (open bars) and dead (closed bars). Figure 5a is after Midgley et al. (1997) and involved 66 individuals (52 alive and 14 dead) and Figure 5b from the survey in April 2004 involving 111 individuals (72 alive and 42 dead).

Figure 6: Gilbert Reynolds's original photograph (top) of part the north facing slope on Cornell's Kop, taken circa 1950 and re-photographed (middle) in 1995 (Midgley 1997) and then re-photographed (bottom) again on the 1st of April 2004. Living trees are indicated by red arrows. The camera position is at 28. 41700 S, 16. 88558 E. (see Landscape Match 1 in Appendix 3)

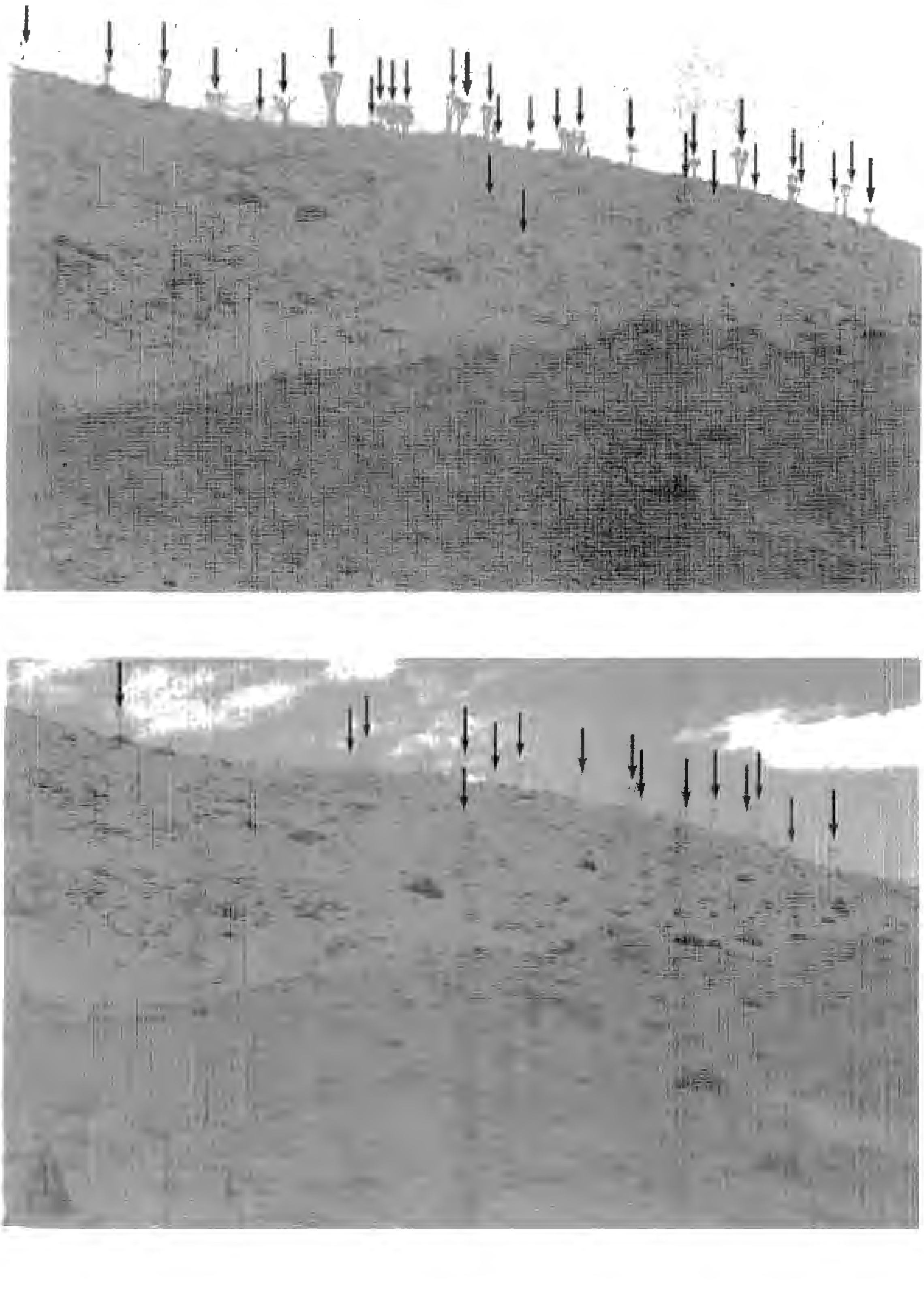

Figure 7: Piet van Heerde's original photograph (top) of the skyline of Cornell's Kop looking south, taken circa 1950 and re-photographed (bottom) on the 1st of April 2004. Living trees are indicated by red arrows. The camera position is at 28. 41594 S 16. 88425 E. (see Landscape Match 5 in Appendix 3)

The two examples of landscape matches (Figure 6 & 7) indicate the number of deaths that have occurred in the population since the original photograph was taken. It is generally the larger adult trees that have died. Smaller trees which are evident in the original photograph are still present in the 2004 photograph. The original photographs also indicate that the population in the past was made up of trees from many different cohorts, with their sizes ranging from small to large while the present day population does not appear to consist of as many large individuals (like the large tree in the foreground in Reynolds' 1950 photograph (Figure 6)), nor are there any juvenile sized trees (<3 m) present. The dead tree skeletons generally remain standing for at least a decade after their death. Since seedlings are too small to be identified in the photograph analysis, their positions have not been indicated.

Table 1: Mortality figures for matched photograph pairs. Every original photograph that contained five or more living individuals was used in the analysis. Photograph numbers LM1 – 7 and LM9 - 11 refer to repeat landscape photographs (see Appendix 3) while M15 and M21 refer to repeat photographs of individual trees (see Appendix 4)

Photo No.	Date of original photo	Date of repeat photo	Time interval (years)	No. of live individuals in original photo	No. of live individuals in repeat photo	No. of deaths since original photo	Annual extinction rate (% deaths per year)	Predicted lifespan of remaining adult population (years)
M 21	2001	2004	3	6	5	1	5.56	15
LM 3	2000	2004	4	15	13	2	3.33	26
M 15	1991	2004	13	10	7	3	2.31	30
LM 6	1985	2004	19	5	3	2	2.11	29
LM 2	1971	2004	33	15	7	8	1.62	29
LM 7	1953	2003	51	11	6	5	0.89	61
LM 9	1953	2003	51	9	5	4	0.87	64
LM 10	1953	2003	51	6	3	3	0.98	51
LM 5	1950	2004	54	30	15	15	0.93	54
LM 1	1949	2004	55	14	6	8	1.04	41
LM 11	1946	2003	58	10	4	6	1.03	39
LM 4	1937	2004	67	12	4	8	1.00	34
Average			38.25	11.92	6.50	5.42	1.80	39
Std. Dev			22.73	6.64	3.78	3.92	1.35	15

Mortality figures from matched photographs (Table 1) indicate that on average 1,8% of the population is dying annually, although there is considerable variation in the mortality rate, which has a range of 4. 7%. The predicted lifespan of the remaining adult population indicates that on average all the adult trees in the photographs will be dead within 39 years, although this figure does not take into account any recruitment that may have occurred in the population since the original photograph was taken and which is not evident in the repeat photographs. A further mortality analysis (Figure 8) plots the mortality rate in a population subset of 23 plants on Cornell's Kop, which were regularly recorded in a number of photographs over a period of 67 years. Of the original population of 23 plants (22 alive and 1 dead), 12 have since died during the 67-year period. The mortality amongst this population subset appears to have occurred at a fairly steady rate, without any catastrophic mortality events apparent. The trees that have died were generally large adult trees at least five metres high or taller.

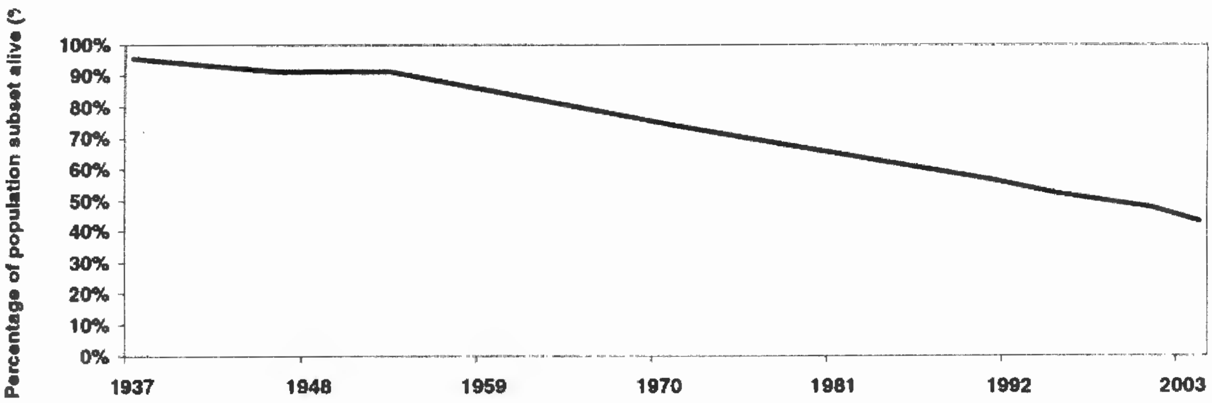

Figure 8: Mortality rate (deaths per year) within a subset of the *Aloe pillansii* population (n =23) over a period of 67 years.

Figure 9: Piet van Heerde's original photograph (left) taken circa 1950 of three Aloe pillansii trees which were re-photographed (right) on the 1st of April 2004. Only plant numbers 60 (foreground) and 63 (right background) remain. The camera position is at 28.41813 S 16.88479 E. (see Match 5 in Appendix 4)

Figure 10: Original photograph (top) of plant number 19 with the north facing slope of Cornell's Kop in the background, taken by Harry Hall in February 1953 and re-photographed (bottom) by Rick Rohde on the 6th of September 2003. The camera position is at 28.41667 S 16.88581 E (see Landscape Match 7 in Appendix 3)

Individual tree heights were matched using matched photograph pairs of 21 individual trees such as in Figures 9 and 10, in which the growth of individual plants could be discerned from the photographs. In Figure 9, tree number 60 grew 68 mm and its right-hand branch has since forked while tree number 63 grew 46 mm over the 54-year period between repeat photographs. In Figure 10, plant number 19 has grown noticeably taller and wider and its branches have since forked, growing 80 mm over the 51-year period between photographs. The extent of population mortality on the hillside in the background of the photograph is also evident.

While some of the adults recorded growth rates of over 2 $mm.yr^{-1}$, other adult trees had not grown at all since the original photograph was taken. A summary of these growth statistics (Table 2), gained from both photograph matching analysis and repeated surveys, indicates that on average, seedlings (29.6 $mm.yr^{-1}$) grow at almost twice the rate of adults (15.5 $mm.yr^{-1}$). Adult growth rates showed very little variation, while individual seedling growth rates were far more variable. An absence of reliable data for plants in the juvenile size class meant that growth rates could not calculated for them (see Appendices 3 & 4 for data on individual trees).

Table 2: Growth rates for each size class of the *Aloe pillansii* population on Cornell's Kop. The data for the seedlings was taken from repeat surveys while the data for the adults was taken from matched photograph analysis. None of the *Aloe pillansii* trees on Cornell's Kop fell into the juvenile size class and thus no data on them was available.

Size Class	Sample Size (n)	Mean Annual Growth Rate ($mm.yr^{-1}$)	Std. Dev	Variance	Range
Seedlings (< 1 m)	7	29.6	35.7	1.27	100.0
Juveniles (1 - 2. 5 m)	No data	No data	No data	No data	No data
Adults (> 2. 5 m)	21	15.5	10.8	0.11	30.0

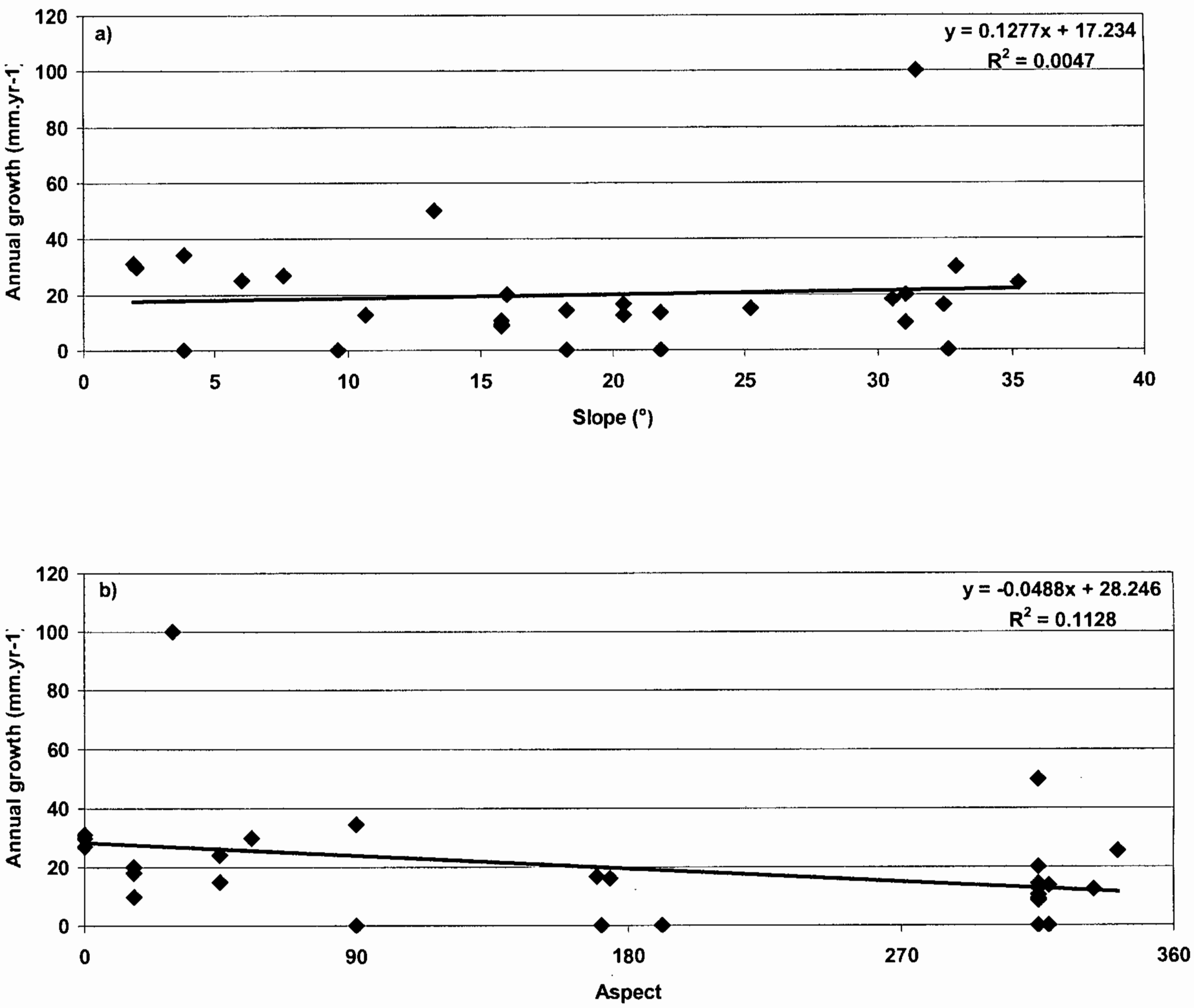

Figure 11: Individual annual growth rates plotted against microhabitat variables of a) the slope on which the plant was situated and b) the aspect of each plant. In neither of the graphs were annual growth rates related to these variables ($p>0.05$, $n = 28$, in both cases).

The individual growth rates were used to investigate relationships between growth and microhabitat (Figure 11a & b) and biological variables (Figure 12a & b). Individual annual growth rates were not related to any of these individual variables that were measured. All R^2 values were less than 0.12, indicating that they explained less than 12% of the variance in the annual growth rate.

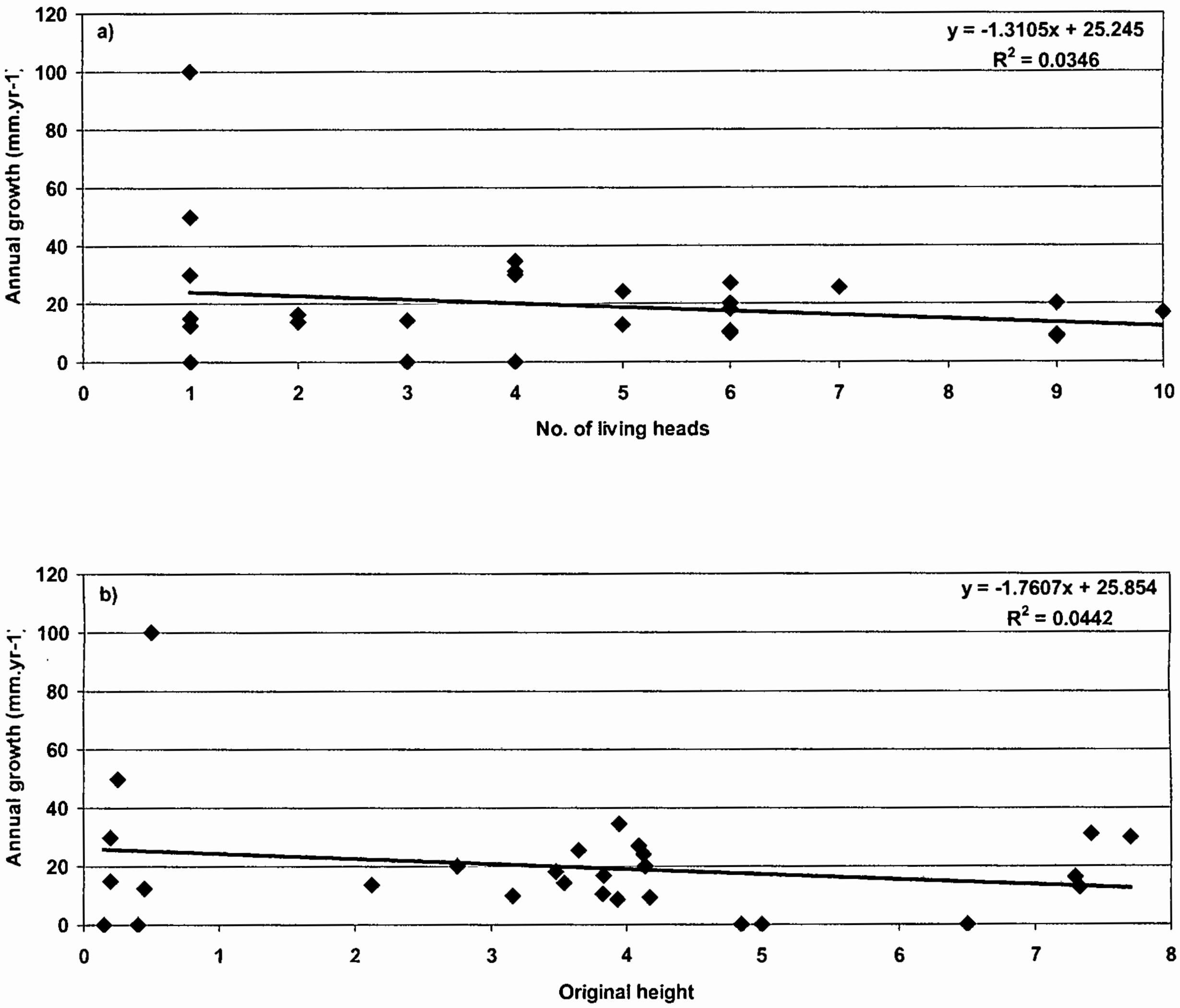

Figure 12: Individual annual growth rates plotted against the biological variables of a) the number of living heads on the plant and b) the height of the plant in the original photograph. In neither of the graphs were annual growth rates related to these variables ($p>0.05$, n = 28, in both cases).

Annual rainfall records from Lekkersing (Figure13), which is 65 km southwest of Cornell's Kop, indicate that annual rainfall in the region is highly variable, with some years experiencing almost no rainfall whatsoever. Estimates of the recruitment date (year when an *A. pillansii* seedling entered the population) are also displayed in order to examine whether these two variable are related. Dates of seedling recruitment were calculated using seedling growth figures from the surveys to trace when seedlings might have entered the population over the last 30 years. Estimates of recruitment numbers were grouped into five-year periods of which only the last year is shown i.e. the seedlings could have recruited in the year illustrated or at some time during the preceding four years, the data is presented like this in order to illustrate the possible time lag between above-average rainfall events and seedling recruitment.

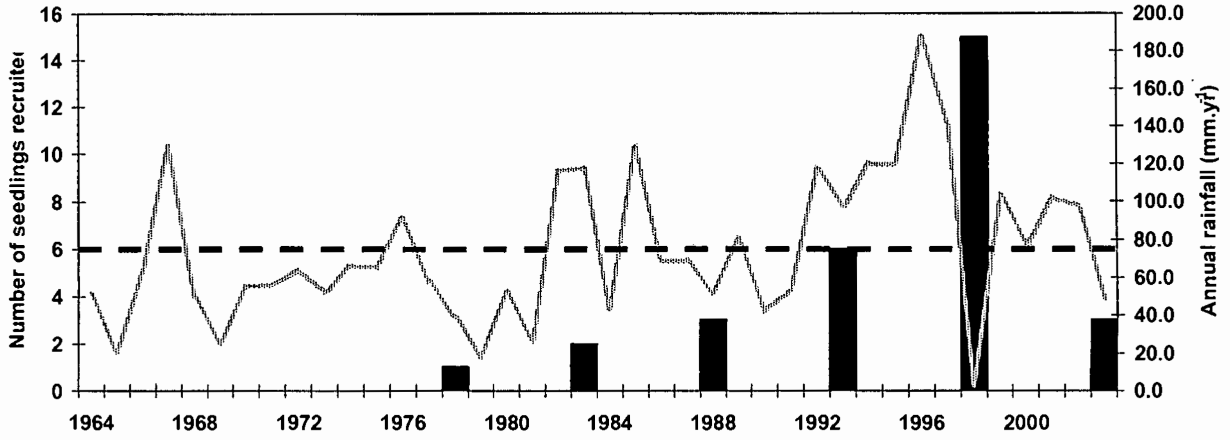

Figure 13: Annual rainfall for Lekkersing (solid line) from 1964 to 2004 and estimates of the number of *Aloe pillansii* recruits (n =30) on Cornell's Kop for the last 30 years, using an average seedling growth rate of 30 mm.yr^{-1} (see Table 2). The average annual rainfall of 74.8 1 mm.yr^{-1} is shown with a dotted line.

The graph indicates a period of six successive years from 1992 to 1997 in which the rainfall was well above the average annual rainfall, there also appears to have been a specific pulse in recruitment between five and ten years ago associated with these highly productive years (1994 – 1999). Prior to 1992 there were only five years out of 28 that had above-average rainfall, all of which have associated recruitment events. These results do not include five seedlings, which were found in the 2000 survey but which had either died or had been removed by 2004.

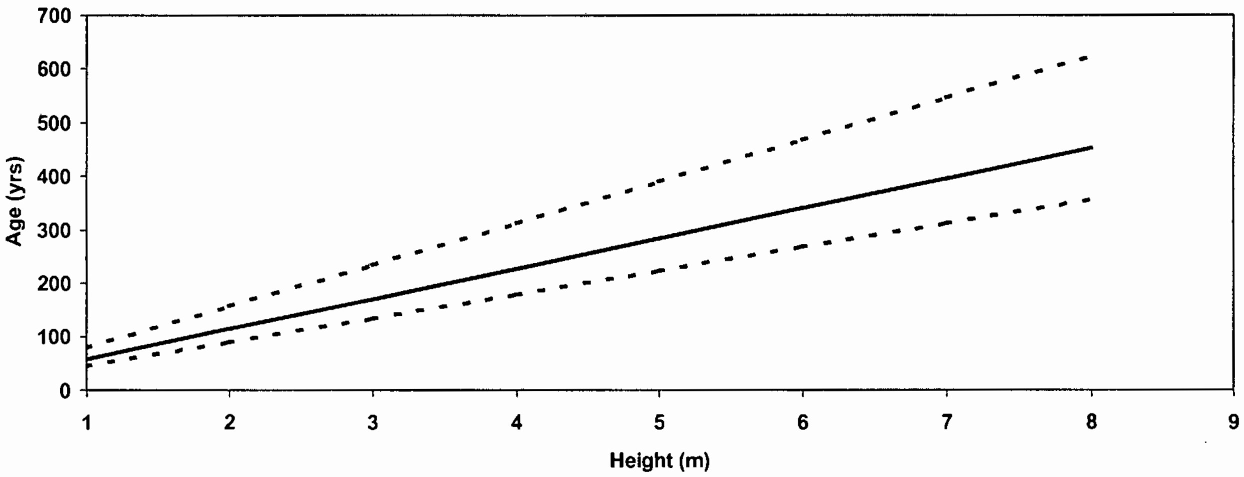

Figure 14: Predicted ages of plants of different heights calculated at an average growth rate of 17.7 mm.yr^{-1} (solid line). Both the mean (solid line) and the 95% confidence limits (dotted lines) are indicated.

The average ages of different sized individuals were calculated using an average growth rate of 17.1 mm.yr^{-1} (Figure14). This rate was calculated by using adult growth rates measured in repeat photographs in which the original photographs were taken in 1985 or before. This rate is likely to be the most accurate estimate since it is calculated over a longer period of time than the recent repeat photographs and will thus incorporate long term climatic effects. Since there is very little variance between the individual growth rates (<0.0001), the mean adult growth rate should be a fairly accurate predictor of individual plant ages. However, seedling growth rates were not included and are generally expected to be higher than adults and thus the figures displayed are likely to be over-estimates. The analysis suggests that the tallest individual on Cornell's Kop at eight m, could be 453 years old.

DISCUSSION

Status of *Aloe pillansii* on Cornell's Kop

Aloe pillansii was first collected from Cornell's Kop in 1926 and later described in 1928 (Reynolds 1950). The first reliable information on the population on Cornell's Kop is from a photograph by Reynolds in 1937 (see Landscape match 4, Appendix 3). Since then the aloe population on the hill has been partially photographically documented at approximately ten-year intervals. The first attempts at surveying the population were made by Midgley (1997) and later by Powell *et al.* (2000). From these cursory analyses of the population, it appears that the *A. pillansii* has declined dramatically since it was first documented in 1937.

However, it is not clear whether this decline is merely part of *A. pillansii* 's long-term recruitment strategy or whether the population is really at risk of extinction. It is clear that the *A. pillansii* population on Cornell's Kop has been declining over the last 50 years. There are more skeletons present on the hill today than ever before and the mortality rates calculated from repeat photographs indicate that the number of living adults has declined rapidly from when the first photographs were taken by Reynolds in1937. Although the adults are dying, it seems that the vast majority of them are dying naturally as they reach the end of their long lifespan, which appears to be well over 400 years for an eight m individual. Midgley's (1997) size class distribution study of the Cornell's Kop population failed to take into account the fact that the dead tree skeletons would have degraded after being exposed to the extreme conditions on Cornell's Kop. Thus, it reported results which indicated that many of the dead trees on the hill had died when they were only 2 or 3 metres tall. The more recent survey in which more accurate heights at death were calculated indicates that this is not the case and that most of the trees had died when they were well into the adult phase of their lives.

Photographic evidence suggests that trees, which were in the juvenile phase in the original photographs, are generally still present in the repeat photographs, indicating that conditions on Cornell's Kop are still habitable for *Aloe pillansii.* Similarly, by assessing the vegetative cover of other plant species in repeat photographs, such as *Euphorbia hamata* among others, it appears that very little has changed on the hill as there hasn't been any identifiable die-back of any other species apart from *Aloe pillansii*. Coupled with this is the fact that during the 2004 survey 30 seedlings were found to be present in the population, which indicates that Cornell's Kop is still very much the same as it was 50 years ago.

Aloe pillansii's Life History Strategy

The size-class distributions of the population indicate that the *A. pillansii* individuals on Cornell's Kop fall into discrete age cohorts. There are a number of seedlings (<1 m), but no juveniles ((1-2. 5 m) whatsoever while the majority of the population present are in the adult phase (>2. 5 m). This is indicative of a life history pattern in which recruitment is infrequent and relies heavily on periodic favourable climatic events in order for seedling recruitment and survival to occur. This is supported by similar studies on other large desert succulents such as *Agave deserti* (Jordan & Nobel 1979), *Ferocactus acanthodes* (Jordan and Nobel 1981) and *Carnegiea gigantea* (Jordan & Nobel 1982, Drezner 2004) in the Sonoran desert, which indicate that all of these species also rely heavily on large episodic rainfall events in order for recruitment to occur.

Analysis of the annual average rainfall records for Lekkersing, which is situated 65 km southeast of Cornell's Kop but is likely to experience similar weather patterns, indicates that there were six years of above-average rainfall from 1992-1997 in the Cornell's Kop region. Estimated recruitment dates correspond remarkably well to years of above-average rainfall. It was found that 50% of all seedlings present were likely to have germinated during the years between 1994 and 1999 and these corresponded well to this period of consistently above-average rainfall. Similarly, every other above-average rainfall year over the last thirty years, which is approximately how long a plant is likely to be in the seedling size class, had a proportional recruitment event associated with it. The absence of consecutive years of above-average rainfall prior to 1992 might explain why Midgley's survey in 1995 found only two seedlings, since the above-average rainfall years had only just begun. If seedlings were present, they would have been difficult to spot by 1995, particularly if the survey team had limited time and manpower. Jordan and Nobel's (1979) study on *Agave deserti* reported very similar findings, in which only six seedlings were found over a period of seventeen years, all of which dated back to one significant rainfall event at the beginning of the seventeen year period.

It is unlikely that annual rainfall is the only climatic determinant of *A. pillansii* distributions. Bolus (2004) suggests that there are a number of important climatic variables such as mean annual minimum and maximum temperatures, annual fog incidence among others, which in combination may affect the distribution of *A. pillansii* populations. There are also a number of potential biotic barriers to recruitment for *A. pillansii*, such as pollination and seed dispersal. However, Williamson (1998) noted that the flowers are visited by a number of insects as well as two nectar-seeking birds and that pollination is thus usually good for most of the seeds on a mature inflorescence, Williamson also stated that if all of the seeds from one single inflorescence were to germinate, they would produce five times as many plants as there presently are on the hill. Thus, it seems unlikely that the population would be declining because of a lack of viable seed set. Similarly dispersal is unlikely to be problematic on Cornell's Kop, since the seeds are relatively small and would easily be dispersed by the strong winds which blow all year round on the hill. Another important factor, which may determine recruitment success is the presence of nurse plants, which provide seed-traps for the collection of wind blown seeds as well as protection for young seedlings (Jordan & Nobel 1979). Photographic evidence suggests that nurse plants are indeed important to *A. pillansii* recruitment as the majority of seedlings found growing on Cornell's Kop were associated with nurse plants while the remaining seedlings were generally found growing in rock crevices or other protected niches. Analysis of repeat photographs however, suggests that there has not been any loss of cover of potential nurse plants on Cornell's Kop, thus this would not appear to be limiting *A. pillansii* recruitment.

Growth rates measured from the surveys and repeat photographs indicate that growth rates in *A. pillansii* are generally very low (somewhere between 20 and 30 mm.yr^{-1}), although it is known from individuals grown under optimal conditions in a nursery, that growth can reach up to 250 mm.yr^{-1} (Bayer 1974). The repeat photography analysis also revealed that some individuals stop growing while others continue to grow, irrespective of their age or height. In another study which used repeat photography to measure growth in a remarkably similar species of tall desert succulent, cirio (*Fouquieria columnaris*), Escoto-Rodriguez and Bullock (2002) found very similar results to this study and noted that growth is often infrequent or even negative, and may also be lagged in relation to climate. Thus, it seems that growth is particularly complex and is clearly dependant not only on the climatic conditions but on some of the individual plant's microhabitat or physical variables as well. This is also clear from their positioning only on the north-facing slopes of Cornell's Kop between the altitudes of 130-180m. This study's attempts to correlate individual growth rates to the microhabitat variables of slope and aspect or the physical variables of plant height and the number of living heads on the plant were unsuccessful. Individual annual growth rates were also plotted against the decade in which the photograph was taken in order to establish whether there had been a specific spike in growth during one particular time period, however there was no relation found between the year of the photograph and the annual average growth. It is likely that some other feature of the plants microhabitat, such as soil particle size, may account for some of the plants recording annual growth rates of 30 mm.yr^{-1} while other plants had not grown at all over the same period. In the future, further studies could be done to determine whether individual growth rates are genetically predetermined and if so, how do external factors such as climate and microsite, interact with this intrinsically set growth rate.

Another important factor related to both growth rates and seedling success in three of the American succulent species studied (Jordan and Nobel 1979, 1981, 1982, Drezner 2004), was that they all exhibit Crassulacean Acid Metabolisms (CAM), which appears to influence seedling survival after germination. Vogel (1974) noted that *A. pillansii* is likely to exhibit this same metabolic system. CAM is characterized by nocturnal stomatal opening and CO^2 uptake (Jordan & Nobel 1979), which although it is important for survival in desert environments, this type of metabolism does result in slow growth rates. Slow growth rates in turn limit the water storage capacity generated by the plant and often, in the case of seedlings, plants are not able to build up adequate water stores in order to survive extended periods of drought.

Causes of Mortality on Cornell's Kop

The most noticeable feature of the size class distribution of the *A. pillansii* population on Cornell's Kop was the absence of any juvenile plants (1-2.5 m) on the hill. This suggests that prior to the germination of the oldest seedling in the population (±30 yrs ago), there has been no recruitment in the population for over half a century. Although it is likely that *A. pillansii* only recruits episodically, it is unlikely that there would have been no recruitment for such an extended period of time. Rainfall records do record that the majority of years during this period did receive less than average rainfall, however, it seems unlikely that no recruitment at all would have occurred during these years. The disappearance of this integral size class might be explained by suggestions of theft by collectors and animal damage (Midgley 1997, Midgley *et al.* 1997, Williamson 1998). However, similar size class distributions, with the missing juvenile class, were found in other, more remote *A. pillansii* populations (Bolus 2004), which suggests that this is characteristic of the entire species rather than a specific population.

Anecdotal evidence reports that during the 1960's & 70's, collectors removed truckloads of succulent seedlings from the Richtersveld (L. Thamm, pers. com). Because of the difficulty of transporting fully-grown plants, it is more likely that small seedlings and juveniles were removed. The possible removal of one size class in this manner could well account for the missing juvenile size class today, which would have been seedlings during the time that theft was rife in these areas. Cornell's Kop's readily accessible location would also have made it an easy target for collectors.

After finding evidence of chewed shreds of *A. pillansii* at the base of the trees, Midgley (1997) stated that mortality might be caused by herbivory from baboons and porcupines. However, an earlier report by Van Jaarsveld (1987) noted that the aloe's leaf sap is very bitter and generally avoided by livestock. In his report, Williamson (1998) cites trampling by goats as the most severe influence on *A. pillansii* seedlings. Both of these theories are highly plausible explanations of mortality but are very difficult to quantify without intensive monitoring of the populations. They could well account for losses of seedlings that might have recruited during the period between 1900 and 1970, although they would not explain the presence of the 30 seedlings in the recent survey.

The *A. pillansii* population on Cornell's Kop appears to have a recruitment strategy which relies on highly infrequent recruitment events, namely above-average rainfall years in the area. Previous studies on Cornell's Kop have suggested that this *A. pillansii* population may be at risk of extinction based on the amount of mortality present on the mountain. The new evidence, in the form of the thirty new seedlings, presented in this study indicates that *A. pillansii's* population dynamics are perhaps more complex than previously thought. 'Snapshot' studies of the population fail to capture data that may be pertinent to understanding the species life history strategy but not evident at the time that the study was conducted. Long term monitoring of the population, in the form of surveys and repeat photography, are crucial techniques needed when trying to unravel complex life histories of long-lived species such as *A. pillansii.*

Links between *Aloe pillansii* and Climate Change

As the topic of climate change becomes more and more prominent in environmental studies, changes in indicator species distributions are becoming important tools in environmental modeling. However, misinterpretations of changes in indicator species populations can lead to ineffective conservation programs and are likely to be labeled as 'environmentalist propaganda'. Thus it is vitally important that potential indicator species such as *A. pillansii* are properly researched before they are used to describe changing climates.

In the earlier half of this century, a number of scientists believed that that the desert environment was one of perennial stability (Shreve 1917) and thus any observed population or climate changes must be of anthropogenic origin. However, there is in fact, little evidence to back up these claims. As more and more long-term studies are conducted, there seems to be more evidence to suggest that deserts are in fact, dynamic and responsive environments, in which plant populations have been fluctuating for many centuries, before and after the impact of humans became apparent (Turner 1990). Thus, there appears to be a large amount of natural variation in desert populations, and one must therefore be careful not to be too quick to ascribe all observed changes to humankind.

Climate change does not appear to be affecting *A. pillansii* as detrimentally as previous reports have suggested (Foden 2002, Rogers 2004). The apparent health of Namibian populations (Loots & Mannheimer 2003), where climate change should be more apparent, agrees with this finding. There also don't appear to be any range shifts of the species occurring, which would be expected if *A. pillansii's* original environment was becoming uninhabitable due to changing climatic variables. Bolus's (2004) study of all the known *A. pillansii* populations in South Africa, also suggests that although some populations are unhealthy in that they are very small and do not have any have any seedlings present, in general most of South Africa's *A. pillansii* populations are considered healthy. There are also a number of more southerly areas, which receive higher annual rainfall than Cornell's Kop does, and yet *A. pillansii* does not occur there. This may be because these areas do not yet fall into *A. pillansii's* discrete environmental niche, but it must also be noted that because of its long-lived life history strategy and infrequent recruitment, the population will have a very slow turnover time and will thus be unable to adapt to rapid environmental and climatic changes. However, as yet, there is no evidence to suggest that inhabitable areas for *A. pillansii* are moving south as a result of global warming as Kaleme (2003) and Foden (2002) suggest is happening with *A. dichotoma.*

A. pillansii appears to be an incredibly hardy species which continues to survive and recruit in extremely harsh environments. The differing findings between this study and those done on *A. dichotoma* (Foden 2002, Kaleme 2003) may also suggest that perhaps *A. pillansii* is not as similar to *A. dichotoma* as has previously been assumed, while *A. dichotoma* may be shifting its range because of climate changes, *A. pillansii* may be too resilient to be used as an indicator species to provide the early warning signs of climate change in Southern Africa. However, it is clear that *A. pillansii* does rely on periodic high rainfall years in order for recruitment to occur. If the climate changes predicted in Midgley *et al*'s (2002) GCMs do occur and high rainfall events do become scarcer in the Richtersveld, *A. pillansii* populations in these areas may well start to decline as a direct result of climate change.

Conservation Measures

As an addendum, it is important to discuss future conservation measures which are needed in order to ensure the survival of this species in the wild. Unfortunately, the lack of long-term data for existing *A. pillansii* populations makes it difficult to accurately assess whether populations are just in a senescent phase of their lifecycle or whether they are in fact headed towards extinction. In this regard, the recent survey by Powell *et al.* (2000) is good starting point and follow up surveys and repeat photography should be done on a regular basis in order to gain a better understanding of this complex species. Further information could be also gained from setting up a weather station on, or near Cornell's Kop to provide more accurate climatic information for the area.

Although *A. pillansii* populations may not be declining due to climatic change , conservation of this species is nonetheless necessary, as *A. pillansii* still faces a number of threats, anthropogenic and other, to its continued survival in areas like Cornell's Kop. *A. pillansii* is known keystone species within its natural environment of the Succulent Karoo, providing important vantage points for raptors as well as nesting sites for smaller birds in an otherwise empty landscape (Midgley *et al.*1997). They are also known to act as reservoirs for hundreds of litres of water, which a number of species may well rely on during particularly arid times (Midgley 1996). According to Powell *et al.* (2000), at present only 28% of the total *A. pillansii* population occurs on conserved land in the Richtersveld National Park, the remaining 72% is found on privately owned land (Williamson 1998) with no apparent conservation measures in place.

The presence of 30 seedlings on Cornell's Kop in the recent survey indicates that *A. pillansii* may not be under such threat from collectors and animal damage as previously thought (Midgley 1997, Williamson 1998). However these threats could be further minimised by fencing off areas with high concentrations of seedlings in them to protect them from trampling and collection. SANParks could also erect a signboard at the base of Cornell's Kop explaining the situation to tourists in order to reduce human disturbances on the hill.

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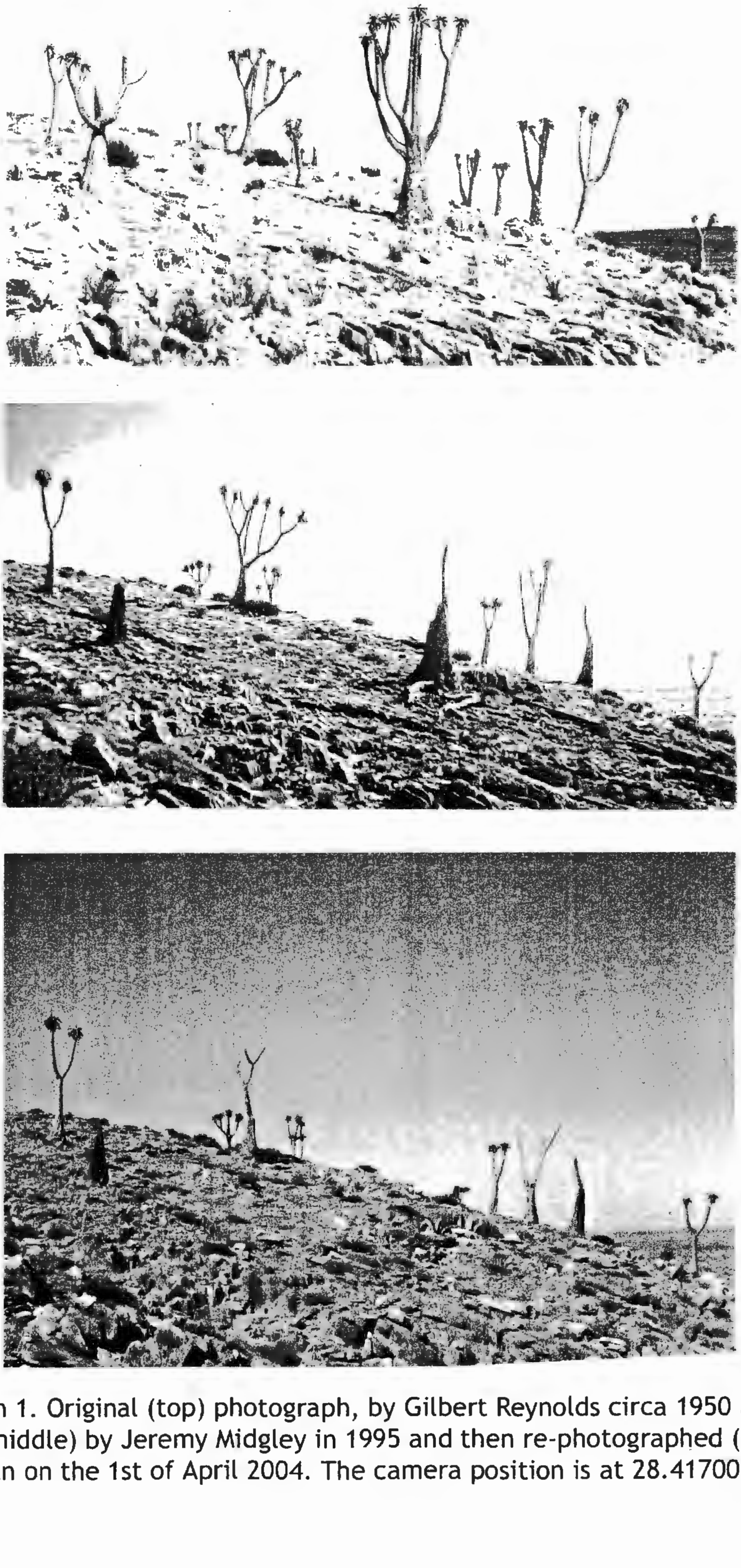
APPENDIX 1: Growth measurements for adults from repeat photographs

Plant No.	Age class	Year of original data	Year of repeat photo	No. of years between photos	Height in original photo (m)	Height (m)	Annual growth rate (mm.yr^{-1})	No. heads in original	No. heads today	Aspect (°)	Altitude (m)	Slope (°)
13	Adult	Match 11 (1950)	2004	54	3.83	4.40	10	5	6	314.9	99	16
16	Adult	Landscape Match 8 (1946)	2003	57	2.12	2.90	10	1	2	318.3	117	22
19	Adult	Match 16 (2000)	2004	4	3.48	3.55	20	6	6	16.4	141	31
		Landscape Match 2 (1971)	2004	33	3.16		10	5	6			
		Landscape Match 7 (1953)	2003	50	2.75		20	4	6			
22	Adult	Match 17 (2001)	2004	3	4.13	4.20	20	5	5	45.1	149	35
24	Adult	Match 26 (1995)	2004	9	6.50	6.50	0	4	4	191.3	130	10
26	Adult	Match 25 (1976)	2004	28	3.83	4.30	20	9	10	169.7	126	20
27	Adult	Match 2 (1991)	2004	13	7.29	7.50	20	2	2	174.0	130	32
30	Adult	Match 3 (1991)	2004	13	3.95	4.40	30	4	4	90.0	142	4
34	Adult	Match 23 (2000)	2004	4	4.85	4.85	0	3	3	90.0	148	4
35	Adult	Landscape Match 6 (1985)	2004	19	7.41	8.00	30	4	4	0.0	145	2
		Match 4 (1991)	2004	13	7.70		30	4	4			
36	Adult	Landscape Match 6 (1985)	2004	19	4.09	4.60	30	6	6	0.0	148	8
38	Adult	Match 22 (1996)	2004	8	3.65	3.85	30	7	7	341.5	152	6
53	Adult	Match 20 (2000)	2004	4	5.00	5.00	0	3	3	314.9	129	18
55	Adult	Landscape Match 11 (1946)	2003	57	3.54	4.35	10	2	3	314.9	139	18
60	Adult	Match 5 (1950)	2004	54	7.32	8.00	10	4	5	314.9	129	11
62	Adult	Match 19 (2001)	2004	3	4.17	4.20	10	9	9	314.9	128	16
		Match 18 (2001)	2004	3	4.14		20	9	9			
63	Adult	Match 5 (1950)	2004	54	3.94	4.40	10	9	9	314.9	129	16

APPENDIX 2: Growth measurements for seedlings from surveys

Plant No.	Age Class	Year of original data	Height in 2000 survey (m)	Height in 2004 survey (m)	Annual growth rate (mm.yr^{-1})	Heads today (#)	Aspect (°)	Altitude (m)	Slope (°)
15	Seedling	Survey (2000)	0.40	0. 40	0	1	318. 3	115	22
20	Seedling	Survey (2000)	0.50	0. 90	100	1	29. 4	141	31
33	Seedling	Survey (2000)	0.15	0. 15	0	1	171. 0	136	33
43	Seedling	Survey (2000)	0.20	0. 26	20	1	45. 1	143	25
44	Seedling	Survey (2000)	0.20	0. 32	30	1	55. 5	148	33
47	Seedling	Survey (2000)	0.45	0. 50	10	1	333. 4	135	20
64	Seedling	Survey (2000)	0.25	0. 45	50	1	314. 9	134	13

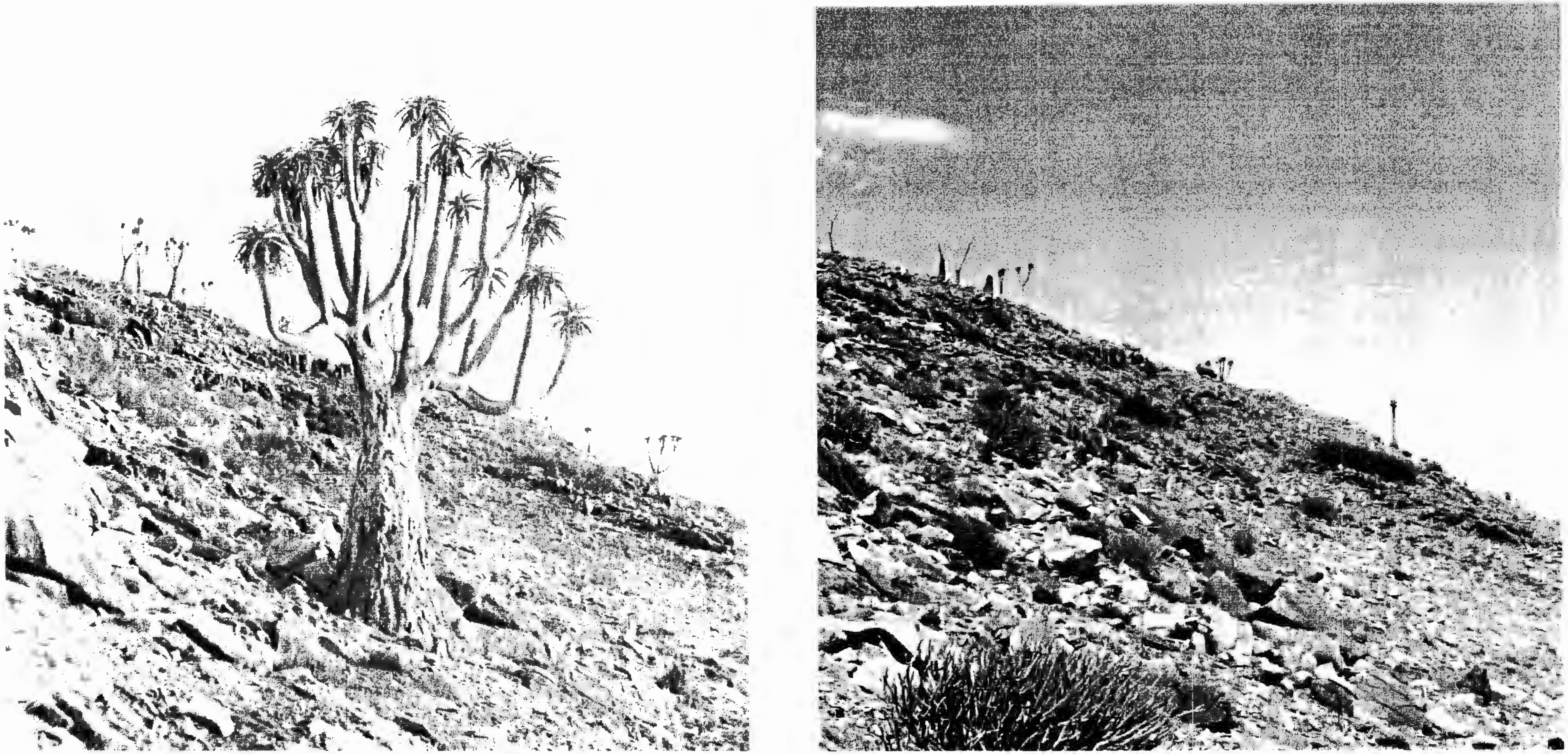


Landscape Match 1. Original (top) photograph, by Gilbert Reynolds circa 1950 and re-photographed (middle) by Jeremy Midgley in 1995 and then re-photographed (bottom) by Timm Hoffman on the 1st of April 2004. The camera position is at 28.41700 S 16. 88558 E

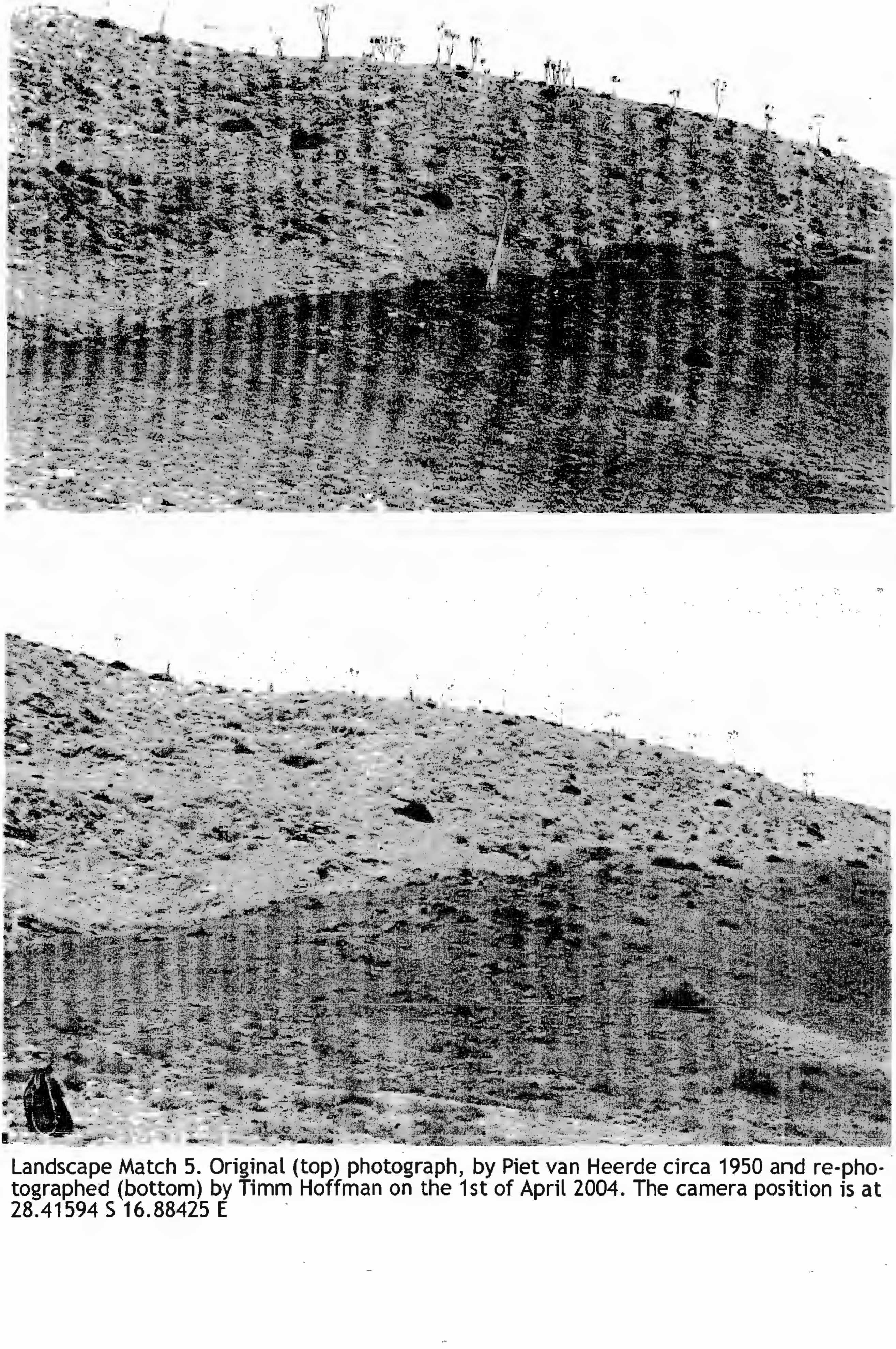
Landscape Match 2. Original (top) photograph of plant number 19, by K.M. Cunliff in October 1971 and re-photographed (bottom) by Timm Hoffman on the 1st of April 2004. The camera position is at 28.41672 S 16.88578 E

Landscape Match 3. Original (top) photograph, by Ernst van Jaarsveld in August 2000 and re-photographed (bottom) by Timm Hoffman on the 1st of April 2004. The camera position is at 28.41667 S 16.88586

[redacted]



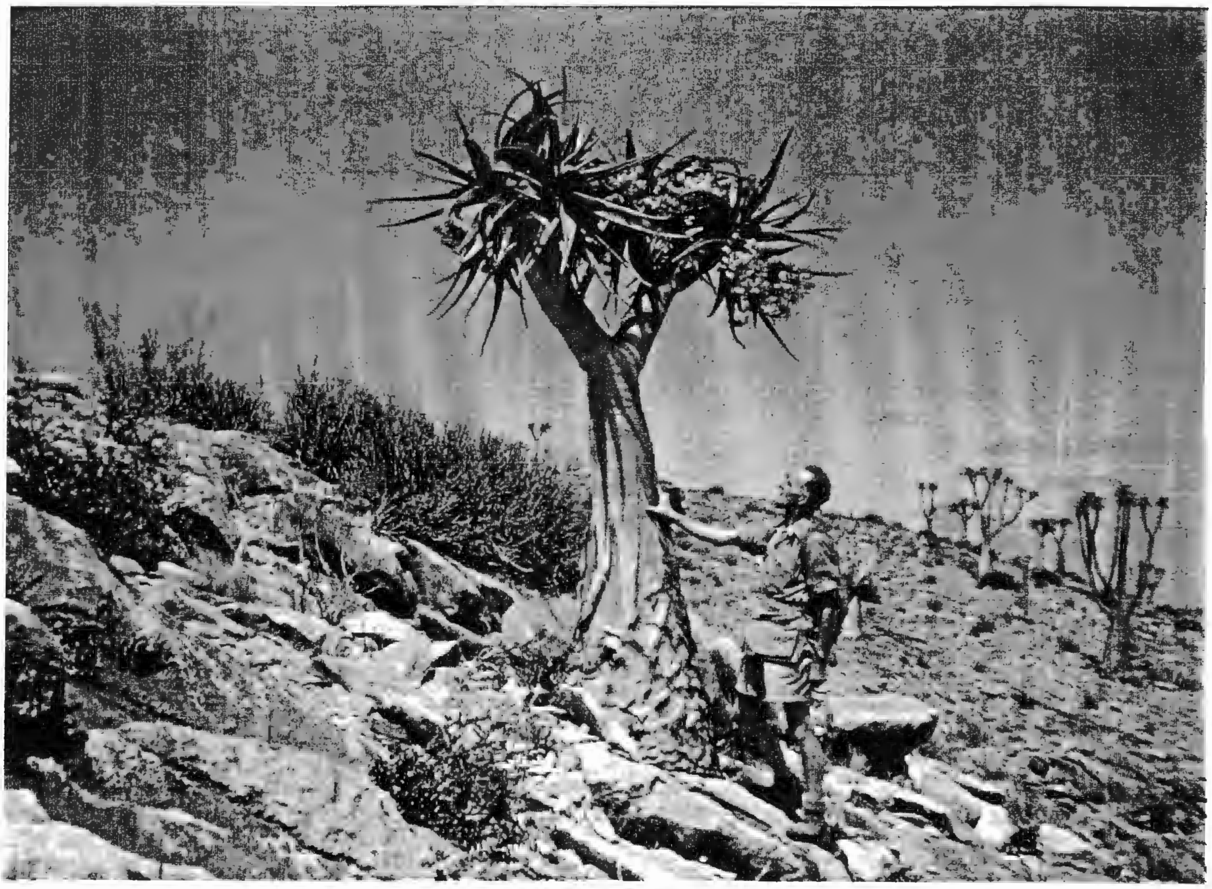
Landscape Match 4. Original (left) photograph, by Gilbert Reynolds on the 24th of July in 1937 and re-photographed (right) by Timm Hoffman on the 1st of April 2004. The camera position is at 28.41642 S 16.88542 E

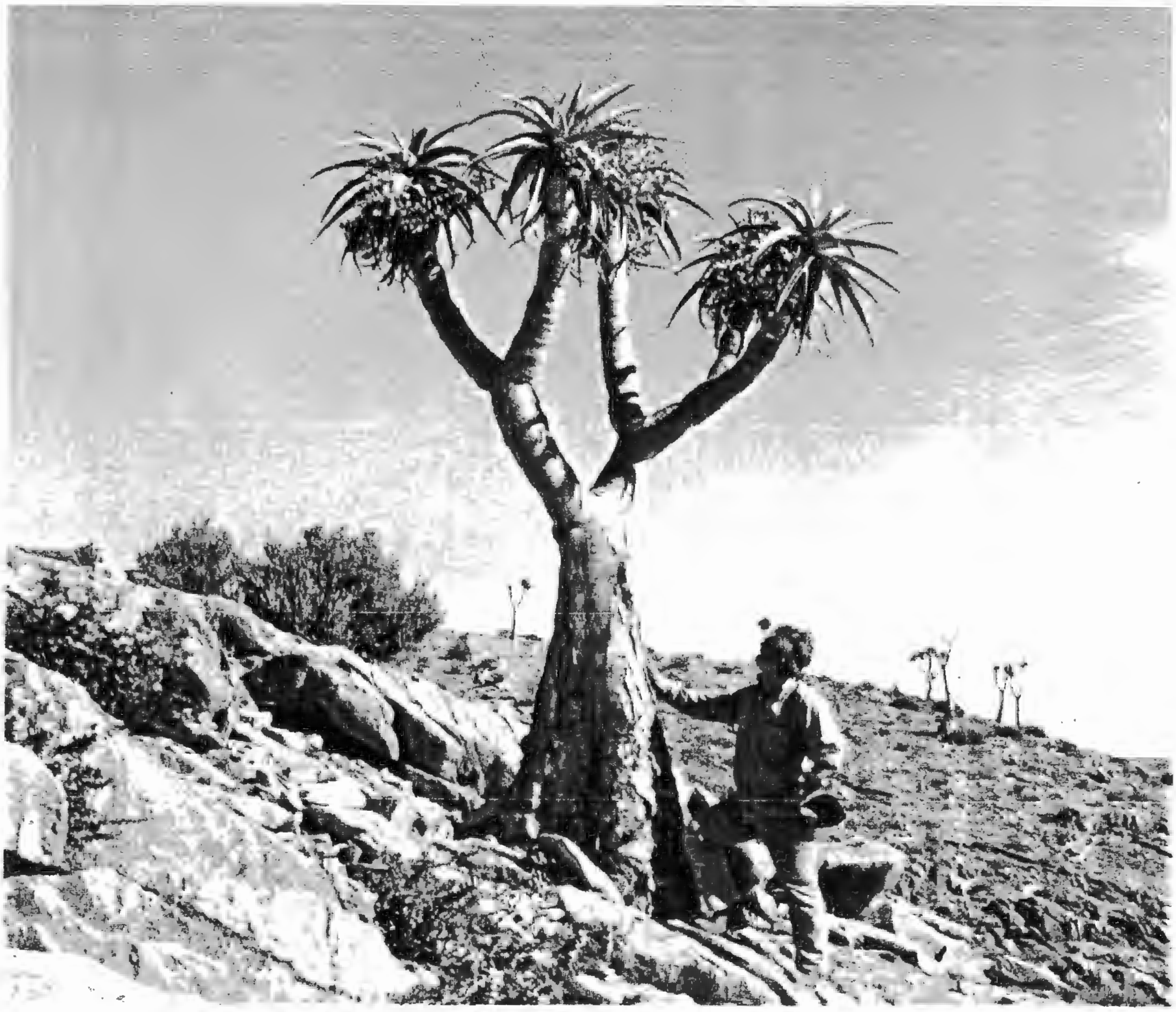


Landscape Match 5. Original (top) photograph, by Piet van Heerde circa 1950 and re-photographed (bottom) by Timm Hoffman on the 1st of April 2004. The camera position is at 28.41594 S 16.88425 E

Landscape Match 6. Original (top) photograph, by Graham Williamson in August 1985 and re-photographed (bottom) by Timm Hoffman on 1st of April 2004. The camera position is at 28.41767 S 16.88525 E

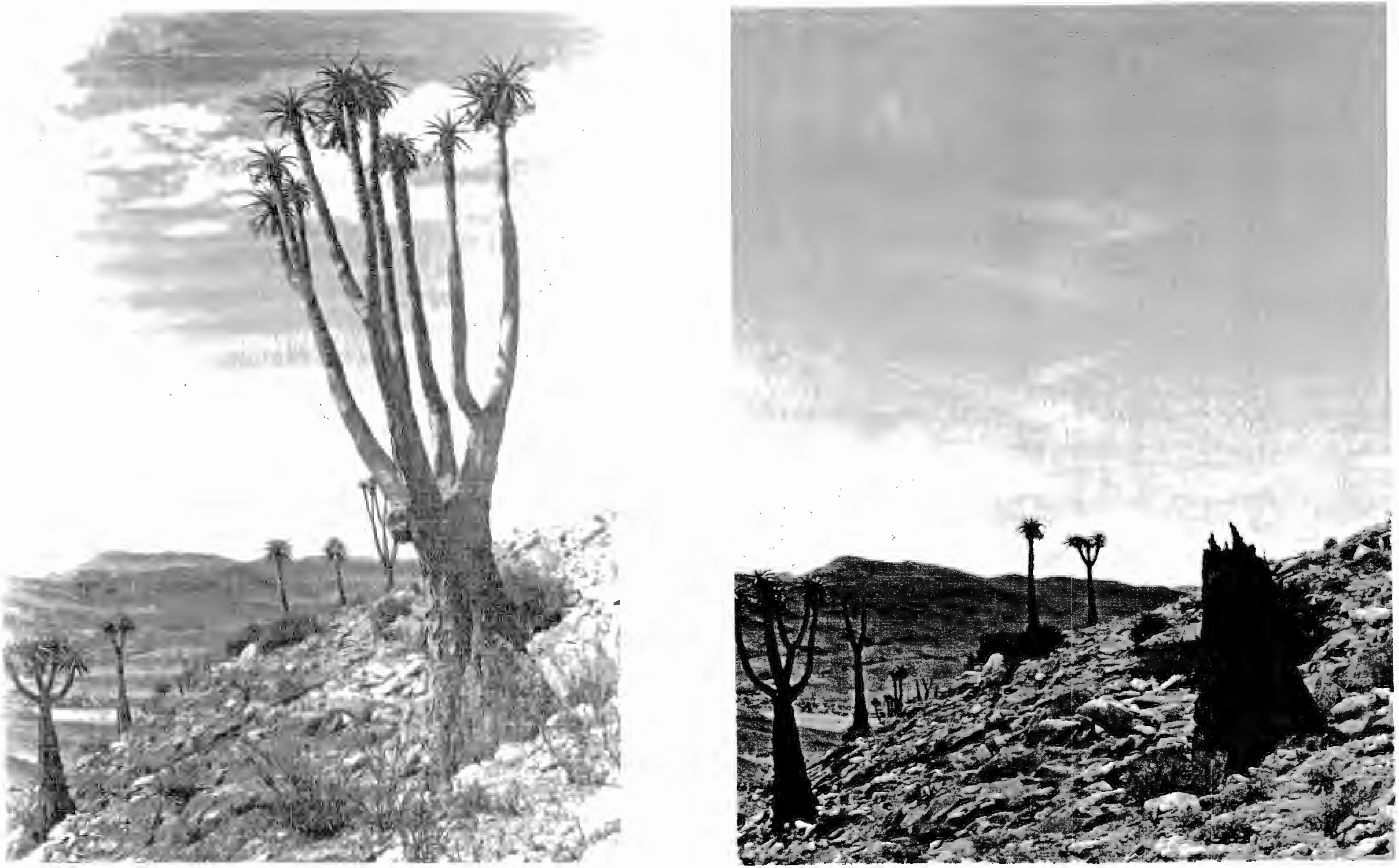
Note the original picture was altered to remove inset photographs from the sky. Also note the presence of goats in the original photograph





Landscape Match 7. Original (top) photograph of plant number 19, by Harry Hall in February 1953 and re-photographed (bottom) by Rick Rohde on the 6th of September 2003. The camera position is at 28.41667 S 16.88581 E

Landscape Match 8. Original (left) photograph of plant number 16, by Gilbert Reynolds on the 6th of December 1946 and re-photographed (right) by Timm Hoffman on the 6th of September 2003. The camera position is at 28.41733 S 16.88522 E



Landscape Match 9. Original (left) photograph, by Harry Hall in February 1953 and re-photographed (right) by Timm Hoffman on the 6th of September 2003. The camera position is at 28.41822 S 16.88492 E

Landscape Match 10. Original (top) photograph, by Harry Hall in February 1953 and re-photographed (bottom) by Timm Hoffman on the 6th of September 2003. The camera position is at 28.41639 S 16.88531 E

Landscape Match 11. Original (left) photograph, by Gilbert Reynolds on the 6th of December 1946 and re-photographed (right) by Timm Hoffman on the 6th of September 2003. The camera position is at 28.41794 S 16.88506 E

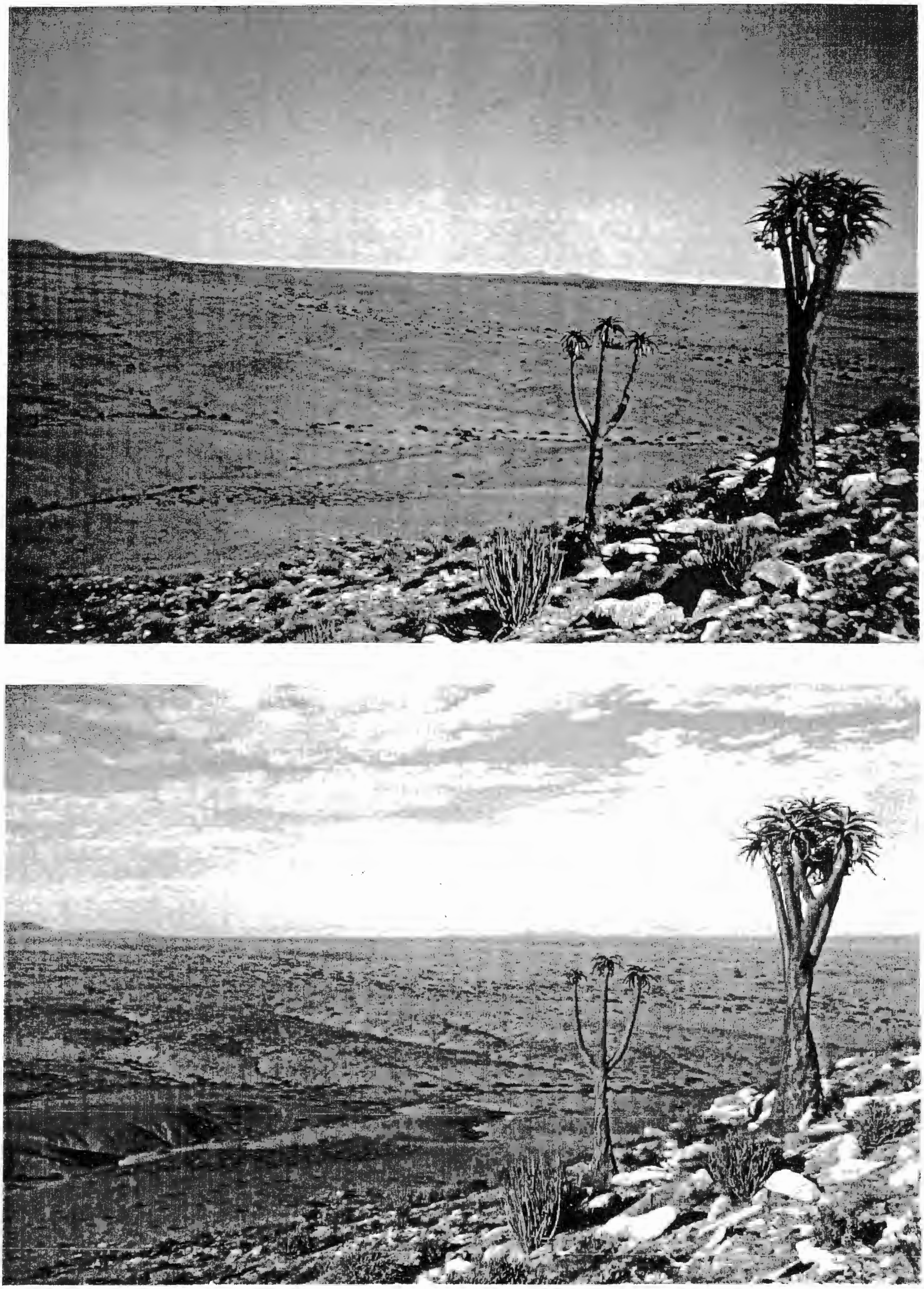
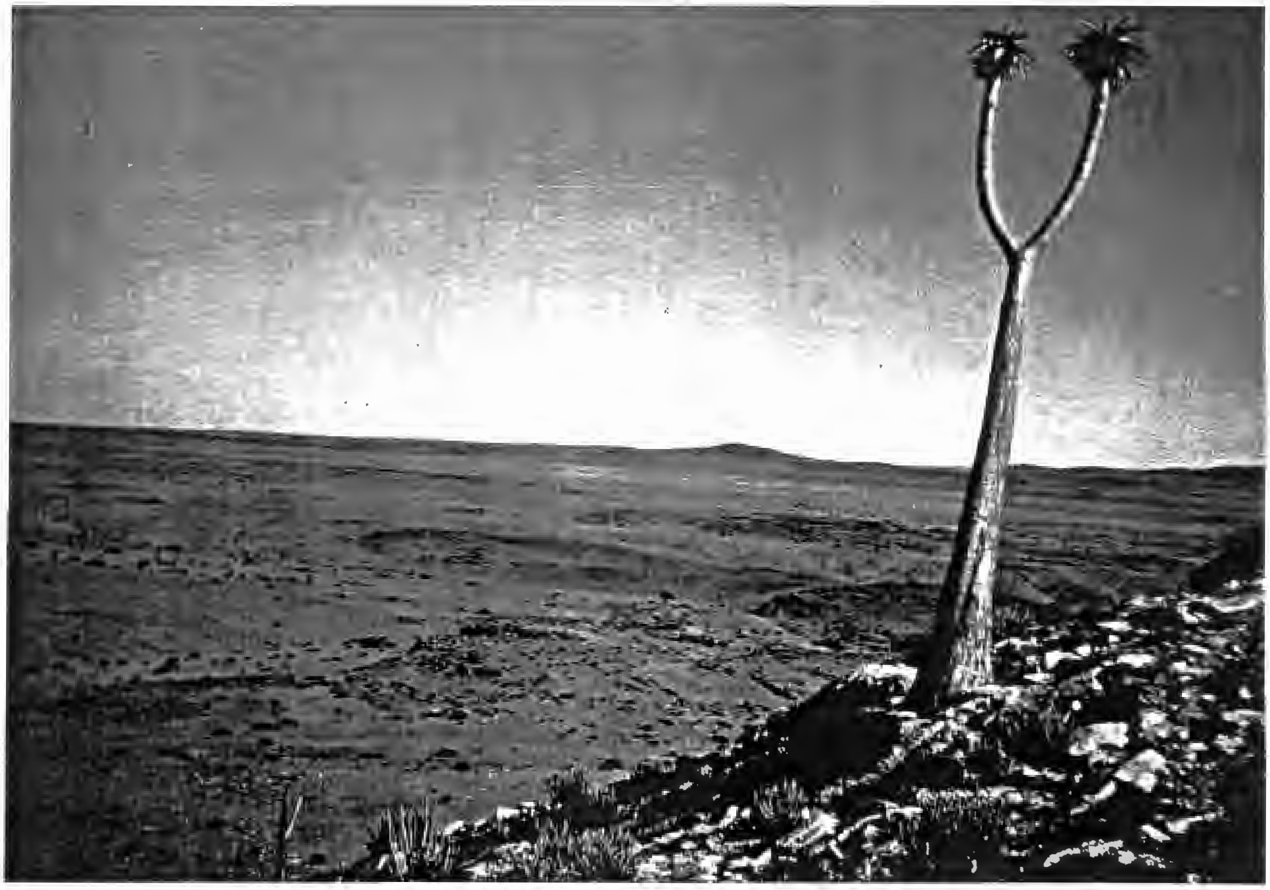
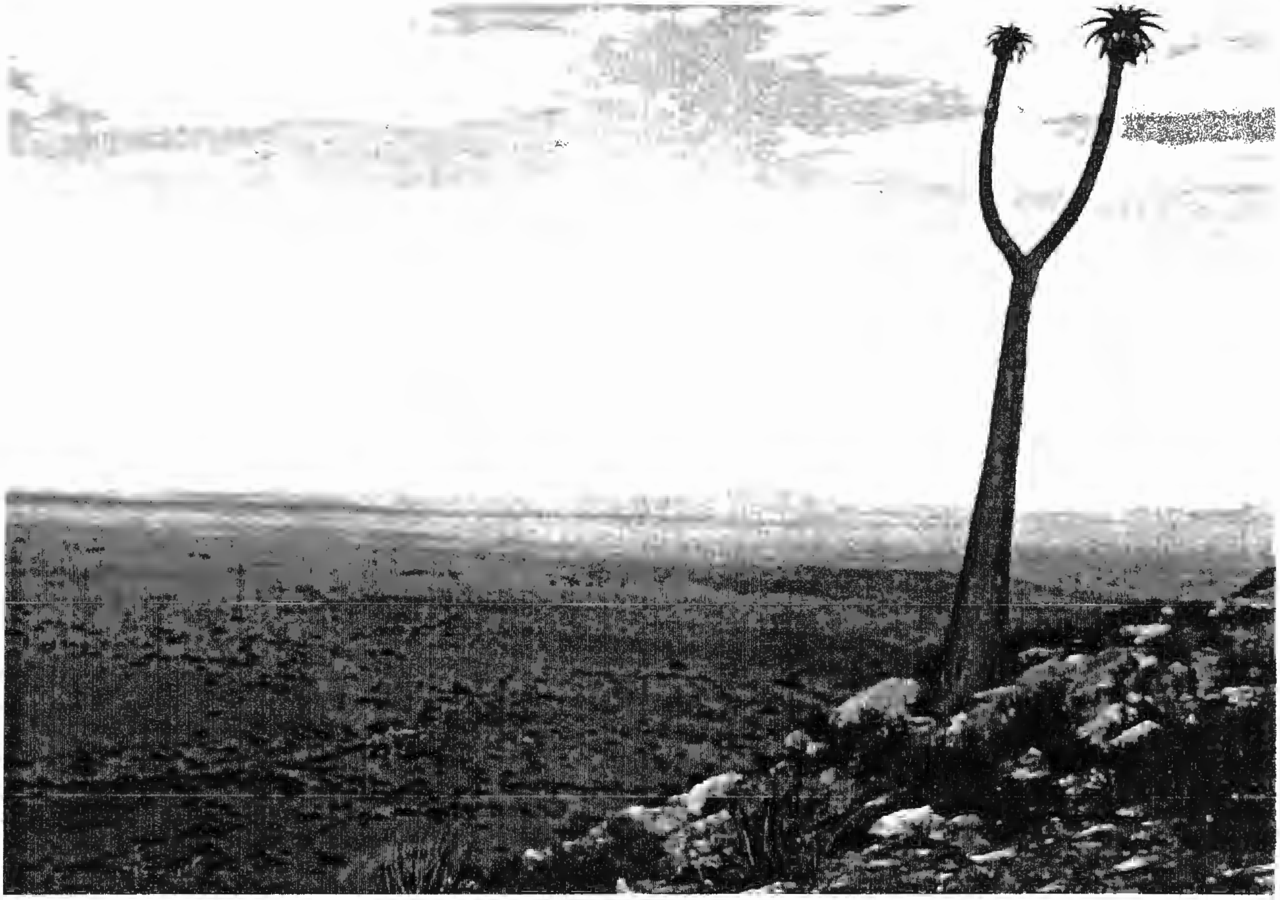


Figure 1. Match 1. Original (top) photograph of plant numbers 25 and 26 from left to right, photographed by Timm Hoffman on the 28th of June 1991 and re-photographed (bottom) by Duncan et al. on 1 April 2004. The camera position is at 28.41905 S 16.88521 E.

Note that the vegetation is less green in the recent photograph, this can probably be explained by the fact that the earlier photograph was taken during the winter rainfall season while the more recent photograph was taken at the end of a long dry summer.



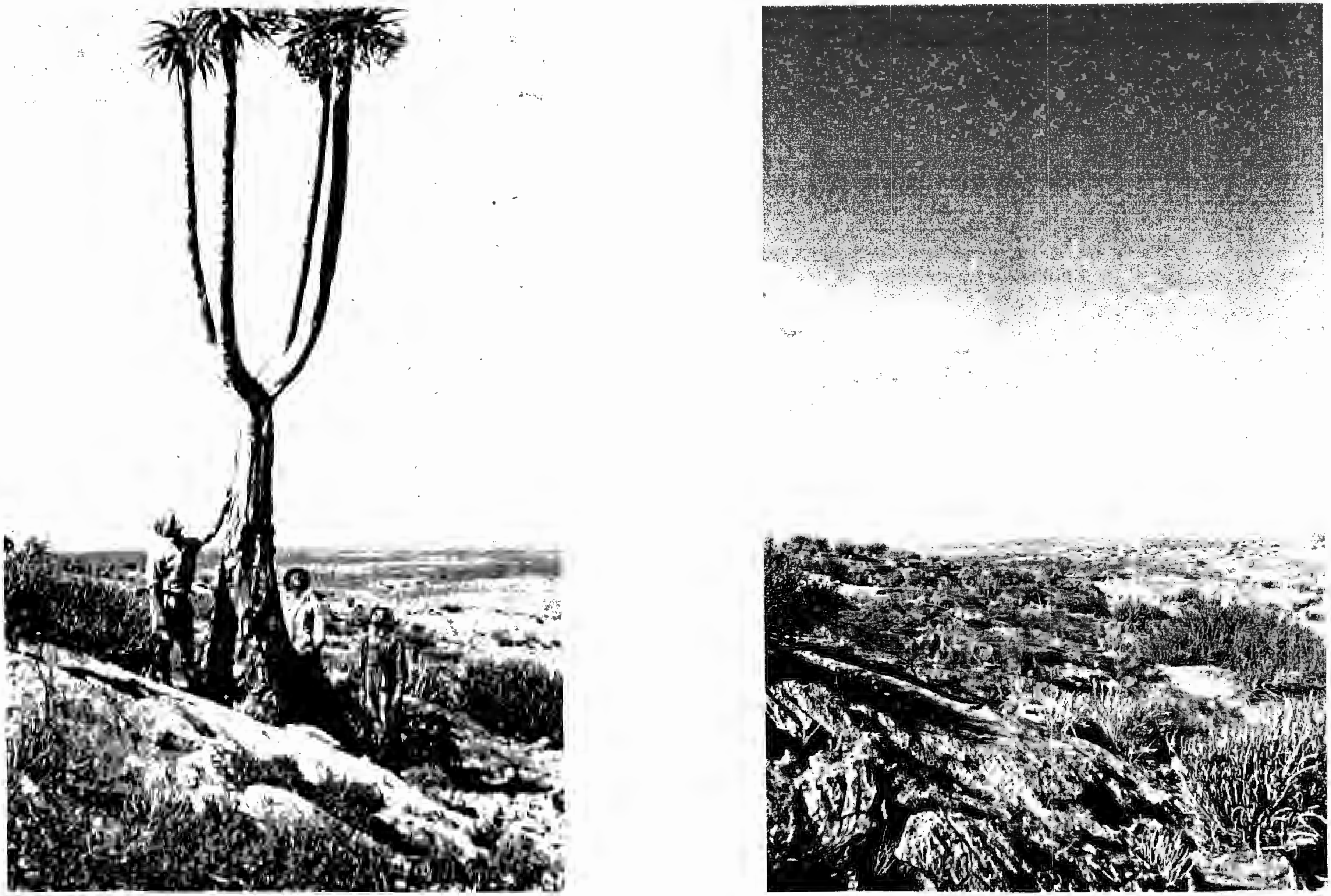


Match 2. Original (top) photograph of plant number 27, by Timm Hoffman on the 28th of June 1991 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41900 S 16.88503 E

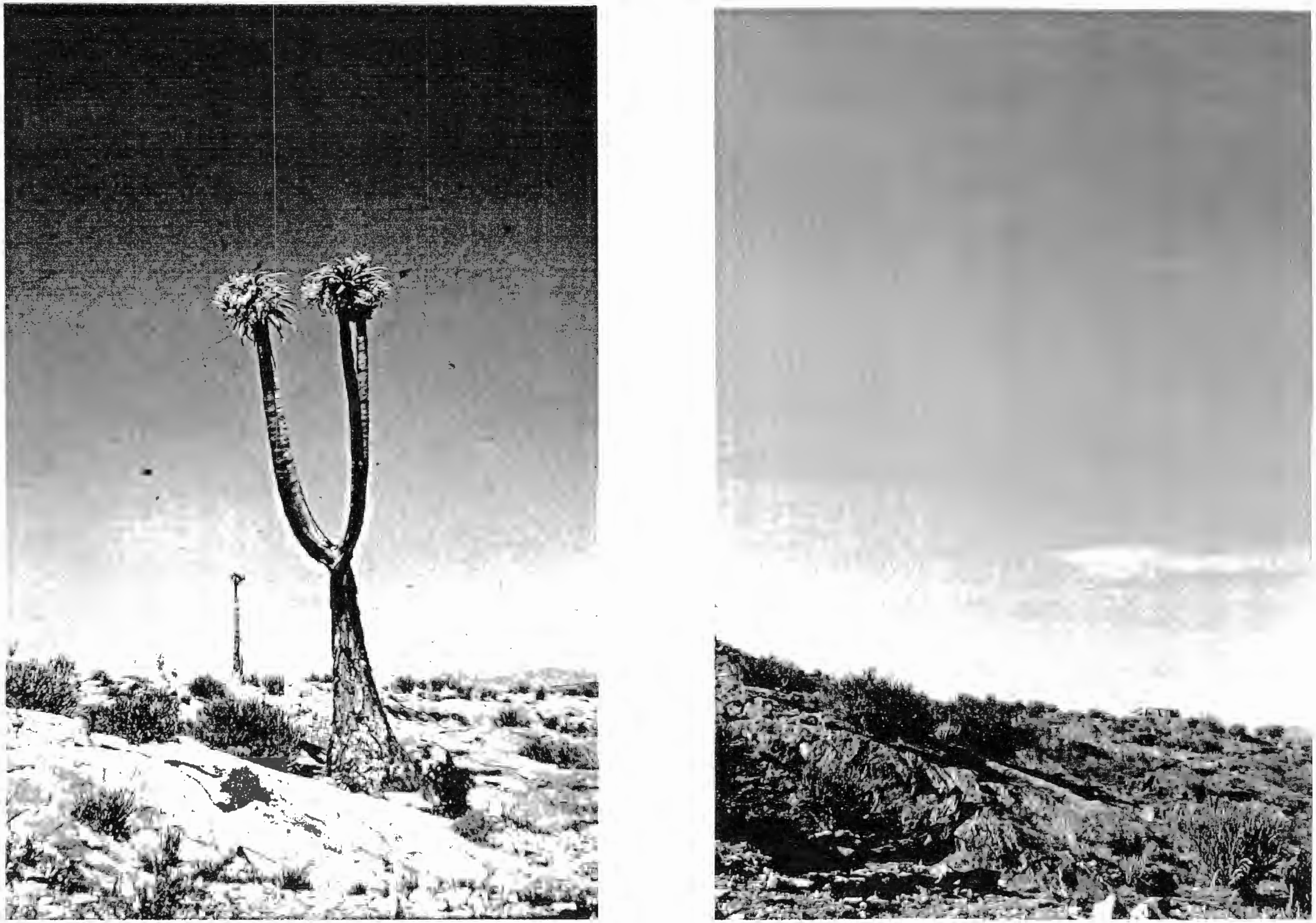
Match 3. Original (top) photograph of plant number 30, by Ernst van Jaarsveld on the 10th of June 1991 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41845 S 16.88507 E

Match 4. Original (top) photograph of plant numbers 35, 56 and 55 from left to right in the more recent photo, by Ernst van Jaarsveld on the 10th of June 1991 and rephotographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41812 S 16.88526 E

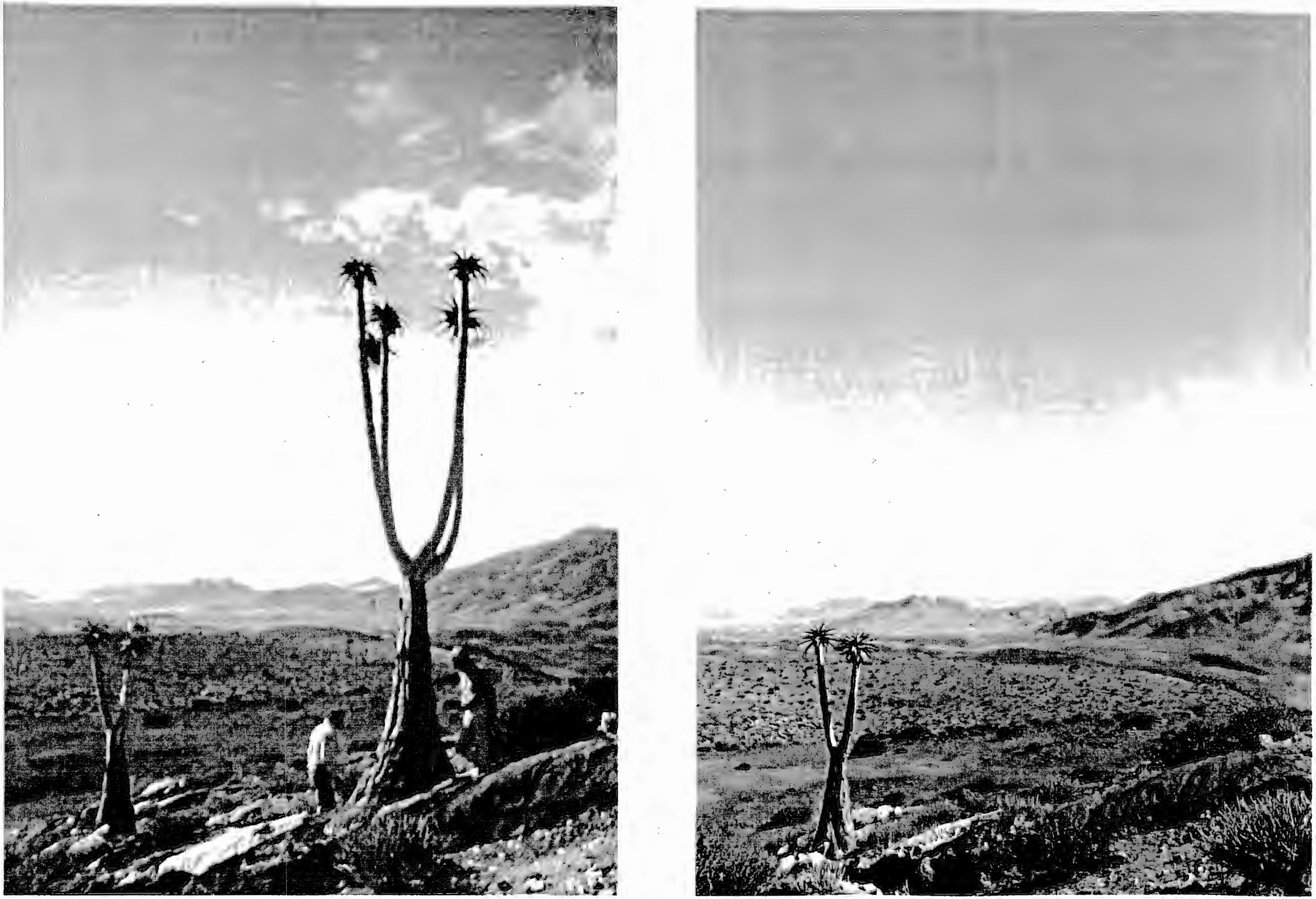
Match 5. Original (left) photograph of plant numbers 60 and 63 from left to right in the recent photo, by Piet van Heerde in 1950 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41813 S 16.88479 E
Note the growth of both the numbered trees while the largest individual in the original photo has since died.



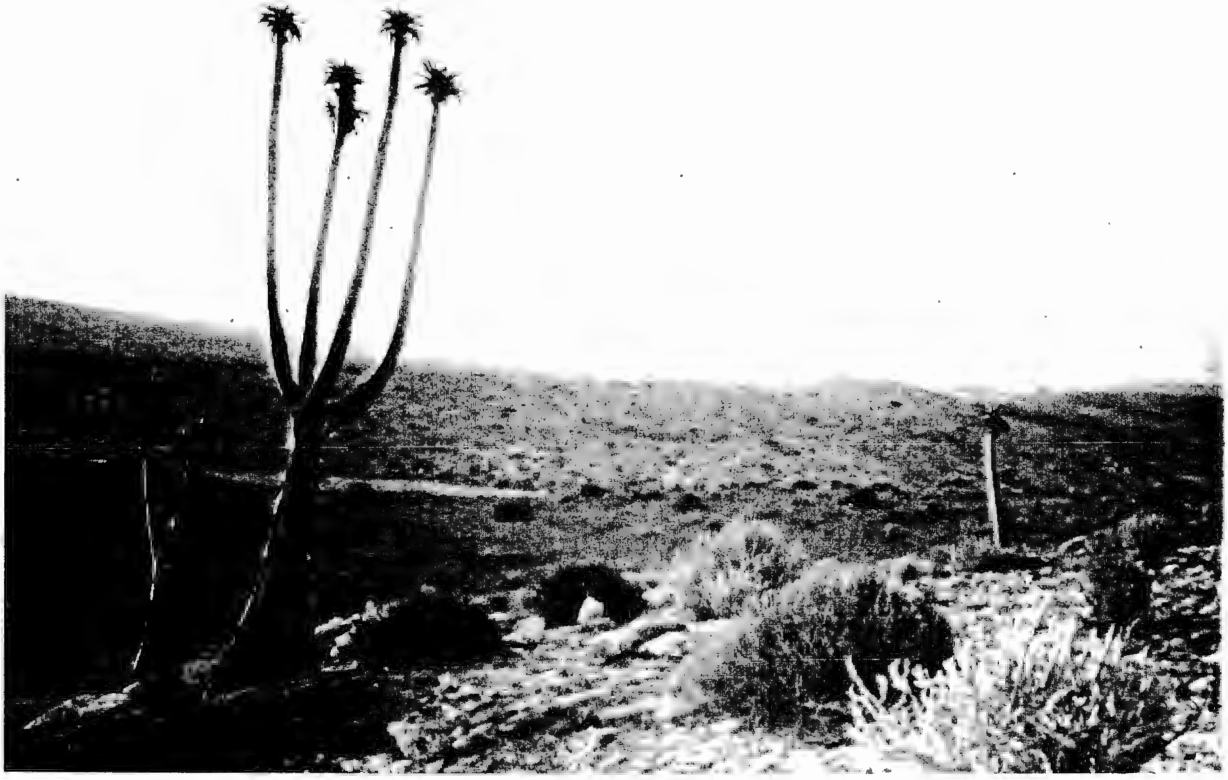
Match 6. Original (left) photograph, by Leslie Hill on an unknown day in September 1956 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41865 S 16.88395 E
Note this tree has died since the original was taken, the same tree features in matches 7,8 and 9



Match 7. Original (left) photograph, by Piet van Heerde in 1950 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41867 S 16.88381 E



Match 8. Original (left) photograph, photograph in the NBI collection taken in 1984 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41896 S 16.88409 E



Match 9. Original (top) photograph, photograph in the NBI collection taken in 1984 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41887 S 16.88404 E

Match 10. Original (top) photograph of plant numbers 60, 62 and 63 from left to right, photograph in the NBI collection taken in 1984 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41843 S 16.88442 E

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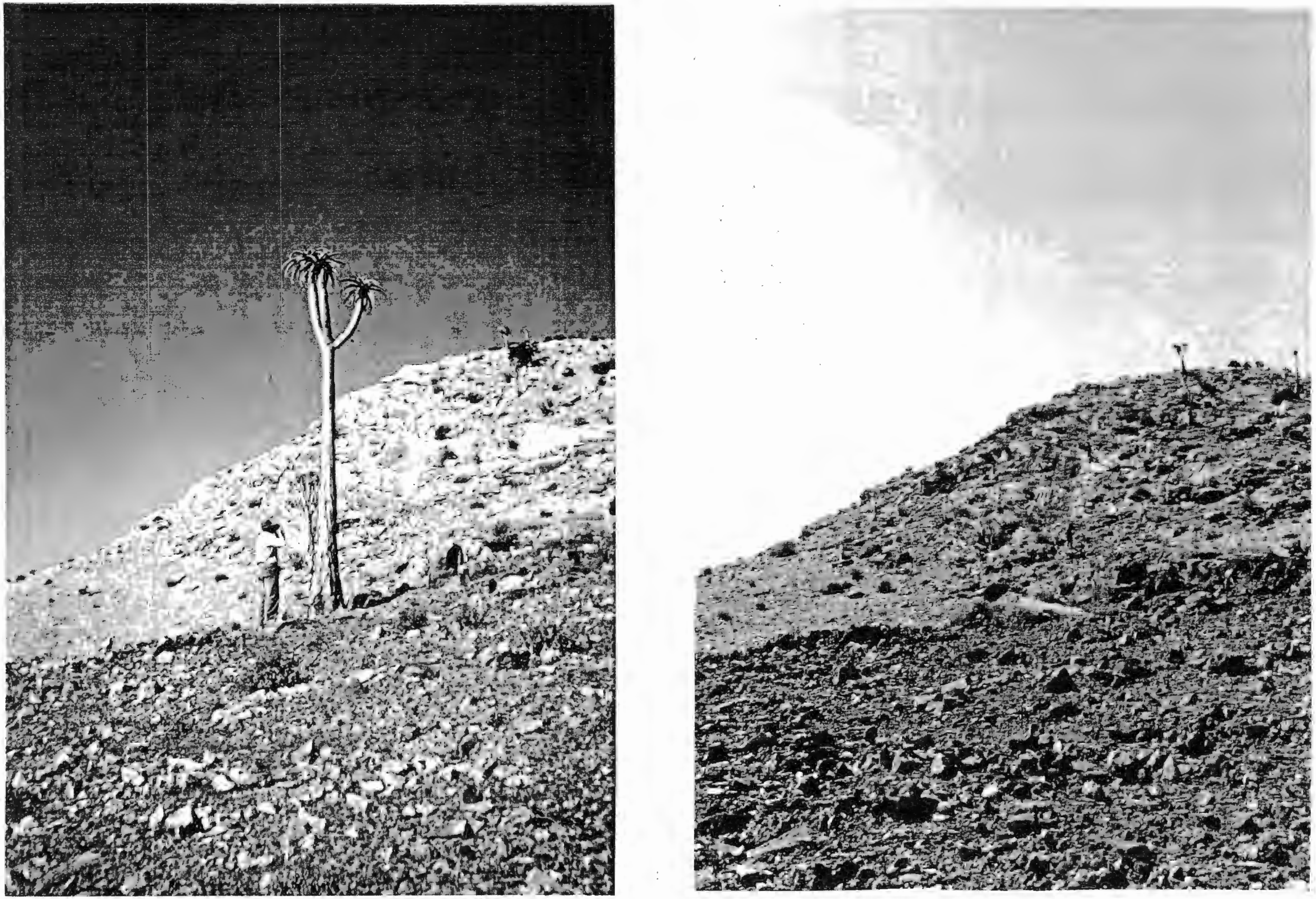
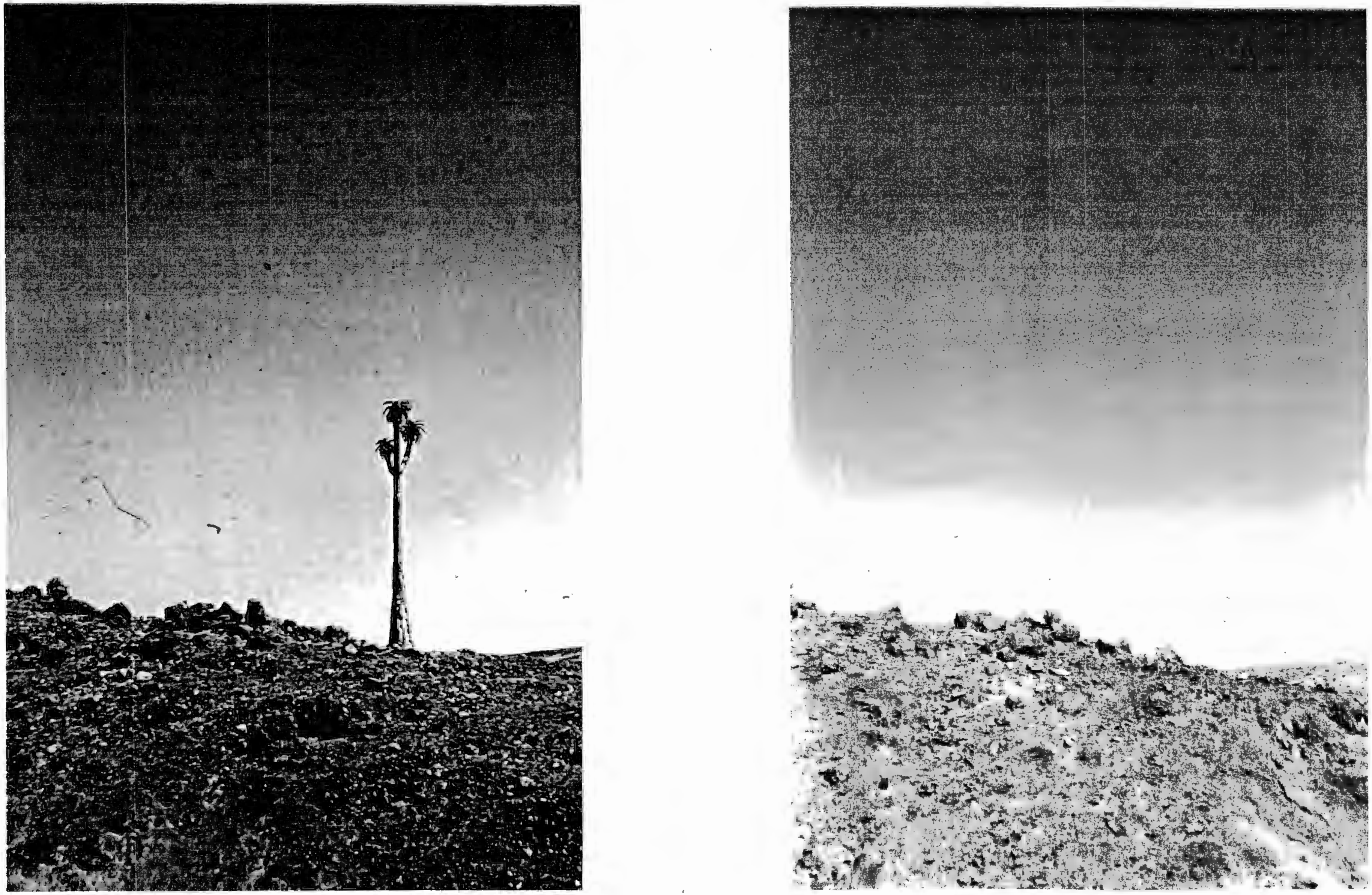
Match 11. Original (left) photograph of plant number 13, by Piet van Heerde in 1950 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41778 S 16.88363 E



Match 12. Original (left) photograph, by Piet van Heerde circa 1950 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41779 S 16.88363 E

Note this tree has died since the original was taken, the same tree features in match 13

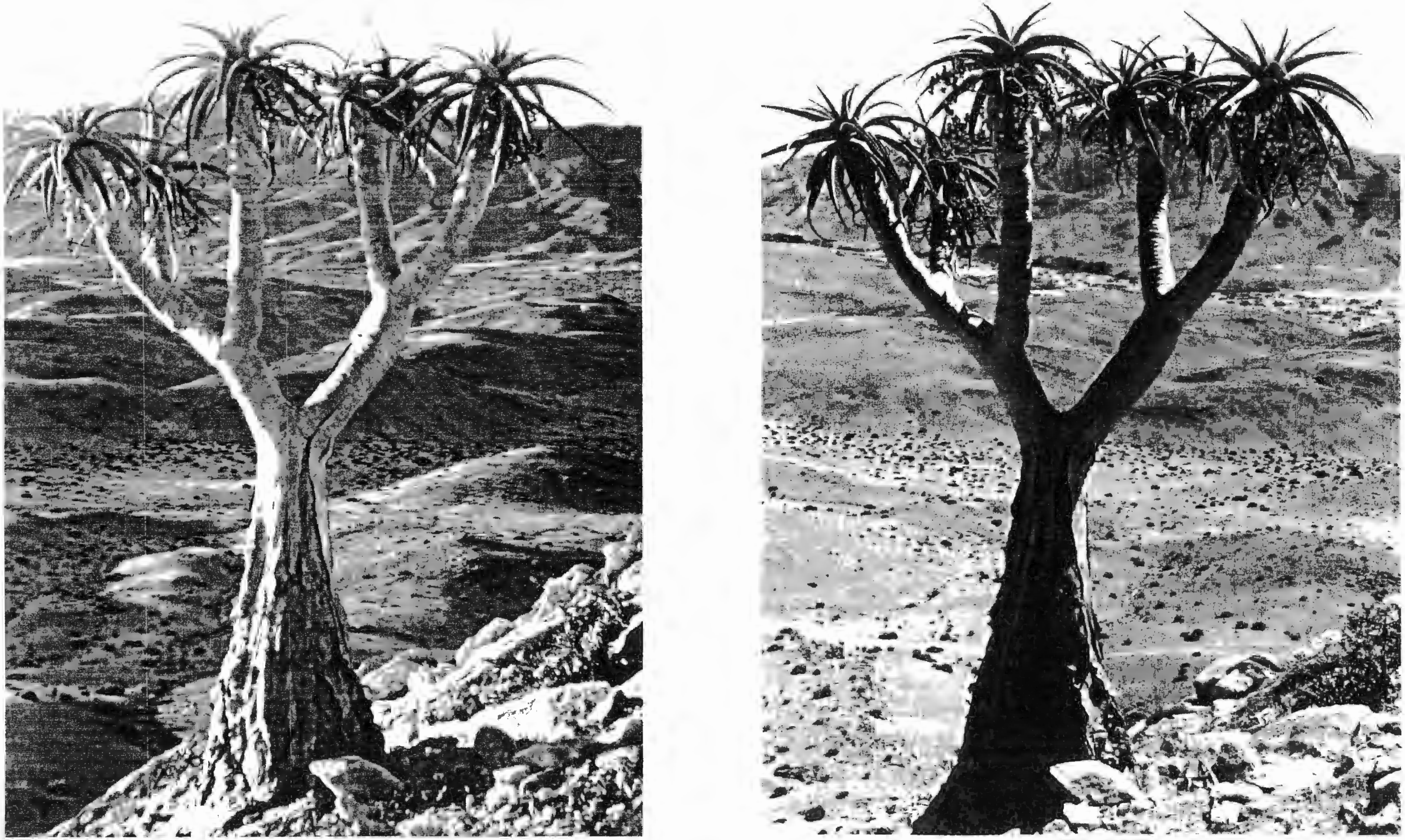


Match 13. Original (left) photograph, by Piet van Heerde circa 1950 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41698 S 16.88467 E

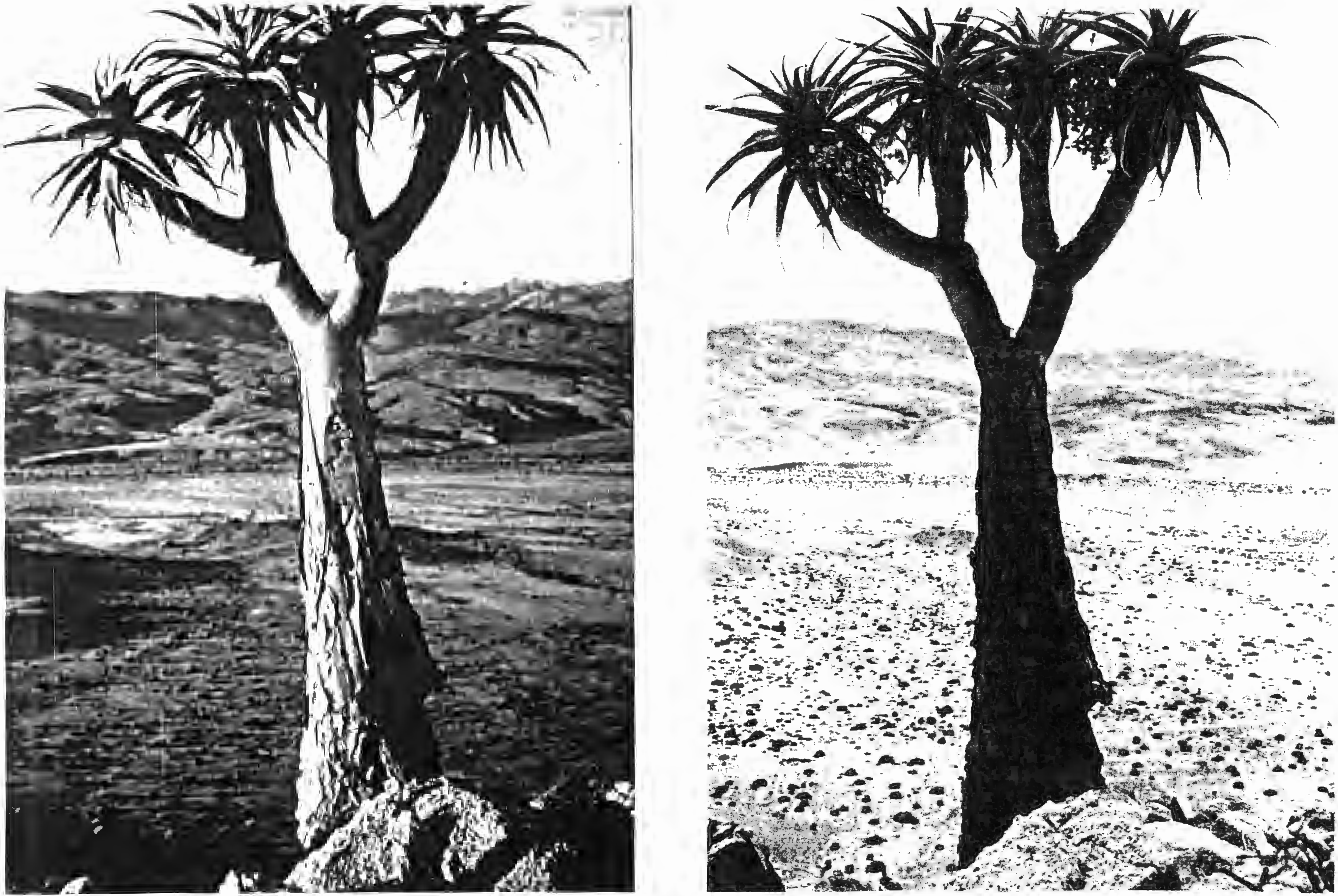
Match 14. Original (left) photograph, by Leslie Hill on an unknown day in September 1956 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41700 S 16.88500 E
Note this tree has died since the original was taken

Match 15. Original (top) photograph of plant numbers 39, 38, 40, 46 (dead) and 45 from left to right in the recent photo, by Timm Hoffman on the 28th of June 1991 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41774 S 16.88600 E

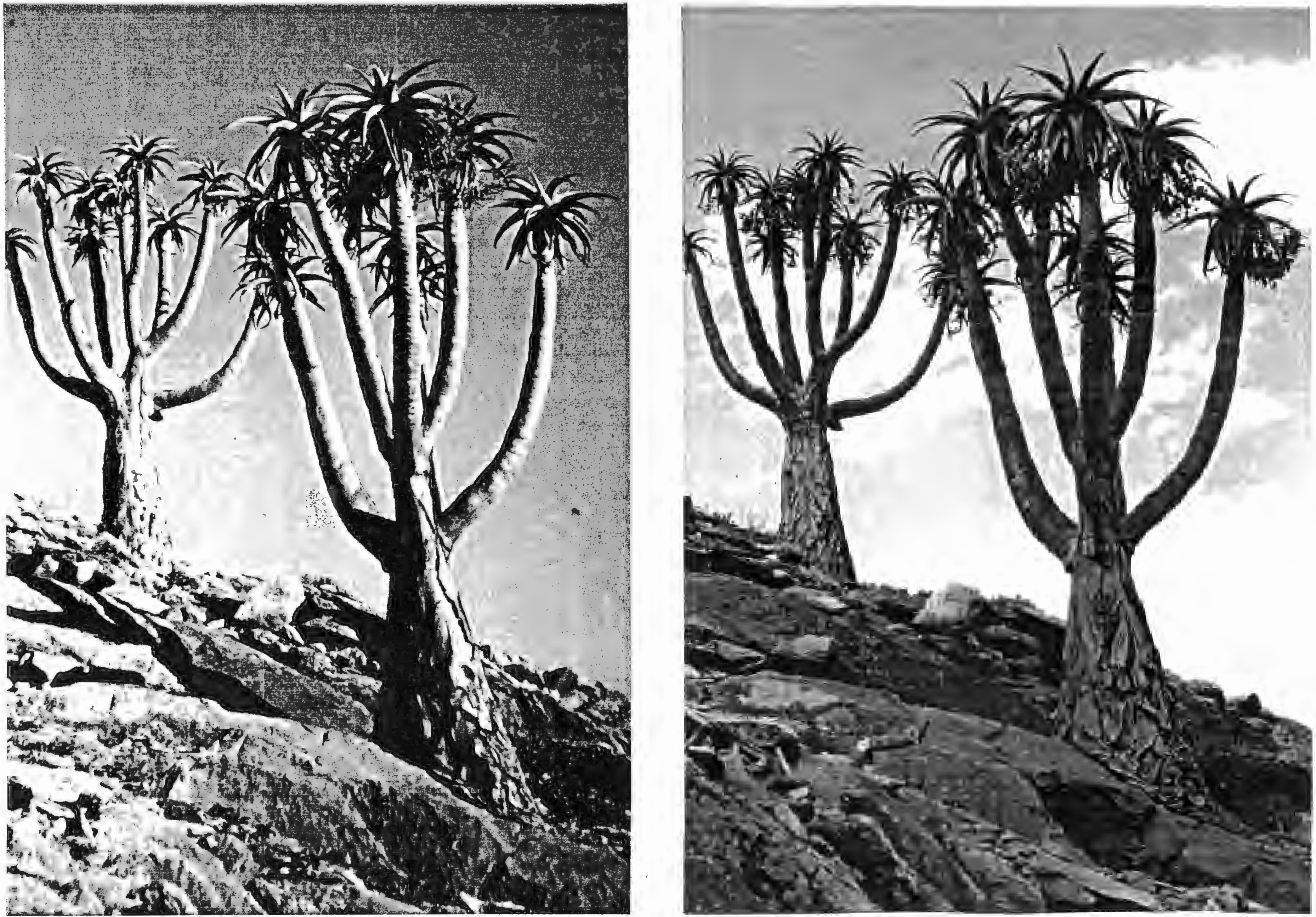
Note only the trees with their trunks visible in the photo have had their numbers recorded in the photo



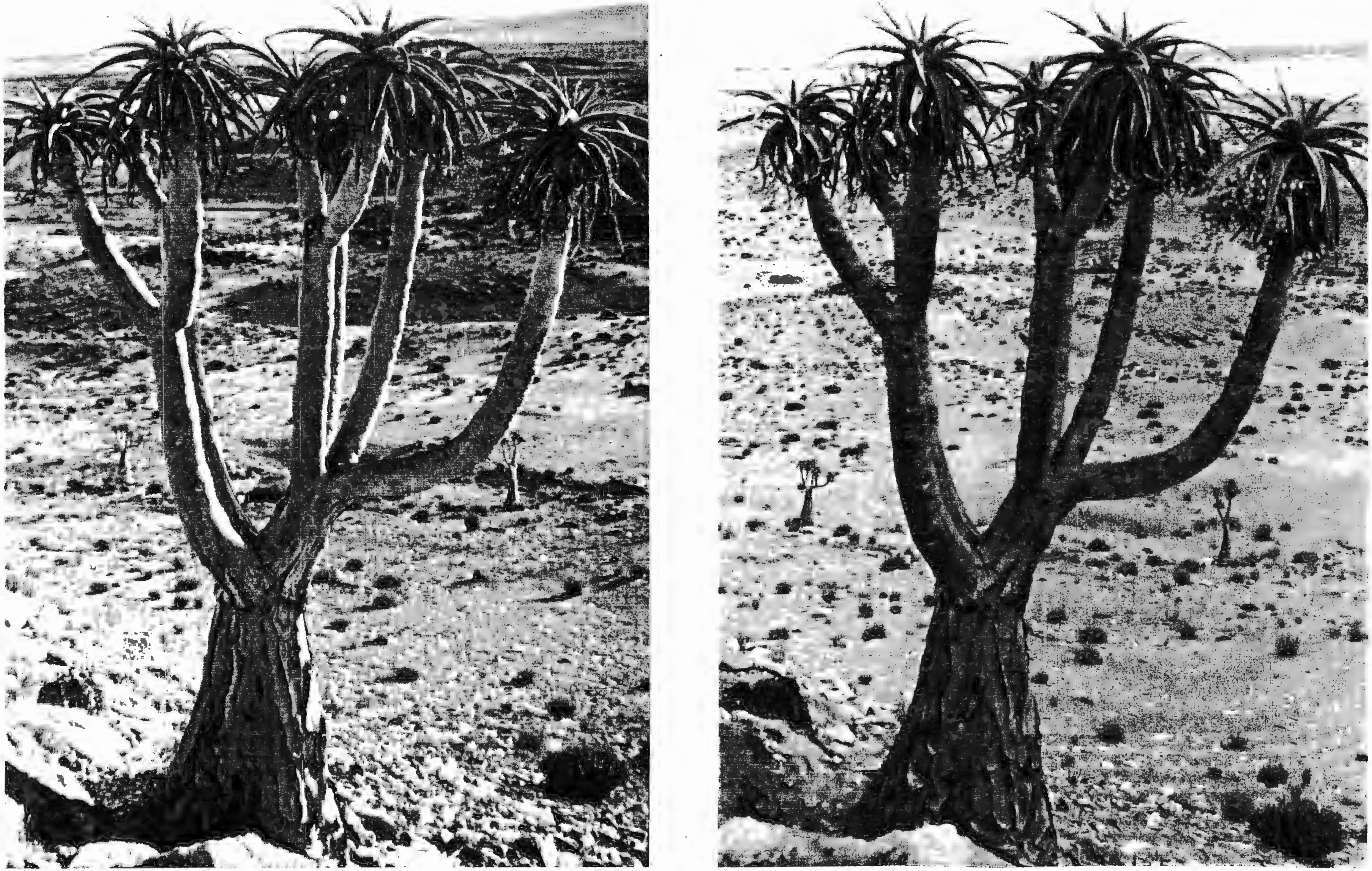
Match 16. Original (left) photograph of plant number 19, by Ernst van Jaarsveld in August 2000 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41682 S 16.88583 E



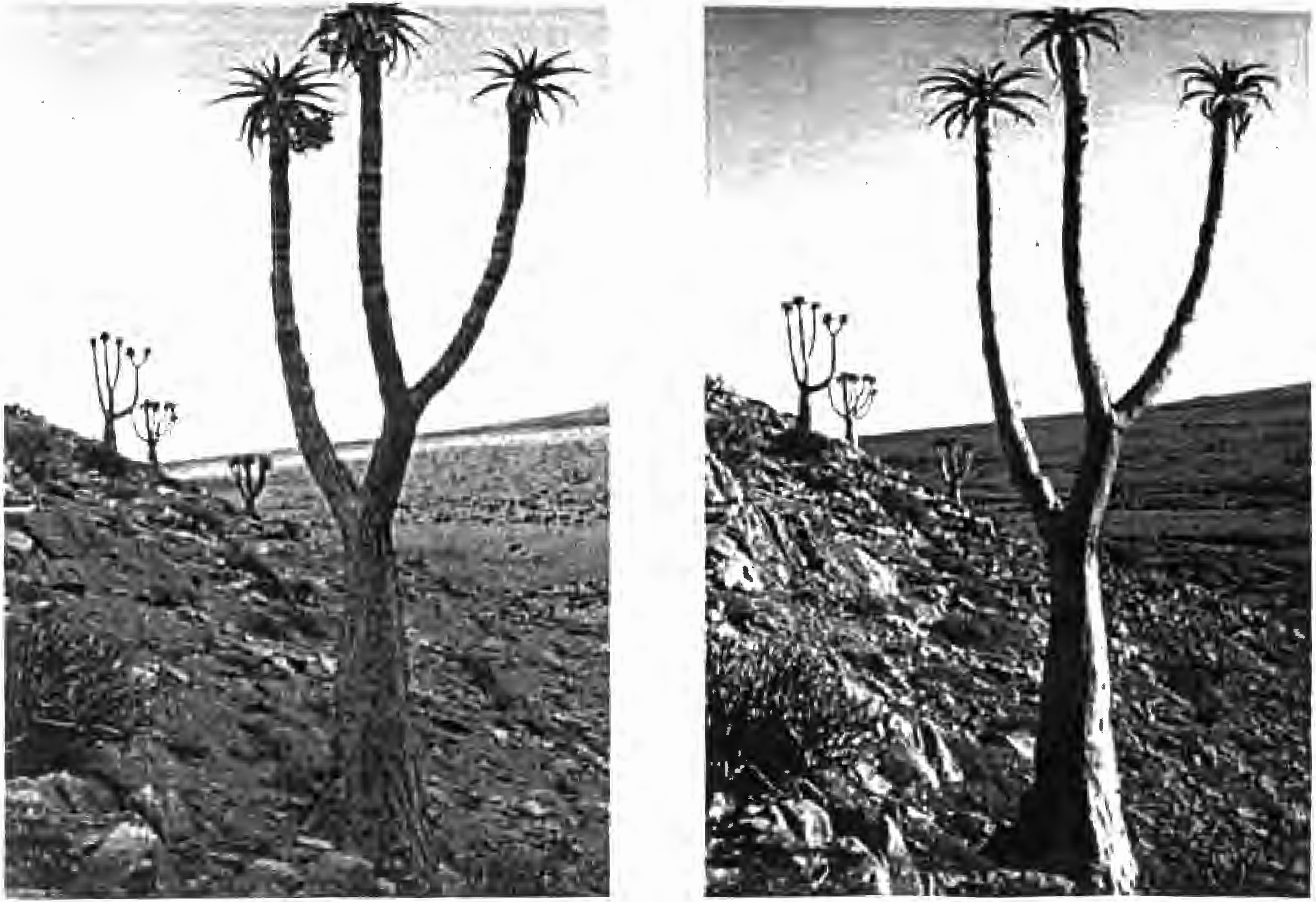
Match 17. Original (left) photograph of plant number 22, by Ernst van Jaarsveld in 2001 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41698 S 16.88591 E



Match 18. Original (left) photograph of plant numbers 62 and 63 from left to right, by Ernst van Jaarsveld in August 2000 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41832 S 16.88463 E

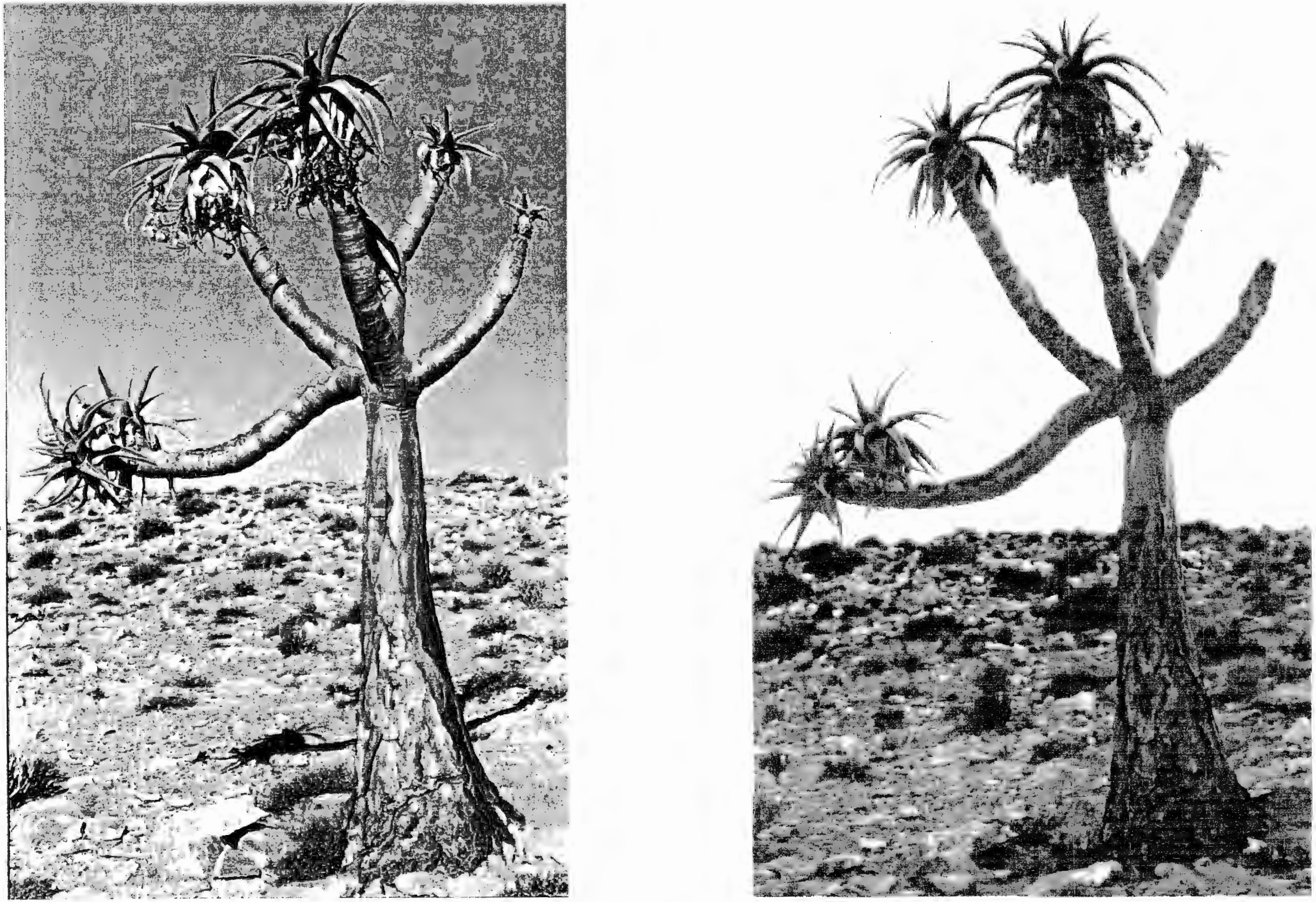


Match 19. Original (left) photograph of plant number 62, by Ernst van Jaarsveld in 2001 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41834 S 16.88462 E



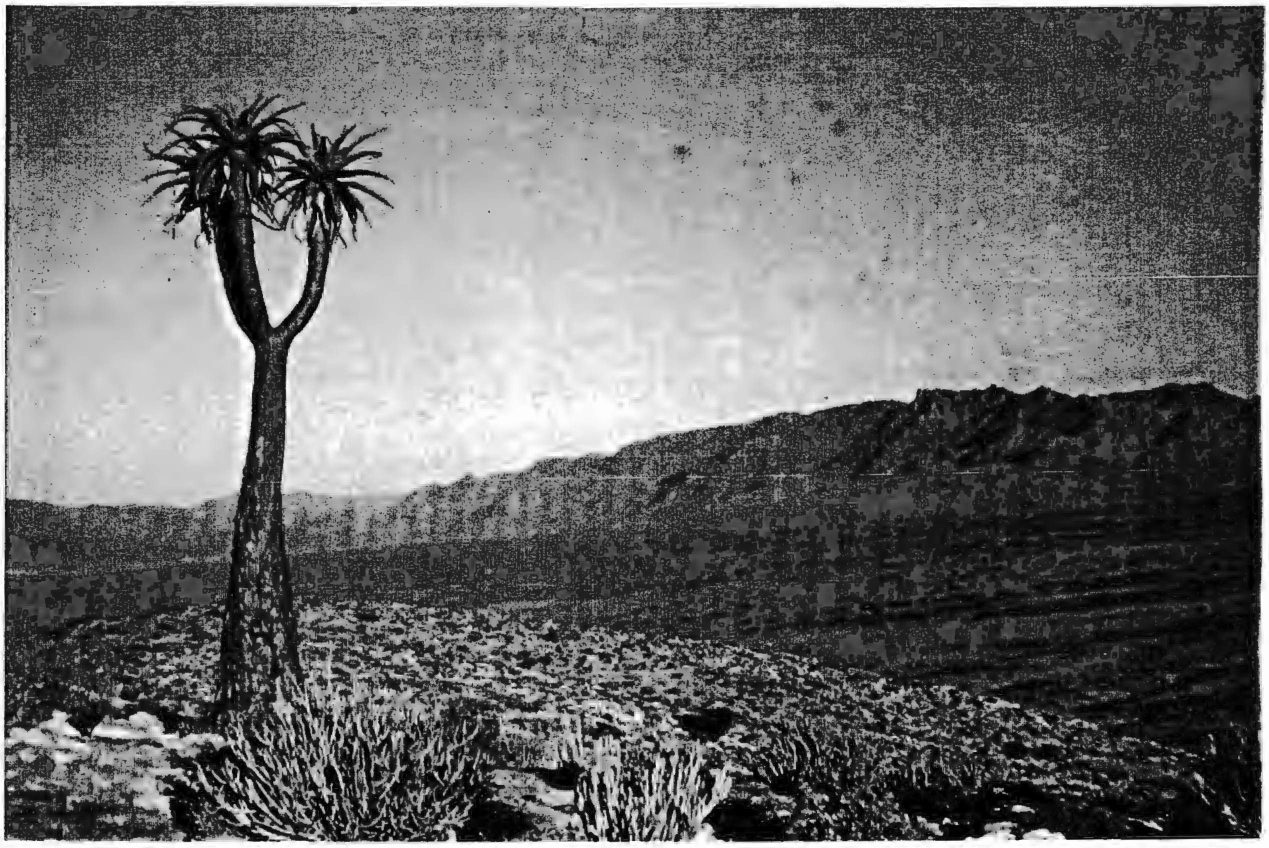
Match 20. Original (left) photograph of plant numbers 59, 60, 63, 62 and 53 from left to right, by Ernst van Jaarsveld in August 2000 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41765 S 16.88494 E

Match 21. Original (top) photograph of plant numbers 18 (dying), 17, 46 (dead), 19, 22 and 45 from left to right, by Ernst van Jaarsveld in August 2001 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41766 S 16.88533 E



Match 22. Original (left) photograph of plant number 38, by Graham Williamson in November 1996 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41783 S 16.88533 E

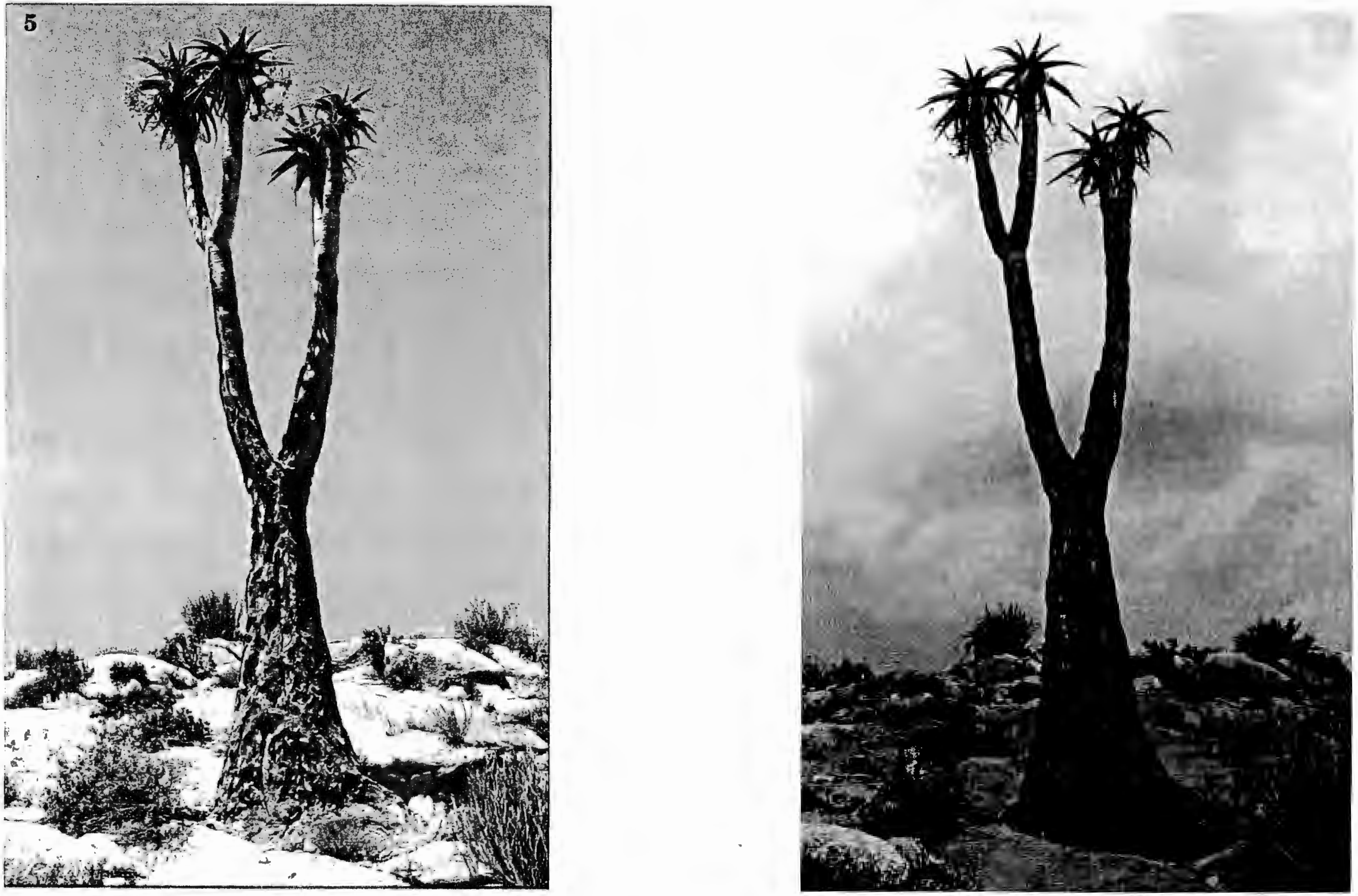
Note in the original the plant is already in the process of amputating two of its heads, one of which has disappeared since then



Match 23. Original (top) photograph of plant number 34, by Ernst van Jaarsveld in August 2000 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41831 S 16.88514 E

Match 24. Original (top) photograph of plant number 30, by Ernst van Jaarsveld on the 10th of June 1991 and re-photographed (bottom) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41851 S 16.88483 E

Match 25. Original (left) photograph of plant number 26 with 24 visible between its branches, by Ernst van Jaarsveld on the 14th of September 1976 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41907 S 16.88950 E



Match 26. Original (left) photograph of plant number 24, by Graham Williamson in November 1995 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41922 S 16.88662 E

Match 27. Original (left) photograph of plant number 35 and 36 from left to right, by Ernst van Jaarsveld in August 2000 and re-photographed (right) by Duncan et al. on the 1st of April 2004. The camera position is at 28.41785 S 16.88528 E