Branching patterns in *Aloe dichotoma* – is *A. ramosissima* a separate species?

A.G. REBELO [1], P.M. HOLMES[2], C. HILTON-TAYLOR[2], C. SAMPER[1,4], R.S. KNIGHT[2], H. KURTZWEIL[3] AND P. BAPST[2,5]

[1] Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700, South Africa
[2] Ecolab, Botany Department, University of Cape Town, Rondebosch, 7700, South Africa
[3] Bolus Herbarium, Botany Department, University of Cape Town, Rondebosch, 7700, South Africa
[4] Current address: Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA
[5] Dedicated to Peter Bapst (1967–1987)

Received April 1988; accepted July 1988

ABSTRACT

The proposal that *Aloe ramosissima* be reduced to varietal rank under *A. dichotoma*, based on a low incidence of *ramosissima*-type branching pattern (less than 100 mm above ground level) in most *A. dichotoma* populations, is invalid, as the *ramosissima*-type branching pattern has a different cause in the two taxa. Branching patterns in *A. dichotoma* populations show a majority of first branchings at between 1.5 m and 2.5 m above ground. Branching below 1 m in *A. dichotoma* populations is caused by ungulate destruction of the apical meristem, whereas in *A. ramosissima* branching below 1 m is initiated by spontaneous meristematic division.

INTRODUCTION

Aloe dichotoma Masson is one of three species in the section *Dracoaloe* Berger of the genus *Aloe*. The Dracoaloe are characterized by dichotomous branching and cylindric-ventricose, fleshy, yellow flowers about 33 mm long (Reynolds 1982). The three species (*A. dichotoma, A. ramosissima* Pillans and *A. pillansii* L. Guthrie) are differentiated by their height and degree of branching, leaf size, and orientation of inflorescences. All three species are confined to dry, rocky areas: *Aloe dichotoma* is the most widespread, occurring in the northwestern Cape Province, South Africa, and southern South West Africa/Namibia (its southern distributional range), and isolated populations at Brandberg (Jankowitz 1977; Reynolds 1982). Both *A. ramosissima* and *A. pillansii* are confined to a few populations in the northern Richtersveld and near Rosh Pinah in the Luderitz magisterial district of South West Africa/Namibia.

Aloe dichotoma grows to 9 m tall, with a trunk of about 1 m diameter, and has pronounced dichotomous branching above this height. The leaves are 250–350 mm long and 50 mm broad at the base. The inflorescence is a branched panicle, up to 300 mm long, and usually branched into three (occ. 4 or 5) racemes. *Aloe ramosissima* differs in being shorter, up to 3 m tall, and in branching at a height of less than 600 mm. It also has smaller leaves, 150–200 mm long and about 22 mm broad at base, thinner branches and smaller rosettes of leaves at the branch tips. However, it is indistinguishable from *A. dichotoma* on inflorescence and floral characters (Reynolds 1982), and on microscopic leaf characters (Glen & Hardy 1987).

Recently, Glen & Hardy (1987) proposed that *Aloe ramosissima* be reduced to varietal rank under *A. dichotoma* Mason as *A. dichotoma* Mill. Although based on microscopic and macroscopic data, their major argument is that the branching from near ground level, the major diagnostic feature of *A. ramosissima*, occurs at low levels in all populations of *A. dichotoma* (H.F. Glen pers. comm.).

The aims of this study were to investigate the levels of branching in *A. dichotoma* in its southern distributional range and to determine whether the pattern of branching differed among populations and between *A. dichotoma* and *A. ramosissima*.

METHODS

Eleven populations of *A. dichotoma* Masson were sampled in southern South West Africa/Namibia and the northwestern Cape (Figure 1) during July 1987. Sampling was undertaken on a minimum of 100 live

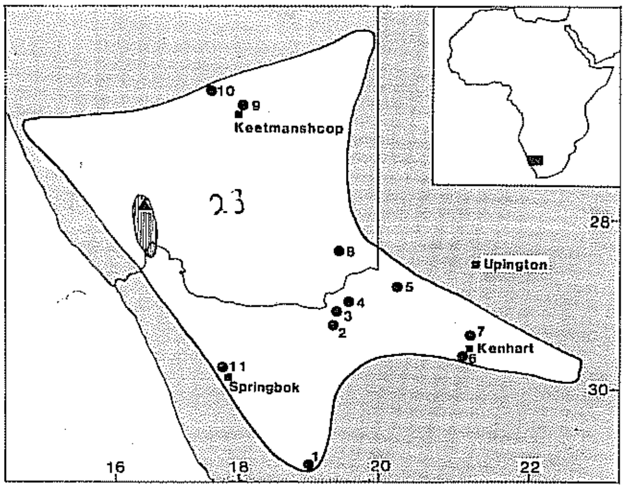

FIGURE 1: Location of populations of *Aloe dichotoma* (●) and *A. ramosissima* (▲) investigated in this study. Locality names are given in Table 1. The unshaded area denotes the southern distributional range of *A. dichotoma* based on herbarium records and Jankowitz (1977). Similary, the hatched area denotes the distributional range of *A. ramosissima*.

plants in an area not less than 500 m by 500 m, or, where assemblages consisted of fewer than 100 plants, the entire population. In each population, plants' absolute height, height to first branching, and the number of branching occurrences were determined. Only a single population of *A. ramosissima* was visited. Due to lack of field time, height to first branching in this species was estimated from photographic records.

RESULTS

The proportion of *A. dichotoma* plants branching below 1 m varied among populations from 0 to 45 % (Figure 2). This proportion was significantly and positively correlated with the proportion of the population less than 1 m tall ($r = 0.60$, $p<0.05$). The distribution of height to first branching showed distinct primary peaks at between 1.5 and 2.25 m, with smaller secondary peaks at 0.25–0.75 m in all populations with appreciable numbers of plants shorter than 1 m. However, among populations there was no correlation between the average height of plants taller than 1 m and their average height to first branching ($r = 0.17$, $p>0.5$).

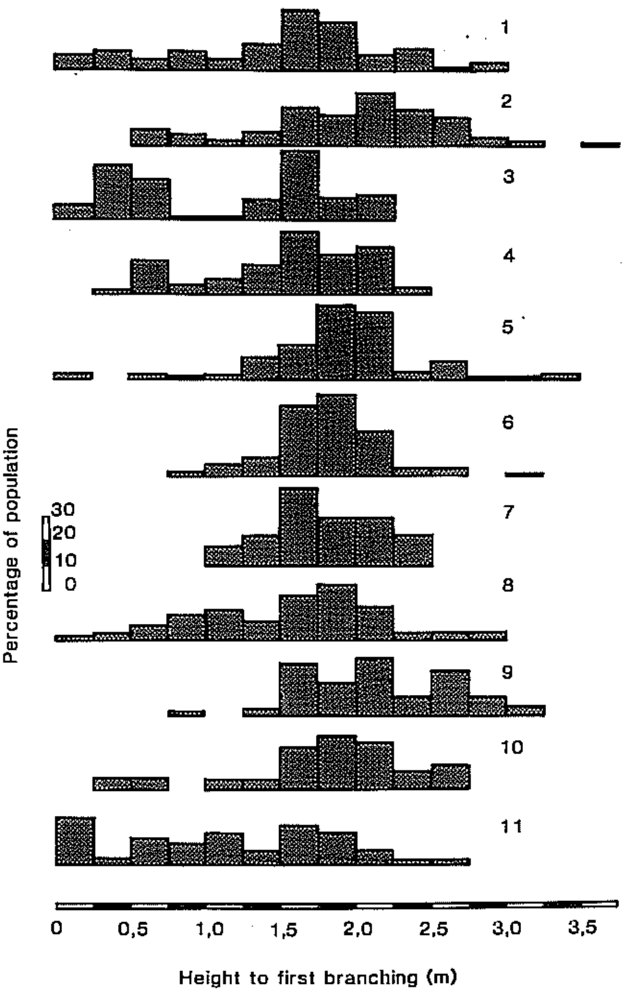

FIGURE 2: Proportion of first branching of *Aloe dichotoma* in different height classes for populations at the southern portion of its distributional range.

The geographical distribution of branching patterns is shown in Figure 3. Eastern populations had fewer plants branching below 1 m than those in the west and south.

The proportion of plants less than 1 m tall that were damaged in the different populations varied between 0 and 51 % (Table 1). Damage was largely due to ungulates breaking off tops of plants, presumably when browsing the apical meristems. However, such browsing, by goats, was only positively identified at Onseepkans (28°57'S, 19°24'E). At Snyfontein (26°30'S, 17°51'E) 26 % of the plants had stems gnawed by donkeys and horses, apparently as a source of water (D. Clark pers. comm.), and 3 % of aloes greater than 1 m tall (average 1.25 m) had been knocked over within the

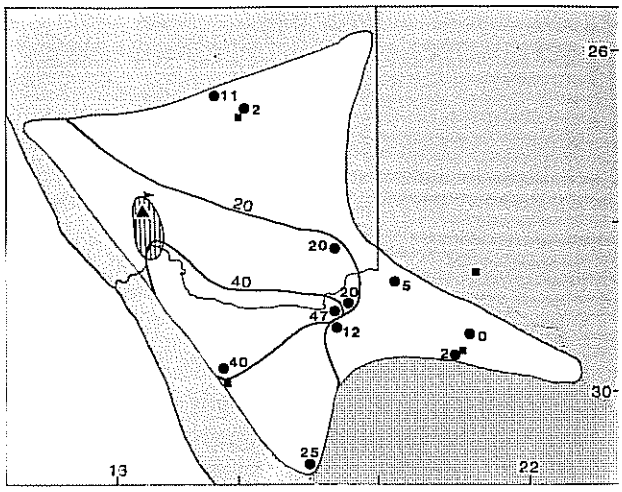

FIGURE 3: Geographical variation in the proportion of *Aloe dichotoma* plants per population branching below 1 m height (given for each site). Extrapolation of isodendrons into the Richtersveld is based on Reynolds (1982).

past year. There were no significant differences between height to first branching in damaged plants less than 1 m tall and the height to damage in those which either died as a consequence thereof or were damaged too recently to have branched (*t*-test, $P>0.05$, Onseepkans) (Table 1). The height at which plants less than 1 m branched was significantly higher in areas containing goats than those containing sheep (*t*-test, $P<0.05$). There were no undamaged plants which branched below 1 m.

All plants in the single population of *A. ramosissima* visited branched below 0.3 m. All plants less than 1 m tall branched below 0.1 m. No damage by herbivores was evident.

DISCUSSION

True dichotomous branching (by apical meristem division) is rare in the Monocotyledonae (Tomlinson *et al.* 1970). Schoute (1918) investigated branching patterns in *Aloe succotrina* Lam and concluded that branching in *Aloe* is always triggered by the formation of a terminal inflorescence, i.e. the branching is pseudodichoto-

TABLE 1: Number of plants less than 1 m tall showing signs of damage or branching and the mean height of damaged plants in 11 populations of *Aloe dichotoma*. All the plants which had branched below 1 m tall were damaged. Plants above 1 m tall were not included as it is not usually possible to determine the cause of first branching.

Population	Total plants < 1 m tall (A)	Damaged plants		Mean (±SD) height (mm)		Agents
		branched (% of A)	unbranched (% of A)	to branching	to damage[1]	
1 Klipdrift	86	8	0	234 ± 96	–	Sheep
2 Poffadder	15	0	7	–	0	Goats
3 Onseepkans	65	26	25	402 ± 146	418 ± 268	Goats
4 Skietskipkop	45	9	0	495 ± 134	–	Goats
5 Augrabies	14	7	0	190	–	Goats
6 Kenhardt	1	0	0	–	–	Goats
7 Strausheim	8	0	0	–	–	Sheep
8 Kokerboom	0	–	–	–	–	Sheep
9 Keetmanshoop	3	0	0	–	–	Goats
10 Snyfontein	39	15	0	408 ± 217	–	Donkeys, horses & Goats
11 Springbok	71	4	1	219 ± 168	400	Sheep

[1] Including both dead and recently damaged plants.

mous. In the case of branching in *A. dichotoma* (and presumably the section *Dracoaloe),* two side-branches emerge below the terminal inflorescence which usually dies while only a few mm long in the first few branchings (Schoute 1918; pers. obs.). In *A. dichotoma* apparently dichotomous branching from the two topmost lateral buds may also occur following damage to the apical meristem (pers. obs.).

Branching patterns in *A. dichotoma* show a bimodal distribution with the majority of first branchings occurring between 1.5 and 2.5 m. This natural branching is quite distinct from the branching which occurs between 0.1 and 0.9 m, which is largely caused by destruction of the apical meristem by ungulates. Goats appear to eat apical meristems, whereas some damage may be caused by trampling activities of goats and other ungulates. Plants over 1 m tall were apparently safe from destruction by sheep and goats, although horses and donkeys occasionally damaged plants up to 1.5 m tall, usually by knocking them over. The height of damage and its variation between areas containing sheep and goats may reflect either browsing height preferences or damage done by animals tramping over plants and breaking off their tops. The production of axillary buds in the remaining leaves generally follows, giving rise to 2–3 (occ. up to 7) branches. Although not always a dichotomous branching pattern, it is difficult to distinguish such branching from dichotomous branching when specimens have matured.

The pattern of branching between the *A ramosissima* and *A. dichotoma* populations investigated differs considerably. In the former all plants below 1 m tall appear to branch spontaneously, whereas any branching at comparable heights in the latter appears to be largely due to damage by ungulates. The inclusion of *A. ramosissima* into *A. dichotoma,* based on a small proportion of plants with *A. ramosissima* branching patterns in all *dichotoma* populations, is therefore questioned, as the branching has different causes.

A further complication results from the spatial distribution of young *A. dichotoma* plants: seedlings may occur in clumps of up to six plants in favourable microhabitats (pers. obs.). Although young plants in such clumps are distinct, the stems may fuse with age and thus appear to branch from the base of 'single' mature specimens. As plants age this apparent height of branching increases as fusion progresses. This 'pseudobranching' was proposed by Reynolds (1982) to account for the proportion of *ramosissima* types in *A. dichotoma* populations.

Furthermore, the proposed rank of *variety* cannot be upheld. Since the distribution of the spontaneously low-branching *ramosissima* taxon is geographically distinct (Reynolds 1982) and does not occur in all *A. dichotoma* populations, as suggested by Glen and Hardy (1987), *ramosissima* must be ranked as either a species or subspecies. Reynolds (*loc. cit.*) states that there appear to be hybrid populations south of Kuboos. Unfortunately we were unable to visit the Richtersveld, and thus could not determine whether the branching patterns in these populations may be due to hybridization or ungulate damage. The high grazing levels in the Richtersveld (A. Le Roux pers. comm.) warrant a closer investigation of the latter possibility. The two taxa are quite distinct in the northern Richtersveld (Reynolds 1982) and north of Rosh Pinah (pers. obs.) where they coexist without any apparent hybridization (Jankowitz 1972, 1977). Whether *A. ramosissima* has sufficient distinguishing characters to warrant the status of a separate species, is beyond the scope of this paper.

ACKNOWLEDGEMENTS

The authors wish to thank C.P. Cornelius and G. Lottig for permission to work on their farms; the Kenhardt Municipality, the South West Africa/Namibian Department of Agriculture and Nature Conservation for permits; D. Clark and R. Hawthorne for assistance in SWA/Namibia; and, W.J. Jankowitz, W.R. Siegfried, P.F. Stevens and P.J. Vorster for comments on earlier drafts of the manuscript. This paper forms part of a project on *Aloe dichotoma* undertaken by the Botany Club of the University of Cape Town. Y. Harrison, N. Helme, D. Law, D. Le Roux and C. Wyeth assisted in the field. The project was sponsored by the University of Cape Town. Authors were funded by the Council for Scientific and Industrial Research through its Nature Conservation Programme and the University of Cape Town.

REFERENCES

GLEN, H.F. & HARDY, D.S. 1987. Variation in *Aloe dichotoma* Mill. Abstract, *South African Association of Botanists 1987 Ar nual Congress:* 37.

JANKOWITZ, W.J. 1972. Die verspreiding van die genus *Aloe* in di verre suide van Suidwes-Afrika. MSc thesis, University of Orang Free State.

JANKOWITZ, W.J. 1977. The distribution of the genus *Aloe* in th districts Bethanien, Luderitz and Warmbad, South West Africa *Madoqua* 10: 33–53.

REYNOLDS, G.W. 1982. Reynolds' Aloes of South Africa. Cap Town: Balkema.

SCHOUTE, J.C. 1918. Über die Verastellung von Monocotylen Bäu men III: Die Verastellung einiger baumartigen Liliaceen. *Rec Trav. Bot. Neerl.* 15: 263–335.

TOMLINSON, P.B., ZIMMERMANN, M.H. & SIMPSON, P.C 1970: Dichotomous and pseudodichotomous branching c Monocotyledonous trees. *Phytomorphology* 20: 36–39.