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Dead Leaves and Fire Survival in Southern African Tree Aloes
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Source: *Oecologia*, Vol. 58, No. 1 (1983), pp. 110-114
Published by: Springer in cooperation with International Association for Ecology
Stable URL: http://www.jstor.org/stable/4217000
Accessed: 15/12/2014 11:04

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Oecologia (Berlin) (1983) 58:110–114

Oecologia
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Dead leaves and fire survival in Southern African tree aloes

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Summary. Many aloe species in southern Africa have stems clothed with a layer of persistent dead leaves. The degree of stem coverage is species-specific. The suggestion that persistent dead leaves have an insulatory function and are adaptive in fire-prone habitat was tested on *Aloe ferox*. Field surveys demonstrated a significant negative relationship between mortality and degree of stem coverage and laboratory studies confirmed the insulating properties of dead leaves. The distribution of southern African tree aloes supports the prediction that bare-stemmed species would be confined to fire-free habitat whilst fully clothed species would occur in both fire-prone and fire-free habitat. The study suggests that harvesting of *Aloe ferox* leaves for medicinal purposes could result in significant mortality in fires.

Introduction

Aloe is a large genus of the Liliaceae widely distributed in Africa and occurring over a broad range of habitats from forests to deserts and frequently on rocky outcrops. Several species, which I shall refer to as "tree aloes", develop a conspicuous stem 1.5 m or more in height. A few of these species have a single main stem with several branches, but most are unbranched with a characteristic "pedestal" form topped by a rosette of large succulent leaves usually with spiny margins.

Many tree aloes of southern and central Africa have a skirt of persistent dead leaves clothing the stem (Fig. 1). The extent of stem coverage is more or less constant within a species and has been used as a character for field identification (Coates Palgrave 1977; Moll 1981), but the functional significance, if any, of dead leaf retention has not been systematically studied. Jeppe (1969), in writing on aloe cultivation, recommends that bare-stemmed aloes should have their stems protected from "cold and sunlight" implying a thermoregulatory role for dead leaf retention. Alternatively, the mass of dried, spiny leaves may act as a deterrent against browsers, such as kudu on *Aloe excelsa* (West 1974) or nectar thieves and seed-eaters such as baboons (Marloth 1915 and personal observations).

West (1974) has pointed out that aloes vary in fire sensitivity and are habitat specific in relation to the incidence of fire. Tree aloes lack a continous phellogen – the meristematic tissue giving rise to bark in woody dicotyledons (Eames, MacDaniels 1947). Aloe bark is, instead, a complex mass of overlapping, irregular layers lacking the completeness of bark tissues in dicot woody groups.

The skirt of dead leaves and their tightly overlapping leaf bases could act as additional insulation and protection for the stem. Lack of leaf abscission would be a useful strategy in regularly fired vegetation providing a functional analogue to the thick, fire-resistant bark of many woody dicot species (Martin 1963; Hare 1965; Gill, Ashton 1968; Vines 1968). I propose that fire has selected those species able to maintain a continous layer of dead leaves to ground level and that they would be at a selective advantage over naked-stemmed types in fire-prone environments.

Study material

Aloe ferox Miller is a tall (2 m–5 m) single-stemmed aloe with the stem densely covered with dead leaves, usually to ground level. It is a common and widespread species in South Africa, occurring from the shrublands in winter rainfall areas of the Cape Province to grasslands in summer rainfall areas of Natal. Most of its habitat within this wide range is subject to periodic fire. The species is the source of the drug "Cape aloes" which is extracted by stripping leaves off plants in wild populations and expressing the sap (Marloth 1915). After harvesting, only a thin layer of persistent leaf bases remains attached to the stem. Harvesting activity has increased enormously in recent years in response to the opening up of export markets in Europe and North America with up to 600 tons of the dried sap being exported annually (A. le Roux, pers. comm. 1981).

This paper reports a test of the hypothesis that the skirt of persistent dead leaves in some aloe species, and in particular *Aloe ferox*, imparts fire resistance by insulating the stem. I then discuss some ecological and economic implications.

Methods

Survival following fire

Populations of *A. ferox* in the all-year round rainfall zone of the southern Cape were investigated. Here the species commonly occurs in shrublands dominated by *Elytropappus rhinocerotis* (L.f.) Less., associated with *Pteronia* spp., *Rel-*

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Fig. 1. A *Aloe ferox* showing the characteristic skirt of persistent dead leaves. The vegetation is renosterveld burnt three years previously.

B *Aloe ferox* after regular leaf harvesting. Note the ring of leaves midway up the stems representing a missed harvest. Vegetation is renosterveld unburnt for several decades

hania genistaefolia (L.) L'Her. and *Dodonea viscosa* Th. on shaley soils and warm, relatively dry slopes. These shrublands, called renosterveld (Acocks 1953), are periodically burnt by fire ignited by lightning or man, at frequencies varying from five or six years to several decades.

Three aloe populations, two on the northern foothills of the Outeniqua range bordering Robinson's Pass (33° 50′ S 22° 02′ E) and one on the southern foothills west of Swartberg Pass (33° 25′ S 21° 58′ E) were studied for relationships between fire induced mortality and the presence of a skirt of persistent dead leaves. The populations were studied within 12–18 months after fire. Easily accessible areas, relatively free of boulder outcrops and cliffs (which may act as fire refugia), were selected for sampling.

All *A. ferox* with distinct stems in an area of ± 2 ha were recorded until a total of 100 individuals had been counted. Each individual was rated as dead or alive, placed in one of three height categories (<1 m, 1–2 m, >2 m) and the presence of an inflorescence in the current flowering season recorded. Plants which had died since the fire could be recognized by their red, wilted leaves, rotting of the stem and severance of any vascular connection with the roots. The length of stem covered by dead leaves was rated in the categories: completely clothed, bare for less than 0.25 m, 0.26 m–0.5 m, 0.51 m–1 m, and >1 m. Only individuals with charred fire scars on the stem were placed in the barestemmed categories to avoid possible inclusion of plants which had dropped leaves after the fire.

Insulating properties of the leaf layer

No suitable areas for experimental burns on defoliated aloes were available. Instead, the insulating properties of leaves and bark were observed under simulated natural conditions. A 2 m tall, fully bearded aloe was tied in its natural vertical position on a trolley. This could be pushed against a platform on which a fire had been built so that the stem was directly exposed to the flames.

Temperatures beneath the leaf layer were measured at two heights, 100 mm and 400 mm, above the fire platform. Chromel-alumel thermocouples in a 3 mm diameter tubular steel sheath were pierced through the aloe stem at these heights with their tips projecting 10 mm beyond the periderm on the fire side of the stem.

Temperatures outside the leaf layer and in the fire were measured at the same heights by piercing two thermocouples through a wooden board placed adjacent to the aloe and at approximately the same distance from the fire.

The aloe was exposed to the fire for eight minutes and, after an hour's interval, for a second period of five minutes.

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Table 1. *Aloe ferox* mortality in three fires in relation to stem coverage by dead leaves. Proportion of each category which died in parenthesis

	Length of bare stem (m)					Total
	0	0.25	0.26–0.5	0.51–1	>1	
a) Robinson's Pass Outeniquas Fire 1						
No. dead	2 (0.03)	0 (0.0)	10 (0.83)	10 (1.0)	10 (0.91)	32
No. alive	58	12	2	0	1	73
b) Robinson's Pass Outeniquas Fire 2						
No. dead	0 (0.0)	1 (0.06)	1 (0.5)	3 (1.0)	22 (0.96)	27
No. alive	56	15	1	0	1	73
c) Swartberg Foothills						
No. dead	1 (0.03)	1 (0.10)	8 (1.0)	20 (1.0)	31 (1.0)	61
No. alive	30	9	0	0	0	39
d) All Fires						
No. dead	3 (0.02)	2 (0.05)	19 (0.86)	33 (1.0)	63 (0.97)	120
No. alive	144	36	3	0	2	185

The dead leaves were then stripped and the aloe exposed again for six minutes. Temperatures were recorded at regular intervals from the four thermocouples during each period of exposure.

Results

Fire survival

Results of the aloe census in three fires are shown in Tables 1 and 2. Sixty one % of the aloes sampled in the Swartberg fire were killed and 27% and 30.5% in the two Outeniqua fires.

Fire survival was strongly related to the degree to which stems were protected by dead leaves. Ninety six% of all individuals with stems bare for more than 0.25 m were killed by the fire. In contrast, 97.3% of aloes with stems completely protected by dead leaves or bare for less than 0.25 m survived, ($X^2 = 85.6$ and 83.0 for the two Outeniqua samples, 88.9 for Swartberg; $P < 0.001$).

Aloe survival appeared to be related to size (Table 2a) in one Outeniqua fire. Smaller individuals suffered the heaviest proportional mortality whilst the tallest suffered the least ($X^2 = 14.49$, $p < 0.01$). There was no statistically significant relationship between size and mortality in the other two fires.

Insulating properties of the dead leaves

The dead aloe leaves were remarkably difficult to burn. In the first trial, two leaves began to char after eight minutes exposure to the fire. In the second trial, one hour later, several leaves began to burn after four minutes exposure. Such extended exposure to flames would be exceptional in a wild fire and burning of leaves thus a very rare phenomenon.

Temperatures at the stem surface (periderm) of the clothed aloe are compared with fire temperatures in Fig. 2a. No change in stem surface temperature was recorded during the first eight minute exposure of the clothed aloe. In the second trial, stem-surface temperatures remained constant with no measurable increase until five minutes after exposure when the temperature rose to 50° C at the 400 mm thermocouple.

In contrast, stem surface temperatures of the stripped aloe rose sharply to 100° C at the 100 mm level one minute after exposure with a more gradual rise at the 400 mm level peaking at 95° C, six minutes after exposure (Fig. 2b).

The experiment thus demonstrated that a) dead leaves are difficult to burn under conditions simulating natural fires and b) the layer of dead leaves insulates the stem against fire heat.

Table 2. *Aloe ferox* mortality in three fires in relation to height. Expected number of deaths, assuming mortality is proportional to size-class representation, in parentheses

	Height (m)			Total
	<1	1–2	>2	
a) Robinson's Pass Outeniquas, Fire 1				
No. dead	12 (4.9)	14 (13.7)	6 (13.4)	32
No. alive	4	31	38	73
Total	16	45	44	105
b) Robinson's Pass Outeniquas, Fire 2				
No. dead	0 (0.8)	11 (8.5)	16 (17.6)	27
No. alive	3	21	49	73
Total	3	32	65	100
c) Swartberg Foothills				
No. dead	16 (13.4)	31 (32.9)	14 (14.6)	61
No. alive	6	23	10	39
Total	22	54	24	100
d) All Fires				
No. dead	28 (16.1)	56 (51.5)	36 (52.3)	120
No. alive	13	75	97	185
Total	41	131	133	305

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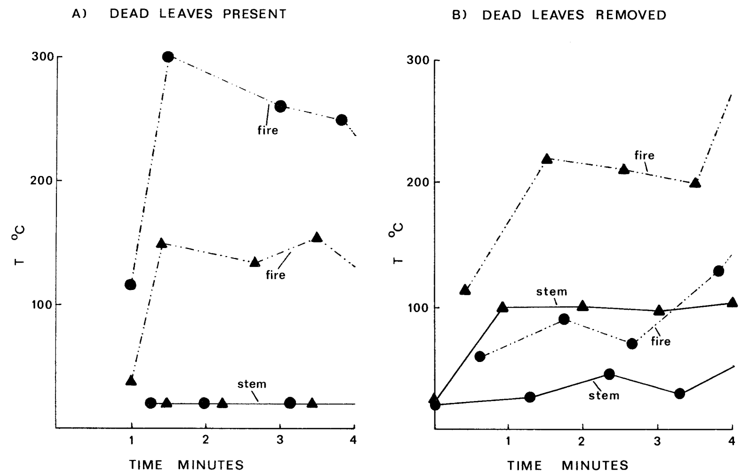

Fig. 2A, B. The insulating properties of the skirt of dead leaves in *Aloe ferox*. An aloe stem was exposed to fire and temperatures measured at two heights, 100 mm (circles) and 400 mm (triangles), above the fire platform. **A** Skirt of dead leaves present (first exposure): Temperatures outside the leaf layer (=fire temperatures). Temperatures inside the leaf layer (=stem, at the periderm) (there was no measurable difference at the two stem heights).
B Skirt of dead leaves removed; Temperatures in the fire and at the stem surface (periderm)

Discussion

Fire is a powerful agent of natural selection and many plant characteristics have been interpreted as fire adaptive (for recent reviews see Gill 1975, 1981a, Noble, Slatyer 1977). Few studies, however, have been able to unequivocally demonstrate increased fitness of populations with a putative trait. Species whose individuals survive fire presumably gain in fitness through increased longevity and the opportunities this offers for successful establishment of offspring in the long term. Variability in bark characteristics within a population and its significance to fire survival are difficult to study partly because of bark measurement problems, but also because of the spatial heterogeneity of fire characteristics (Gill 1981b). *Aloe ferox* is a good subject for studying the adaptive significance of stem insulation because populations vary in their degree of insulation, this variation is easily measured and survivorship with or without dead leaves is relatively clear cut.

Although most individuals with bare stems were killed, this was not always the case. Many of the taller aloes had bare stems immediately above the ground (78% of all plants with stems bare for less than 0.25 m were taller than 2 m). Despite this unprotected zone, only 2 of 38 plants in this category were killed – both small plants with narrow stem diameters. How did the remainder survive despite their bare stems?

The distribution of heat in fires is not uniform. Several studies have demonstrated that fire temperatures are greatest 0.2 m to 1.0 m *above* the soil surface in both grassland and shrubland fires (Whittaker 1961; Vareschi 1962; Kayll 1966; Tunstall, Walker, Gill 1976; Trollope 1978; Trabaud 1979). Fire temperatures have not been measured in Renosterveld, but the studies cited suggest that critical heat loads may only be experienced above a critical height on the stem.

In addition, the lowest and therefore oldest part of the stem has the thickest bark (Table 3) offering the greatest degree of insulation. Microhabitat factors, such as stones around the bole, sometimes also appeared to play a role in deflecting fire heat.

Table 3. Variations in *Aloe ferox* bark thickness with height above the ground. Each value is the mean of eight measurements from a sectioned 2 m tall plant

Stem height (m)	0.1	0.2	0.3	0.4	0.5	1.0
$\bar{x}$ Bark thickness (mm)	5.69	6.00	3.19	2.44	2.64	1.60
Standard error	0.53	0.52	0.46	0.14	0.36	0.07

The distribution of aloes with bearded stems

Since the skirt of persistent dead leaves appears to be important in fire survival of *Aloe ferox,* it is of interest to examine the distribution of this characteristic in other tree aloes. I would predict that aloes with fully clothed stems would be typical of fire-prone environments. The habit would not, however, preclude them from colonising fire-free environments, e.g. *Aloe comosa* in succulent shrublands of the north-western Cape (Reynolds 1950).

Naked or partially naked-stemmed species would be restricted to firefree environments such as desert, forest, dense bush or boulder outcrops and scree where fires are rare or of low intensity. Agricultural activities which reduce fire frequency, such as overgrazing by livestock, might allow these species to expand into less densely vegetated areas than their "typical" habitat.

Information on skirt length and habitat of southern African aloes was gleaned from a number of sources (Reynolds 1950; Jeppe 1969; West 1974; Coates Palgrave 1977) and from personal observation of the genus, mostly in the eastern Cape. Unfortunately these sources are often vague and the classification that follows is preliminary.

Southern African tree aloes listed by Coates Palgrave (1977) were divided into three categories of completely clothed, partially clothed and bare-stemmed species. Species in the first category appear to have the greatest inter – and intra-population variability in leaf retention. Characteristic habitat of each species was classified according to fire likelihood. Fire-prone habitats are grassland, woodland (including savannah, thornveld etc. with grassy understorey), and Cape shrublands (fynbos, renosterveld). Habitats which are fire-free or where fires are rare and of low intensity include forest, "bush" (eg. Acock's 1953 Valley Bushveld), thicket and arid areas of the west coast. Boulder outcrops, cliffs and scree slopes provide fire-free islands in fire prone vegetation, the degree of protection generally increasing with increasing rock size. Since aloes frequently grow in rocky habitats, varying from stony dolerite outcrops to granite inselbergs, the division of these into fire-prone and fire-free is somewhat subjective.

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Table 4. The habitats and their fire likelihood of South African tree aloes in relation to stem protection by dead leaves

Stem mostly fully covered			Stem bare			Stem partially covered		
Species	Habitat[a]	Fire	Species	Habitat	Fire	Species	Habitat	Fire
africana	T, W	−(+)	bainesii	F, T	−	arborescens	T, R	−
candelabrum	W, T	+(−)	dichotoma	D, R	−	angelica	T, R	−
comosa	S, R	−(+)	pearsonii	D, R	−	excelsa	T, R	−(+)
dolomitica	G, W	+	pillansii	D, R	−	munchii	T, R	−
ferox	G, S	+	plicatilis	R, S	−	pluridens	T	−
khamiesensis	S, R	+(−)	ramosissima	D	−	rupestris	T	−
littoralis	G, W	+				speciosa	T	−
marlothii	G, W	+						
spectabilis	G, W	+						
thraskii	T (coastal bush)	−						

[a] Fire-prone habitats (+) are: W = Woodland (thornveld, savannah etc.); G = Grassland; S = Shrubland (fynbos, renosterveld)
Fire-free habitats (−) are: T = Thicket (Bush, scrub etc.); F = Forest; D = Desert (arid lands); R = Rock, boulder, cliffs

Despite these classification difficulties, the data in Table 4 support the contention that dead leaf retention is adaptive in fire environments. All species with bare or partially bare stems are restricted to habitat where fires are rare or absent. All species in fire-prone environments can maintain a skirt of dead leaves that completely covers the stems. Species in this group may occupy both fire-prone and fire-free habitat, for example, *A. ferox* and *A. khamiesensis* in renosterveld (fire-prone) and succulent Karroid shrubland (fire-free). *A. thraskii*, a fully bearded species, is unusual in occurring only in fire-free thicket, but is exposed to salt spray from the sea. *A. sessiliflora* and *A. castanea* have variable habits of leaf retention and plant form and occur in both fire-prone and fire-free habitat. A comparison of stem characteristics in different habitats of these two species would provide a further test of the hypothesis.

Conclusions

Although fires in *Aloe ferox* habitat only occur at intervals of several decades, they exert a strong selective pressure on this slow growing species. The continuous cover of persistent dead leaves appears to have evolved in response to fire in this and other fire-prone aloe species.

It is evident that harvesting of *Aloe ferox* leaves for the drug "Cape aloes" could cause heavy mortality in populations exposed to fire. The Swartberg sample was taken from a harvested population and twice as many aloes died in this fire as in the two unharvested Outeniqua fires. Farmers harvesting aloes should exclude fire, prohibit leaf removal below a critical height (±1 m?) or leave some individuals unharvested to provide a seed source for replacing individuals whose fire defences they are removing.

Acknowledgements. I thank Malcolm Gill for asking a useful question, P. de Kock and R. America for field assistance and G. Breytenbach, F. Kruger, R. Cowling C. Geldenhuys and B. van Wilgen for useful comment. The study forms part of the conservation research programme of the Directorate of Forestry, South Africa, and is published with their permission.

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Received March 5, 1982

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