Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana

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Abstract

Acacia erioloba woodlands provide important forage and shade for wildlife in northern Botswana. Mortality of mature trees caused by browsing elephants has been well documented but the lack of regeneration of new trees has received little attention. Annual growth of new shoots and changes in height were measured to determine the influence of elephants and small ungulate browsers, rainfall and fire on the growth and survival of established *A. erioloba* seedlings from 1995 to 1997 in the Savuti area of Chobe National Park. All above-ground vegetation was removed from 40% of established seedlings in 1995 and 28% in 1997 by browsing elephants, and the mean height of remaining seedlings decreased from >550 mm to <300 mm. When seedlings browsed by kudu, impala and steenbok but not elephants are considered, mean seedling height increased <50 mm per year, even though mean new shoot growth remaining at the end of the dry season was 100–200 mm. Fires burned portions of the study area in 1993 and 1997, killing above-ground vegetation, but most established *A. erioloba* seedlings survived, producing coppice growth from roots. While elephants and fire caused the greatest reduction in established seedling height and number, small browsers suppressed growth, keeping seedlings vulnerable to fire and delaying growth to reproductive maturity.

Key words: Acacia, seedlings, elephants, fire, ungulates, Botswana

Résumé

Les forêts d'*Acacia erioloba* procurent une nourriture et des abris importants pour la faune au nord du Botswana. On connaît bien la mortalité des grands arbres due aux éléphants mais on n'a accordé que peu d'attention au manque de régénération de nouveaux arbres. On a mesuré la croissance annuelle des jeunes pousses et le changement de hauteur pour déterminer l'influence des éléphants et des petits ongulés, des chutes de pluies et des feux sur la croissance et la survie des semis connus d'*A. erioloba*, de 1995 à 1997 dans la zone de Savuti au Parc National de Chobe. Toute la végétation au-dessus du sol a été supprimée sur 40% des semis connus en 1995, et 28% en 1997 par le broutage des éléphants, et la hauteur moyenne des plants restants a baissé de > 550 mm à < 300 mm. Lorsqu'on considère les pousses broutées par les koudous, les impalas et les steenbocks, mais pas par les éléphants, la hauteur moyenne des jeunes pousses augmentait de moins de 50 mm par an même si la croissance moyenne des nouvelles pousses subsistant à la fin de la saison sèche était de 100 à 200 mm. Les feux ont brûlé des portions de la zone étudiée en 1993 et en 1997, tuant toute la végétation au-dessus du sol, mais les pousses d'*A. erioloba* les mieux situées ont survécu, produisant de nouveaux taillis au départ des racines. Alors que les éléphants et les feux causaient les plus fortes réductions de la hauteur et du nombre des pousses établies, les petits ruminants en supprimaient la croissance, ce qui les laissait vulnérables aux feux et retardait la croissance jusqu'à la maturité.

Introduction

Declines in mature acacias and other canopy trees related to elephant (*Loxodonta africana* Blumenbach) browsing have been documented in eastern and southern Africa for over 30 years (Buechner & Dawkins, 1961; Laws, 1970). Elephant browsing alone (Croze, 1974; Leuthold, 1977; Guy, 1981; Barnes, 1983; Lock, 1993) or fire, especially when combined with elephant browsing, can prevent

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 Afr. J. Ecol., **39**, 340–350

woodland regeneration (Field & Ross, 1976; Smart *et al.*, 1985; McNaughton *et al.*, 1988; Dublin *et al.*, 1990; Ruess & Halter, 1990). Fire intensity increases when grass accumulates after high rainfall or low levels of grazing (Norton-Griffiths, 1979; Sabiiti & Wein, 1988; Leuthold, 1996). Giraffe (*Giraffa camelopardalis* L.) (Pellew, 1983b) and small antelope, such as impala (*Aepyceros melampus* Lichtenstein) (Belsky, 1984; Prins & Van Der Jeugd, 1993), can inhibit the growth of seedlings and small trees, increasing the length of time that they are vulnerable to fire (Pellew, 1983a; Dublin *et al.*, 1990).

In northern Botswana, *Acacia erioloba* (E. Mey.) woodlands provide important forage (Coe & Coe, 1987) and shade for wildlife. The decrease of mature acacias and other canopy trees in riverine areas where wildlife concentrates during the dry season has concerned wildlife managers in northern Botswana since the 1960s (Child, 1968; Sommerlatte, 1976; Melton, 1985). While damage and mortality to mature *A. erioloba* trees by foraging elephants has been documented (Moroka, 1984; Wackernagel, 1992; Mughogho, 1995), little attention has been given to the rate of establishment and growth of potential replacement trees in Botswana's wildlife areas.

Acacia erioloba is widespread throughout Botswana and in parts of Zimbabwe, Namibia and South Africa on Kalahari sand (Carr, 1976). The largest trees are usually found on alluvial soils where long tap roots, which extend to a permanent water source, may exceed 40 m (Timberlake, 1980). *Acacia erioloba* seedlings grow slowly above ground for 4–5 years while establishing a deep root system (Barnes *et al.*, 1996). Seedlings on sandy soils may reach 1 m in height during their first year but grow more slowly on heavier soils. Trees may reach 7 m in 15–20 years (Barnes *et al.*, 1996). New *A. erioloba* shoots, leaves and flowers are produced during the dry season using stored energy (Barnes *et al.*, 1997). The canopy remains green throughout the year and provides important forage and shade at a time when many other trees are leafless.

Surface water limits the distribution of elephants and other water-dependent animals (Owen-Smith, 1996), and vegetation changes from elephant browsing increase near permanent sources of water (Leuthold, 1977; Ben-Shahar, 1993). The number of established *A. erioloba* seedlings and small trees has decreased in riverine areas of Chobe National Park and Moremi Game Reserve where wildlife concentrates during the dry season (M. Barnes, unpublished data). This study was conducted in the Savuti area of Chobe National Park, where established *A. erioloba* seedlings were still common. Since the Savuti River stopped flowing in 1981, the number and distribution of elephants and other water-dependent animals have been limited by the amount of water available in artificial water points (AWPs) during the dry season. Prior to the installation of AWPs, elephants were not able to remain in Savuti when the river and other temporary sources of water from the rainy season dried. Rainfall in 1994 and 1995 was $<50\%$ of the annual average (Botswana Meteorological Service), while 1996 and 1997 had near average rainfall of 600 mm each year (pers. obs.). Human-caused fires originating outside the national park burned parts of the study area in 1993 and 1997.

In this study I address the following questions. (1) To what extent does an increased supply of water change the pattern of mortality or the number of established *A. erioloba* seedlings damaged by elephants? (2) In the absence of elephants, can browsing ungulates suppress the growth of *A. erioloba* to reproductive maturity? (3) Does the amount of rainfall during the rainy season influence new shoot growth and height increase in *A. erioloba*? (4) Can the current rate of burning prevent established seedlings from reaching a fire-resistant size?

Study area

Savuti is located in the western part of the 11 000 km^2 Chobe National Park in northern Botswana (Fig. 1). The flat topography is broken by seven rocky outcrops or inselbergs and the Magwikhwe Sand Ridge, which extends over 75 km along the west side of Savuti (Thomas & Shaw, 1991). Soils in Savuti are related more to past and present hydrological processes than to underlying geology (Remmelzwaal *et al.*, 1988). Alluvial and lacustrine deposits provide a diversity of soil types in the Kalahari sands, which cover most of northern Botswana. The Savuti River flowed frequently until the 1880s and then was dry until 1958, allowing *A. erioloba* and other woody vegetation to establish in the flood plain. After 1958, the river flowed every year, except 1966, until it ceased flowing again in 1981 (Shaw, 1984). The Savuti River has remained dry since 1982, leaving a broad dry channel and a dry grassland on the 2–4 km by 15 km flood plain. Trees include *A. erioloba*, *Acacia luederitzii* (Engl.), *Acacia tortilis* ((Forsk.) Hayne), *Acacia hebeclada*

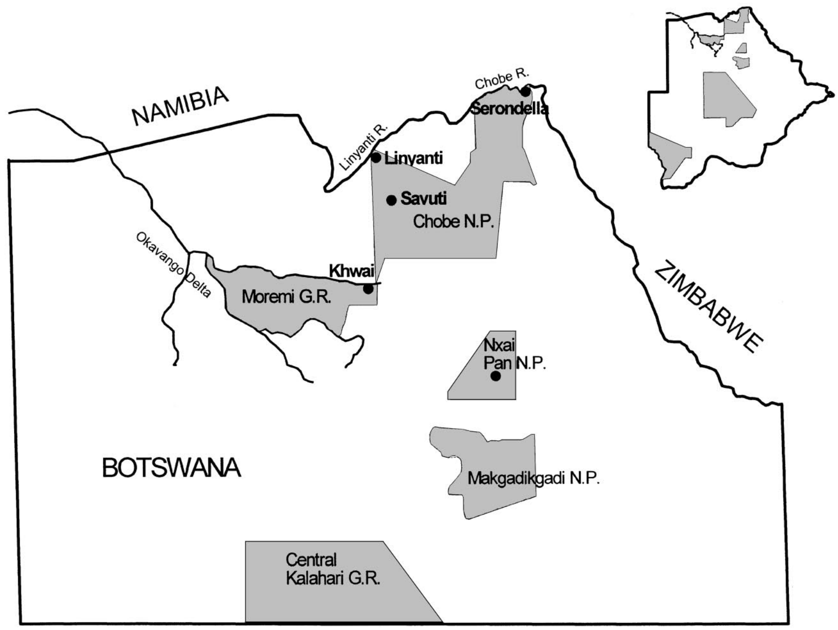

Fig 1 Location of Savuti study area in Chobe National Park, Botswana

(DC.), *Acacia nigrescens* (Oliver), *Combretum imberbe* (Warwa), *Combretum hereroense* (Schinz), *Combretum mossambicense* ((Klotzsch) Engl.), *Lonchocarpus capassa* (Rolfe) and *Lonchocarpus nelsii* ((Schinz) Schinz ex Heering and Grimme). Soils with more clay are dominated by *Colophospermum mopane*.

The November–March rainy season is highly variable and coincides with the period of highest evapotranspiration (Bhalotra, 1987; Bekker & De Wit, 1991). Rainfall varies spatially and temporally with differences of >100 mm annually reported between rain gauges <1 km apart (Vossen *et al.*, 1985) and dry periods of several weeks are not uncommon during the rainy season (Vossen, 1988; Bhalotra, 1989). Savuti is located on the 550 mm average annual rainfall isohyet with a 35% coefficient of variation (Bhalotra, 1989). The first year of the study was extremely dry, occurring at the end of a 7-year drought (Botswana Meteorological Services), with rainfall from 250 to 300 mm. Average annual rainfall of >600 mm was recorded in 1996 and 1997 (pers. obs.). Since the Savuti River dried up in 1982, there is no surface water available after the seasonal pans have dried. In 1988, an AWP was installed north of the dry Savuti River channel near the public campsite to provide water for wildlife during the dry season. Two additional AWPs were installed near the flood plain in 1995. The Linyanti River, 40 km north, is the closest natural source of water in the dry season.

Methods

Grasses in the Savuti flood plain and adjacent woodlands are usually 0.7–1.0 m high from January–March. Rainfall decreases in April (Bhalotra, 1989) and thousands of migrating zebra (*Equus burchelli* Gray) spend several weeks grazing in Savuti before continuing north to the Linyanti and Chobe Rivers (Fig. 1). The large zebra herds, in addition to wildebeest (*Connochaetes taurinus* Burchell), buffalo (*Syncerus caffer* Sparrman) and elephants that graze during the rainy season, substantially reduce the height and amount of grass. In August 1995, 20×50 m plots were established in areas with short ($n = 4$), medium ($n = 4$) and tall ($n = 3$) grass on the flood plain and in adjacent woodland with little grass cover ($n = 4$) during the dry season to monitor new shoot growth, browsing effects and height changes in established *A. erioloba* seedlings. Established *A. erioloba* seedlings (>1 years) were 150–1500 mm high with stem diameters 7–20 mm at ground level and smooth grey or reddish-brown bark. A total of 186 seedlings were marked with plastic tags in 1995. Only 66 seedlings with tags remained in August 1997, after elephants pulled up or broke seedlings off near ground level. Additional established seedlings were marked on the plots in 1997. Most were probably regrowth from roots of previously marked seedlings that had been broken off below the level of the tags, as no new seedlings established in 1995 or 1996. The height of each tagged seedling was measured monthly during the August–November growing season in 1995 and 1997. The lengths of three randomly chosen new shoots were also measured monthly between August and November in 1995 and 1997. Soft new shoots are red or green and turn reddish brown with lignification at the end of the dry season in December. Evidence of browsing was recorded as small browser or elephant. Small browsers, such as impala, kudu (*Tragelaphus strepsiceros* Pallas) and steenbok (*Raphicerus campestris* Thunberg), removed individual new shoots and leaves but rarely lignified or woody vegetation. Elephants used their feet to break off seedlings held in their trunks at ground level or a few centimetres above and pulled branches off with their trunks, consuming woody vegetation in addition to new growth (pers. obs.).

Each year in Botswana, fires are set to reduce woody vegetation and promote new grass growth for livestock. Fires originating outside protected areas often burn uncontrolled into the national parks and reserves. In October 1993, prior to this study, a fire burned most of the grassland seedling sites in Savuti. In late August 1997, all of the tall grass plots and three of the medium grass plots burned. Each plot was visited monthly to determine how many established seedlings survived. Because the plastic tags melted, individual numbered seedlings could not be followed, but the number and mean height of surviving seedlings at the end of November were compared to the number and mean height of seedlings measured on each plot 2 weeks before the fire.

Statistical analysis

Analysis of variance (GLM, SAS, 1990) was used to determine the relationship among the effects of browsing elephants, small ungulates, fire, rainfall and the height of grass at each study site on new shoot growth and mean height change of established *A. erioloba* seedlings in 1995 (<300 mm rainfall) and 1997 (>600 mm rainfall). All established *A. erioloba* seedlings showed evidence of browsing. Additional analyses using only measurements of plants browsed by kudu, impala and steenbok, but not elephants, were used to examine the influence of smaller browsers only. Bonferroni *t*-tests were used for pair-wise comparisons when main effects were significantly different ($P < 0.05$) and the interactions were not significant. Changes in the size distribution of established seedlings between August and November of 1995 and 1997 were compared using Chi-square analysis (SAS, 1990).

Results

Elephant and small ungulate browsing, grass height around seedlings, and burning were all associated with changes in mean height of established *A. erioloba* seedling. Only 59% of established seedlings marked in August 1995 ($n = 186$) remained in November. Because no fires occurred in the area in 1995 and smaller browsers, such as impala, steenbok and kudu, are not capable of breaking main stems >7 mm diameter at ground level, the reduced number and significant decrease in mean established seedling height can be attributed to elephants ($F = 17.90$, d.f. $= 1,25$, $P = 0.003$; Table 1). In 1997, 28% of established seedlings were broken off near ground level on unburned

Table 1 Mean height of established *Acacia erioloba* seedlings with browsing damage attributed to all browsers and with small browsers only (excluding elephants) in the Savuti area of Chobe National Park, Botswana in August and November 1995 and 1997. Height values are means ± SE

	All browsers, including elephants		Small browsers only	
	Mean height (mm)	Bon Grp[1]	Mean height (mm)	Bon Grp
Aug 1995	583 ± 43	A	531 ± 37	A
Nov 1995	403 ± 26	B	579 ± 34	A
Aug 1997	433 ± 49	B	393 ± 44	B
Nov 1997	291 ± 37	C	405 ± 46	B

[1]Bonferroni *t*-test means with same letter are not significantly different from others in same column.

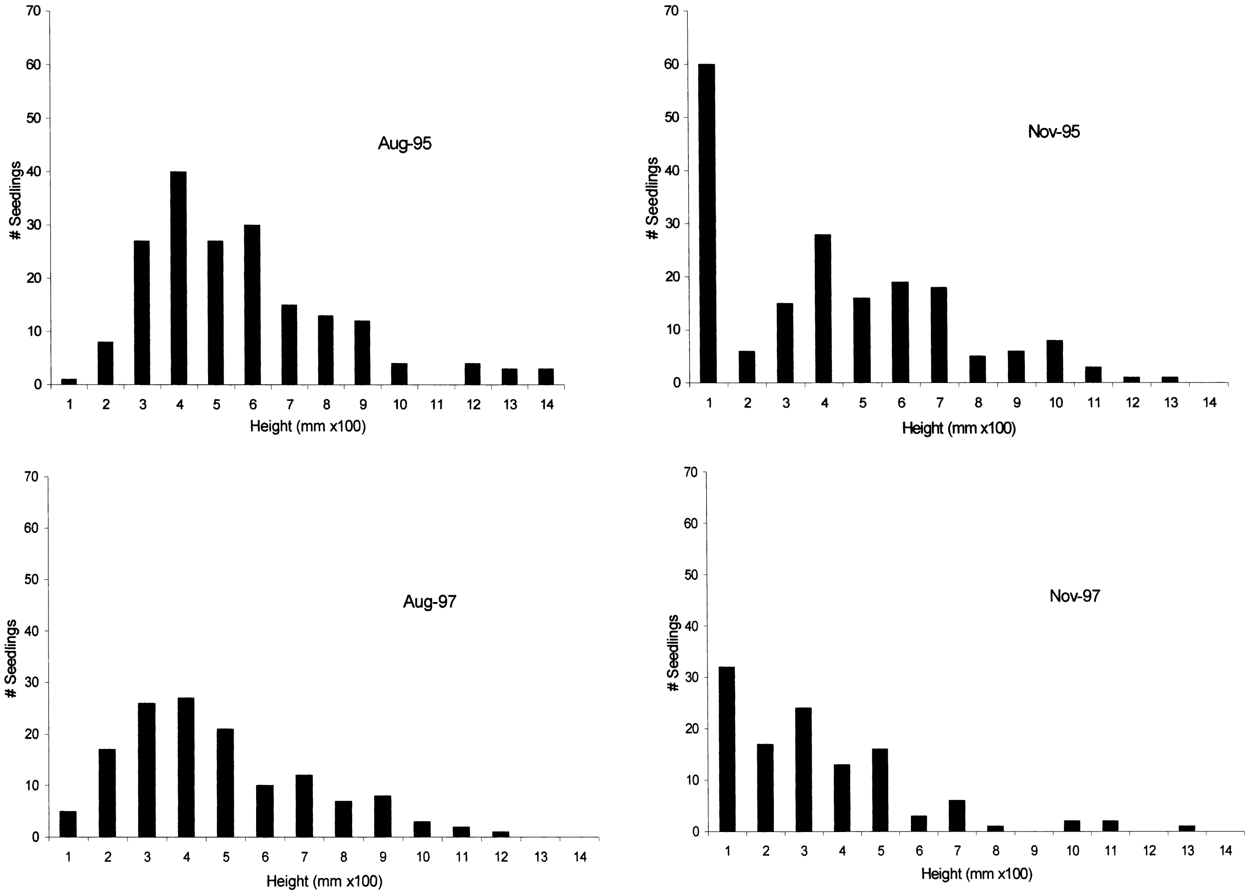

Fig 2 Height distribution in 100 mm increments of established *A. erioloba* seedlings in the Savuti area of Chobe National Park at the beginning and end of the growing season in 1995 and 1997 ($n = 186$). Includes seedlings browsed by elephants and ungulates and seedlings burned in August 1997

plots, again resulting in a significant decrease in mean height ($F = 8.42$, d.f. $= 1,17$, $P = 0.0099$; Table 1). Seedling height distribution changed significantly between August and November 1995 and 1997 ($\chi^2 = 173.581$, d.f. $= 42$, $P < 0.0001$; Fig. 2).

Impala and steenbok were frequently observed browsing new shoots on established *A. erioloba* seedlings in the woodland and grassland. Foraging observations of the more secretive kudu were limited to the woodland. In 1995, mean length of new shoots decreased from August (139 ± 19 mm SE) to November (102 ± 16 mm) ($F = 1.03$, d.f. $= 3,56$, $P = 0.3852$; Fig. 4). In contrast, mean length of new shoots increased significantly during 1997 from 32 ± 4 mm to 165 ± 25 mm by November ($F = 18.81$, d.f. $= 3,24$, $P < 0.0001$; Fig. 3). There was more

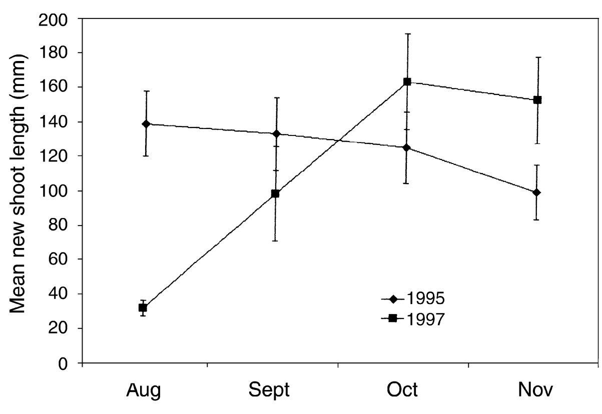

Fig 3 Mean growth of new shoots ($\pm$SE) on established *A. erioloba* seedlings during the August–November growing season in the Savuti area of Chobe National Park in 1995 and 1997

new shoot growth remaining at the end of the dry season in 1997, after unseasonable rainfall in September and October, than in 1995 ($F = 3.67$, d.f. $= 2{,}19$, $P = 0.0724$). Seedling height did not change significantly on seedlings browsed only by small ungulates. Mean increase in seedling height was only 48 mm in 1995 ($F = 2.25$, d.f. $= 1{,}25$, $P = 0.1464$; Table 1) and 12 mm in 1997 ($F = 0.17$, d.f. $= 1{,}10$, $P = 0.6858$), even though the mean new shoot growth remaining on random new shoots in November was >100 mm each year.

At the beginning of the study, there was a positive linear relationship between the height of grass and the height of *A. erioloba* seedlings ($F = 4.988$, d.f. $= 1{,}184$, $P = 0.0067$). The tallest seedlings were found in tall grass and the shortest in woodland and short grass sites, suggesting that seedlings in taller grass might be better concealed from browsers. However, by November 1995 there was no difference in mean height at any of the sites. In November 1997, the tallest seedlings were found on the short grass plots. By November in both years, there was a significant negative relationship between grass height and the amount of new shoot growth remaining on seedlings browsed only by small ungulates ($F = 10.27$, d.f. $= 3{,}7$, $P = 0.0059$; Table 2). Twice as much new shoot growth remained on seedlings in the short grass study area compared to seedlings in the woodland.

All of the tall grass plots and three of the medium grass plots burned in August 1997, 2 weeks after height and new shoot growth had been measured. Within 2 weeks, coppice growth from the roots of established *A. erioloba* seedlings was found on all of the burned plots. Three months after the fire, exactly the same number of established seedlings were found on three plots as had been marked prior to the fire, but two plots each had two fewer seedlings. Mean height of coppiced seedlings (250 ± 12 mm) did not vary among plots in November ($F = 1.24$, d.f. $= 4{,}31$, $P = 0.3154$). Before the fire, mean seedling height on these plots was 631 ± 52 mm. No above-ground vegetation survived on any of the burned seedlings, so all shoot growth was new. New shoots ranged from 130 to 390 mm with no difference among plots ($F = 0.29$, d.f. $= 4{,}31$, $P = 0.8839$). At the end of the growing season in November 1997, there was no difference in mean height between burned established seedlings (250 ± 12 mm) and unburned seedlings browsed by elephants (291 ± 37 mm) ($F = 0.32$, d.f. $= 1{,}7$, $P = 0.5874$). Differences between mean seedling height in the short, medium and tall grass and woodland sites were influenced by browsing and fire (Fig. 4).

Discussion

Elephant browsing

Elephant browsing was the primary cause of mortality or loss of all above-ground biomass in established *A. erioloba* seedlings in Savuti. Elephants frequently browse seedlings <1 m high (Field & Ross, 1976; Jachman & Bell, 1985; Tchamba & Mahamat, 1992; Kabigumila, 1993; Dublin, 1995). However, when elephants break seedlings off near ground level, coppice growth is usually produced from the roots so the highest mortality probably occurs when they are pulled up. Only 35% of the established seedlings marked in August 1995 could be located 2 years later in August 1997; however, many seedlings broken off by elephants below the tag survived and produced new shoots. All of the untagged seedlings on each plot were marked and given a new number in August 1997. Assuming that the newly marked seedlings had been browsed previously and lost their tags, as no new

Table 2 Mean growth of new shoots on established *Acacia erioloba* seedlings browsed only by small ungulates in study areas with short, medium and tall grass heights and woodland in the Savuti area of Chobe National Park, Botswana in 1995 and 1997. Values are means ± SE

	1995			1997		
Site	*n*	Mean shoot length (mm)	BonGrp[1]	*n*	Mean shoot length (mm)	BonGrp
Short	4	175.4 ± 34.1	A	4	285.3 ± 16.3	A
Medium	4	109.1 ± 45.5	B	1	230.8	A
Tall	3	161.5 ± 7.2	A	0	burned	
Woodland	4	87.9 ± 13.4	B	4	118.9 ± 17.4	B

[1]Bonferroni *t*-test means with the same letter in a column are not significantly different ($P < 0.05$).

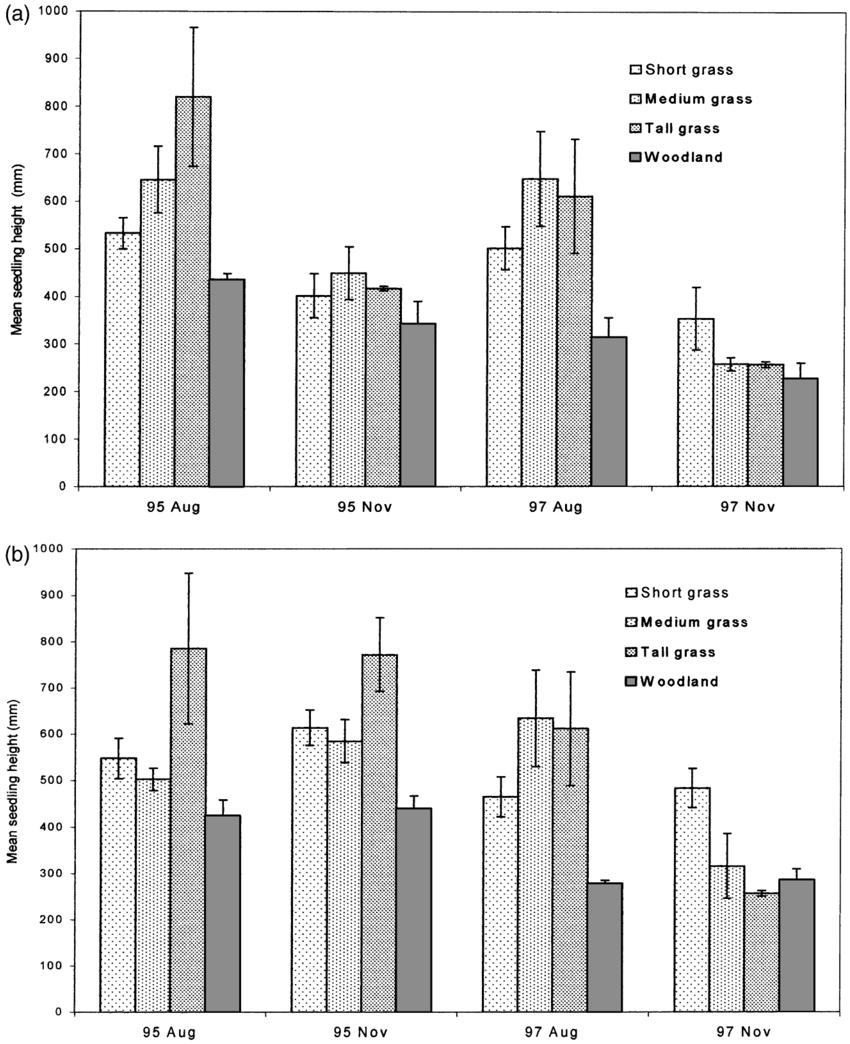

Fig 4 Mean height of established *A. erioloba* seedlings (±SE) at four study sites in the Savuti area of Chobe National Park at the beginning and the end of the growing season in 1995 and 1997. Figure (a) includes all observations including small ungulates, elephants and seedlings burned 2 weeks after the August 1997 measurements; (b) includes burned seedlings and seedlings browsed by small ungulates but not elephants

seedlings established from 1995 to 1997, mortality from elephant browsing between August 1995 and August 1997 was 36%. Twenty-eight percent of the seedlings were pulled up or broken off below tag level between August and November 1997.

Since the Savuti River dried in 1982, the number of elephants in the Savuti area during the dry season has been limited by the amount of water available. Between 1982 and 1988, there were few elephants in Savuti during the dry season. After the installation of Pump Pan AWP in 1988, near the dry Savuti River channel, >200 elephants remained in the area during the dry season but few elephants were observed foraging in acacia woodlands >5 km from Pump Pan. After two additional AWPs were installed south and east of acacia woodlands in 1995, elephants were frequently observed foraging over a much wider area. Elephant paths increased through the acacia woodlands and between AWPs, including across the flood plain where established seedlings were most abundant. Monthly censuses during the dry season in 1995 and 1997 indicate that around 800 elephants remain in Savuti during the dry season when all three AWPs are operating (M. Barnes, unpublished data).

Small ungulate browsing

While browsing elephants were responsible for mortality or removal of all above-ground vegetation on many established *A. erioloba* seedlings, smaller ungulate browsers also inhibited increases in mean height. Solitary or paired steenbok were observed browsing *A. erioloba* on the flood plain and in the woodland during the dry season after green herbs were no longer available. Steenbok are preferential browsers and prefer acacia savannas where low grass cover allows predator detection and escape (du Toit, 1993). Impala herds forage primarily in woodlands and along ecotones but occasionally move >1 km into the open grassland of the flood plain. Kudu browse in the woodland year-round (Owen-Smith & Cooper, 1987; Owen-Smith, 1994). It was not possible to determine which small browser had removed old or new vegetation from established seedlings. Although smaller ungulate browsers do not reverse the growth of established seedlings to ground level as do elephants and fire, the current level of browsing, especially of vertical shoots, can delay growth to a fire-resistant size. In 1997, mean height increase was just 12 mm during the growing season, even though mean new shoot length remaining in November was 165 mm. It appears that small ungulates suppress height increase in *A. erioloba* by removing more new growth from vertical than lateral shoots.

Concealment by tall grass does not protect established *A. erioloba* seedlings from browsing by elephants or small ungulates, even though seedlings in short dry grass or on bare sand were conspicuous as the only green plants during the dry season. There was a significant linear relationship between the height of grass and the height of established *A. erioloba* seedlings in August 1995, with the tallest seedlings found in the tallest grass. However, in November 1995 and 1997, the site farthest from cover, with the shortest grass, had the tallest plants and the most remaining new shoot growth. *Acacia erioloba* and *A. hebeclada* provided the only green forage in the open grassland during the dry season. Daytime temperatures in the late dry season usually exceed 40 °C and animals spend most of the day in the shade. Browsing ungulates in the short grass plots might have an increased risk of predation and no other forage choices except the established seedlings of acacias and dried grass. The woodlands provide shade, cover and a variety of browse species, including the lower shoots of small trees, in addition to seedlings.

As there was not a significant difference in mean new shoot length or height increase between drought and average rainfall years, the amount of precipitation during the rainy season did not appear to influence the vertical growth of established *A. erioloba* seedlings, which produce new shoots only during the dry season. Elephants and impalas forage on green grass >90% of the time when it is available in Savuti and then switch to woody vegetation (pers. obs.), which is higher in protein, after grasses have dried (Field & Ross, 1976). Unseasonable rainfall during the late dry season in September and October 1997 stimulated early growth of grass and herbs. Beginning in mid-September, impala foraged on green grass and herbs >95% of the time. The persistence of more new shoot growth in 1997 than in the dry year 1995 may have resulted in part from the availability of alternative food resources emerging in response to the early rain. In addition to the amount of rain, the timing of the rainfall is important. Mixed foragers, such as elephants and impala, are able to graze grass and herbs longer during years with higher rainfall throughout the rainy season and extending into the dry season, giving woody vegetation, such as acacias, more time to recover and grow.

Fire

Grass height and density are related to rainfall and the fuel load for potential fires increases in wet years (Norton-Griffiths, 1979). Grasses in the Savuti flood plain and adjacent woodlands are grazed and trampled by migrating zebra, wildebeest and buffalo during the rainy season. Much of the remaining short grass stubble is removed by termites during the dry season. In areas where grass is less palatable, grass >1 m high remains throughout the dry season. Heavy grazing and trampling by migratory ungulates reduces the fuel load and, therefore, fire frequency and intensity at Savuti. During the dry year 1995, nearly all grass was removed by grazers and termites, leaving bare sand and no fuel for fires. In 1997, the migrating zebras had used all of the available surface water in temporary seasonal pans by mid-May and left the area before the grass had been depleted, leaving adequate fuel for fires to spread rapidly.

Fires generated by human activities outside the parks burned large areas in Savuti in 1993 and 1997. Some areas of Chobe National Park, especially near park boundaries, burn nearly every year. Small and mature *A. erioloba* trees with thick fissured bark are fire resistant but all aboveground vegetation was killed on established seedlings. Three months after the 1997 fire in Savuti, the number of established seedlings with coppice growth from the roots was the same as the number previously marked on three plots, but two plots had fewer seedlings. Mortality increases with fire intensity (Sabiiti & Wein, 1988). *Acacia erioloba* frequently resprout with more than one stem after burning (Skarpe, 1991) and most at Savuti had more than four new shoots from existing roots.

Skarpe (1991) reported that *A. erioloba* in Botswana livestock areas are vulnerable to fire until their canopies are above 2–3 m. Thick bark increases fire resistance but there was no additional bark on established seedlings at Savuti or other evidence of a transition to the small tree size category during this study. No established *A. erioloba* seedlings >1.5 m were found between 1995 and 1997, so an established seedling with thin smooth bark may remain vulnerable to fire when >2 m high. At the current elephant browsing rate in Savuti, the mean height of established seedlings decreased from >550 mm to <300 mm from 1995 to 1997. However, even if there were no elephants, browsing by smaller animals suppresses height increase to <50 mm each year. As mean seedling height is now <0.5 m, it could take over 25 years for plants to exceed 2 m, when they might be less vulnerable to fire.

The future of Acacia erioloba in Savuti

Ages of *A. erioloba* trees are difficult to determine because they have a dense red heartwood without distinct rings when mature. The number of rings observed has been correlated with age in some known age trees <20-years old protected from fire and browsing (Gourlay & Kanowski, 1991). However, the number of rings in trees from established seedlings that have been reversed to ground level by fire or elephant browsing would not reflect the age since germination and initial establishment, but rather the time since release from fire or browsing (Gourlay, 1995). Prior to the drying of the Savuti River, the area supported large numbers of wildlife during the dry season. When the river and temporary water sources dried after 1982, most water-dependent animals moved to the Chobe-Linyanti River or other areas with surface water throughout the dry season. The seedlings on the flood plain could have established when soil moisture conditions were optimal as the flood plain dried out after the river ceased to flow or during subsequent years with adequate rainfall for germination and establishment, suggesting a maximum age of around 15 years at the beginning of this study. As unbrowsed *A. erioloba* can increase by 0.5 m in height each year (Barnes *et al.*, 1997), a 0.5 m seedling could reach 3.5 m in height after 6 years without browsing. Currently, *A. erioloba* appears to be limited to three size classes; established seedlings (<2 cm diameter with thin, smooth bark and <1.5 m high), small trees (>2 cm diameter with thick, fissured bark and 2.0–6.5 m high) and mature trees (>10 m). There was no recruitment of established seedlings to the small tree size class during this study and no trees between 7 and 10 m high were found.

The current rate of fire or elephant browsing can independently prevent recruitment of established *A. erioloba* seedlings to the small tree size category. Elephant browsing does not always kill seedlings but changes the size distribution, resulting in a decrease in the number of taller seedlings and more seedlings <200 mm, which will be vulnerable to fire for a longer period of time. Vegetation species that are less tolerant of elephant browsing may decrease or disappear from areas near an artificial water source (Owen-Smith, 1996). However, abundant acacia regeneration has been observed when elephants were excluded (Hatton & Smart, 1984) or elephant populations have been reduced in other parts of Africa (Lock, 1993; Leuthold, 1996). At the present level of small ungulate browsing alone, established seedlings may require >20 years to reach a fire-resistant size, far longer than the current fire interval. Impala, the most numerous small browser in Savuti (Vandewalle, 1988), require water if the water content of forage is <30% (Jarman & Sinclair, 1979). However, impala are rarely found more than a few kilometres from water (du Toit, 1990) so there may have been fewer in Savuti between the time the river dried and Pump Pan was installed. Kudu and impala are seen daily at AWPs but it is not known if their populations would change if the AWPs were removed. Although it may be difficult to prevent human caused fires originating outside of the national park, it could be beneficial to extinguish fires that burn frequently through sensitive vegetation. Promoting recruitment and regeneration may be more important than attempting to reduce mature tree loss (Pellew, 1983a; Herremans, 1995) if *A. erioloba* trees are to persist in Savuti.

Acknowledgements

I am grateful to the Botswana Department of Wildlife and National Parks and the Office of the President for permission to conduct this research project. I received support from National Science Foundation dissertation improvement grant 94-12150, Wildlife Conservation

Society, and the Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno. Joel Berger, Gary Haynes, Truman Young, Janet Rachlow and an anonymous reviewer provided valuable comments.

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(Manuscript accepted 1 February 2001)