
Short-term survival and long-term mortality of *Acacia drepanolobium* after a controlled burn

B. D. Okello^{1,2}, T. P. Young^{2,3*}, C. Riginos^{2,3}, D. Kelly² and T. G. O'Connor¹

¹Department of Range & Forage Resources, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, Private Bag X01, Scottsville 3209, South Africa, ²Mpala Research Centre, PO Box 555, Nanyuki, Kenya and ³Department of Plant Sciences, University of California, Davis, CA 95616, U.S.A.

Abstract

We investigated the short- and long-term effects of a controlled burn in *Acacia drepanolobium* woodland in Laikipia, Kenya in 1998. Fire temperatures averaged 250°C at ground level, with a maximum of over 500°C, but were rarely >100°C at 1.5 m above the ground or more. Nine months after the fire, virtually all *A. drepanolobium* trees had survived the fire. Some smaller trees were burnt to ground level, but most were only 'top-killed' and had coppiced. Taller trees suffered less damage than smaller trees. However, a 2003 satellite image suggested a dramatic reduction in *A. drepanolobium* canopy cover at the site. A survey of the site in 2006 revealed that the density of larger *A. drepanolobium* trees was nearly three times greater in adjacent control areas than in the old burn, with a lesser reduction in the density of smaller trees. These data suggest that short-term measures of postburn survivorship may be deceptive, and that an additional source of tree mortality (perhaps elephants) was concentrated on trees in burned areas, even many months after the burn, with long-term consequences for tree and ecosystem dynamics.

Key words: *Acacia drepanolobium*, coppicing, elephants, fire, Kenya, Laikipia, top-kill

Résumé

Nous avons étudié les effets à court et à long terme d'un feu contrôlé dans la forêt à *Acacia drepanolobium* située à Laikipia, au Kenya, en 1998. La température du feu avoisinait les 250°C au niveau du sol, avec un maximum de 500°C, mais elle dépassait rarement les 100°C à 1,5 mètre au-dessus du sol et plus haut. Neuf mois après le feu, pratiquement tous les *Acacia drepanolobium* avaient sur-

vécu. Certains des arbres plus petits avaient brûlé jusqu'au ras du sol, mais chez la plupart, seule la partie aérienne avait brûlé et ils avaient fait des repousses. Les arbres plus grands avaient subi moins de dommages. Pourtant, une image satellite prise en 2003 a suggéré une réduction spectaculaire de la canopée d'*A. drepanolobium* à cet endroit. Une étude du site réalisée en 2006 a révélé que la densité des plus grands *A. drepanolobium* était près de trois fois plus forte dans les zones de contrôle adjacentes que sur le site brûlé, où la densité des plus petits arbres était moins réduite. Ces données suggèrent que les mesures de la survie postincendie faites à court terme peuvent être trompeuses, et qu'une source supplémentaire de mortalité des arbres (peut-être des éléphants) s'est concentrée sur les arbres des zones brûlées, même plusieurs mois plus tard, avec des conséquences à long terme pour les arbres et la dynamique de l'écosystème.

Introduction

Fire is a widely studied phenomenon in African savanna ecosystems (O'Connor, 1985; Wein & Edroma, 1986; Sabiiti, Wein & Edroma, 1991; Higgins, Bond & Trollope, 2000; Roques, O'Connor & Watkinson, 2001; Meyer *et al.*, 2005; Govender, Trollope & Van Wilgen, 2006), but its effects are still not well understood. In many rangelands all over the world, fire has been used as an instrument in the management of range vegetation in various ways: to reduce bush cover, influence changes in species composition, to improve the quality of forage to animals, and to reduce disease-causing pests. Fire influences changes in vegetation on its own and in conjunction with other factors like herbivory, climate, and soils (Whelan, 1995).

In the Laikipia plateau of north central Kenya, anthropogenic fire was a common phenomenon until the late

*Correspondence: E-mail: tpyoung@ucdavis.edu

1950s (Heady, 1960). However, in the last 50 years, fires have become infrequent, because ranchers do not want to risk losing forage when rains fail after a burn. Nonetheless, prescribed and accidental fires still do occur. The decline in the frequency of fire coupled with an increase in the number of herbivores (both wild and domestic) has coincided with an increased woody cover in most of the commercial ranches. The tree species *Acacia drepanolobium* Sjoestedt is the dominant species over large areas of Laikipia plateau that have soils of impeded drainage (Young *et al.*, 1998). It is believed that this tree has increased in density throughout its range and expanded to areas where it had been absent previously (Heady, 1960; Pratt & Gwynne, 1977), although this is yet to be formally documented. In many ranches of Laikipia, managers are increasingly harvesting *A. drepanolobium* for charcoal, sometimes in combination with bush control methods designed to eliminate this coppicing species locally, especially along cleared fence lines (Okello, O'Connor & Young, 2001).

Fire has been suggested as an appropriate management tool for encroaching *A. drepanolobium* (Pratt & Gwynne, 1977; Dall, Maass & Isselstein, 2006). We explored the possibility that controlled burns could contribute to the control of *A. drepanolobium* by reducing its overall density and reducing recruitment. We report here both short-term and long-term changes in *A. drepanolobium* density in a wooded grassland after a controlled burn in Laikipia, Kenya.

Study site and methods

Study site

The study was carried out at the Mpala Research Centre in north-central Kenya. The study site is 1800 m above sea level, at 0°17.36'N, 36°51.59'E. Annual rainfall averages 500–550 mm, with high interannual variation. Mean monthly maximum temperatures range from 25 to 33°C and minimum temperatures from 12 to 17°C (Young *et al.*, 1998).

The experimental site is underlain by heavy clay 'black cotton soil' (vertisols) (Ahn & Geiger, 1987). Overstorey vegetation was dominated by *A. drepanolobium*, which accounted for 88–97% of the woody species density (Young *et al.*, 1998). The most common subordinate woody species was *Cadaba farinosa* Forssk., and other shrubs include *Lycium europaeum* L., *Rhus natalensis* Krauss, and *Grewia* spp. The grasses *Pennisetum mezianum*

Leeke, *P. stramineum* Peter, *Themeda triandra* Forssk., *Lintonia nutans* Stapf., and *Bracharia lachnantha* (Hochst.) Stapf. dominated the herb layer (Young *et al.*, 1998) and occurred at densities great enough to sustain a fire.

The area is a working cattle ranch, stocked at a rate of approximately one standard livestock unit (STU) per 5–7 ha. A wide variety of wildlife occurs in the area, the most abundant of which are Burchell's zebras (*Equus burchelli* Gray), hartebeests (*Alcelaphus buselaphus* Pallas), oryx (*Oryx gazella beisa* L.), elands (*Tragelaphus oryx* Pallas), Grant's gazelles (*Gazella granti* Brooke), steinbucks (*Raphicerus campestris* Thunberg), elephants (*Loxodonta africana* Blumenbach) and giraffes (*Giraffa camelopardalis* L.). The latter five are all browsers on *A. drepanolobium*, but only elephants knock down and kill entire trees. Prior to 1998, elephants were uncommon in the black cotton ecosystem, but since then they have increasingly used the area (I. Douglas-Hamilton and N. Georgiadis, unpubl. data).

Burn and data collection

A 4.7-hectare plot bounded on two sides by graded tracks was chosen that had vegetation representative of the surrounding area. A 3-m wide firebreak was graded around the remaining sides. The plot was c. 500-m long along its north–south axis, and 70–140 m wide. Overstorey species composition and density were estimated along ten belt transects of 5 × 50 m each. In each transect, all trees and shrubs were identified and their heights measured to the nearest 0.05 m. One-hundred *A. drepanolobium* trees in four height classes (0–0.8, 0.81–1.5, 1.51–3.0 and >3.0 m) were haphazardly selected throughout the study area and tagged with numbered aluminium tags. However, some of the tags were lost after the burn, either from total combustion of the aboveground canopies of smaller trees or to monkeys.

Tempilstik[®] crayons were used to monitor fire temperatures (Wally, Menges & Weekley, 2006). These crayons melt and change their colour when designated temperatures are reached. Seven Tempilstik[®] temperature markers (66, 101, 124, 149, 204, 302 and 500°C) were painted on asbestos slabs of 20 × 15 cm. The asbestos slabs marked with Tempilstik crayons were placed along the long axis of the plot at ten stations, 50 m apart, at each of four height levels (on the ground, 0.5, 1.5 and 3.0 m). Asbestos slabs monitoring vertical temperature profiles were nailed on *A. drepanolobium* trees at each station. Air temperature and humidity were monitored with a thermohygraph

placed 100 m from the burn plot. Wind speed was monitored using an anemometer mounted on a vehicle by the firebreak and recorded every 10 min. The speed and height of the head fire were visually estimated at the same ten stations. Before burning, 30 quadrats (0.25 m²) of herbaceous material were clipped to determine the fuel load. The clipped material was weighed wet, oven-dried at 70°C for 24 h and reweighed.

At ten positions within the experimental plot, we marked out four contiguous 1 × 1 m plots. On two of these, 100 *A. drepanolobium* seeds were placed on the surface and their positions on the ground marked with coloured pins. In the other two quadrats, an equal number of *A. drepanolobium* seeds were planted just below the soil surface (±2 cm deep) and their positions similarly marked with coloured pins. After the fire, one set of seeds from each quadrat was recovered and taken for germination in a screen house on trays lined with filter paper, while the other set was left to germinate in the field. In total, 40 sets of 100 seeds were used.

The fire was lit on 24 March 1998 at 12.24 hours, and the plot had burned by 1.34 hours. We initially back-burned for 20 m from the south-western corner to guard against the danger of fire jumping over the road/fire break. A head fire was then started from the northern (windward) side. After the fire, the maximum temperatures reached at each station were recorded by observing the melting and colour change of the Tempilstik[®] crayons on the asbestos slabs.

We carried out initial follow-up surveys in March and December 1998. In March, using tagged trees and those from the belt transects, we recorded the numbers of trees and shrubs and scored them for burn damage. We visually estimated tree damage as follows: 1 = 100% top-killed; 2 = 50–75% burned; 3 = 25–50% burned; 4 = <25% burned; and 5 = no damage noticed. We also recorded the height at which the flame visibly burned the tree (this was shown by the change in colour of leaves). In both March and December, we counted the numbers of *A. drepanolobium* trees to determine density.

Follow-up data collection

We acquired from Digital Globe (Fort Collins, CO, U.S.A.) a June 2003 satellite image of the site (51 months after the burn) from the Quickbird satellite. The image was taken the day before the solstice, close to the sun's zenith and

only 30 km north of the equator. These image characteristics provided us with ideal conditions to map woody species with little interference from shadows. Using the panchromatic band (0.6-m spatial resolution), we ran an unsupervised classification using ERDAS Imagine 8.6. This classification module uses Imagine's ISODATA algorithm to group pixels with similar spectral reflectance on the basis of minimum spectral distance formula (Leica Geosystems, 2002). We assigned the pixel groups to one of two classes, woody canopy or nonwoody canopy, on the basis of visual patterns and our knowledge of the field conditions.

These classes were ground-truthed in February 2006 by visiting 34 sites ranging in tree cover from 5% to 50%. At each site, we established a 50 × 50 m plot and counted all the *A. drepanolobium* trees in the plot in each of four size classes (<1, 1–2, 2–3 and >3 m). We then correlated satellite cover values with the total number of *A. drepanolobium* trees >1-m tall, >2-m tall and of all heights. As canopy cover correlated best with total trees, we present only this result.

In February 2006, nearly 8 years after the burn, we resurveyed the site of the old burn as well as the unburned areas adjacent to it. In both areas, we randomly placed four 100 × 10 m transects and recorded every woody plant, as well as height for individuals of *A. drepanolobium*.

Results

Fuel load and fire temperatures

Prefire fuel load within the burned plot was 8.7 ± 0.5 (SE) tonnes ha⁻¹ of dry matter (11.8 ± 0.8 tonnes ha⁻¹ wet weight). The fire took about 70 min to burn the 5-hectare plot. Wind direction was northeasterly and wind-speed ranged from 2 to 12 km h⁻¹, (mean 7.5 ± 1.3 km h⁻¹). Air temperature during the burning was 23°C, and the humidity was 33%.

During the burn, maximum fire temperatures of more than 500°C were recorded at ground level. Temperatures were the highest at the ground level (mean maximum 255°C), and declined with height above the ground (Fig. 1). The fire was not uniform over the burn plot (Fig. 1). The flame height of the head fire also varied across the plot, ranging from 1.0 to 4.0 m. In places within the burn plot, fire smoldered for hours after the flames died out and some spots of unburned grasses remained, especially around *L. europaeum* and *C. farinosa* shrubs.

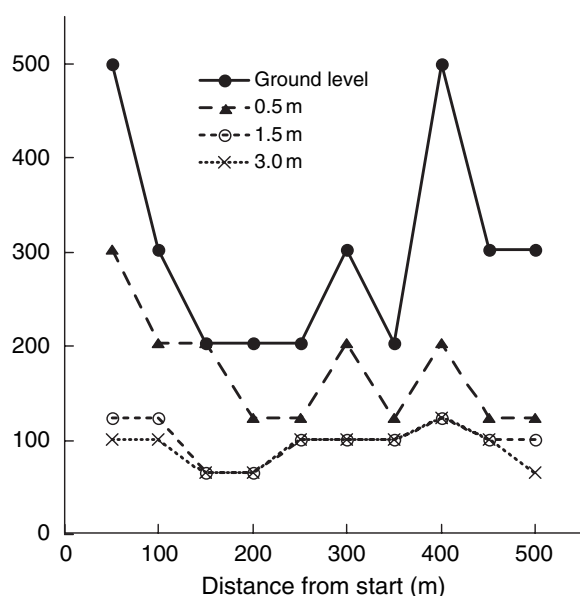


Fig 1 Fire temperature profile across the burn (from north to south). The temperatures represent the critical melting temperature of the highest temperature Templestick crayon that had a positive reading at each site

Short-term effects on the woody layer

Pre- and postfire estimated densities of *A. drepanolobium* trees were 808 and 804 per ha respectively (Table 1). Nine months after the fire, the density of *A. drepanolobium* remained virtually unchanged (808 per ha). However, many *C. farinosa*, *R. natalensis*, *Grewia* spp., and *L. europaeum* individuals died after the fire (Table 1). We did not find any postfire recruitment of new individuals.

Taller *A. drepanolobium* trees suffered less fire damage than shorter trees (Table 2, $\chi^2 = 40.3$, $P < 0.001$). Nine months after the fire, all the top-killed trees were alive and

Table 1 Overstorey species density (per ha) before and after a prescribed fire in an *Acacia drepanolobium* wooded grassland

| Species | Prefire (Mar 1998) | Postfire (Mar 1998) | Postfire (Dec 1998) |
|-----------------------------|-----------------------|------------------------|------------------------|
| <i>Acacia drepanolobium</i> | 808 | 804 | 808 |
| <i>Rhus natalensis</i> | 40 | 32 | 20 |
| <i>Cadaba farinosa</i> | 24 | 20 | 8 |
| <i>Lyceum europaeum</i> | 24 | 8 | 0 |
| <i>Grewia</i> sp. | 8 | 6 | 5 |

Table 2 Fire damage on *Acacia drepanolobium* trees in different size classes expressed on per cent basis

| Height class (m) | Fire damage class | | | | |
|------------------|-------------------|------|------|------|------|
| | 1 | 2 | 3 | 4 | 5 |
| <0.8 | 16.7 | 50.0 | 27.8 | 5.6 | 0.0 |
| 0.8–1.5 | 8.0 | 28.0 | 52.0 | 12.0 | 0.0 |
| 1.51–3.0 | 5.4 | 16.2 | 64.3 | 14.3 | 0.0 |
| >3.0 | 0.0 | 5.5 | 43.6 | 40.0 | 10.9 |

1 = top-killed, 2 = 50–75% burnt, 3 = 25–50% burnt, 4 = <25% burnt, 5 = no damage noticed.

at various stages of coppicing. Trees >3.0 m did not coppice, perhaps because of the lower fire damage index in this class. No other woody species showed signs of coppicing.

Germination of *A. drepanolobium* seeds

More of the buried seeds were recovered than surface seeds (Table 3). Among those seeds recovered, germination was greater for seeds that had been buried beneath the soil surface in both the laboratory (37.2%) and the field (40.1%), compared with those on the surface (2.0% and 3.3% respectively; Table 3).

Table 3 Recovery rates after the burn, and germination rates of seeds placed either on the surface or ± 2 cm below the surface ('buried'), and germinated either *in situ* in the field, or in the laboratory (± 1 SE)

| | Seeds recovered (out of 100) | % Germination of recovered seeds | Seeds recovered and germinated |
|------------------------------------|------------------------------------|--|--------------------------------------|
| Surface | | | |
| Field | 16.9 \pm 1.6 | 3.3 \pm 1.8 | 0.4 \pm 0.2 |
| Screen house | 16.6 \pm 1.7 | 2.0 \pm 0.8 | 0.3 \pm 0.1 |
| Buried | | | |
| Field | 33.9 \pm 2.5 | 40.0 \pm 4.7 | 13.0 \pm 1.5 |
| Screen house | 37.7 \pm 2.6 | 37.2 \pm 2.8 | 13.8 \pm 1.3 |
| P-value (surface versus buried) | <0.001 | <0.001 | <0.001 |

All seeds were subjected to fire only in the field setting, but the recovery rates for the replicates destined for screen house germination trials are reported separately. Sample sizes were ten groups of 100 seeds per treatment. The fates of surface and buried seeds were compared with ANOVA.

Long-term effects on the woody layer

Analysis of the June 2003 satellite imagery revealed that the area of the burn had 38% less cover by darker pixels than the surrounding areas. These 2003 cover values were strongly correlated with total tree densities in 2006 ($r^2 = 0.80$, $P < 0.001$) across our 34 sampled plots. Using the fitted regression equation between the 2003 cover values and the 2006 tree density values suggested a 53% reduction in tree cover in the burn plots compared with the surrounding unburned areas.

The February 2006 ground survey (Fig. 2) revealed that there were 64% fewer adult *A. drepanolobium* trees (height ≥ 1.5 m) in the burned area than in the adjacent unburned areas ($F = 13.24$, $P = 0.01$), but only 27% fewer saplings ($F = 1.11$, $P = 0.33$). The density of *A. drepanolobium* trees of all sizes decreased from the original 808 per ha in 1998 (in the preburn) to 587 per ha (in the unburned area) and 330 per ha (in the burned area). Seven other woody species were found in the surveys, but six of these were too uncommon (<1.0 per transect) for analysis. However, the more common species *C. farinosa* was 64% less abundant in the burned plots than in the unburned plots ($F = 17.44$, $P = 0.006$).

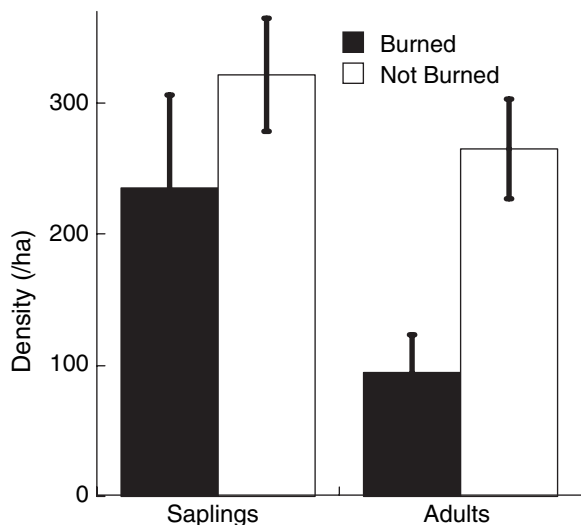


Fig. 2 Two-thousand and six densities of saplings (<1.5 -m tall) and adults (≥ 1.5 -m tall) of *Acacia drepanolobium* trees in the 1998 burn site, and adjacent unburnt areas. The values are the means of four transects, and the bars are ± 1 SE

Discussion

The temperature profile shows how fire temperatures vary across the landscape (Fig. 1). This is probably because of the patchy distribution of fuel load. The spatial distribution of dry grass, which was the primary source of fuel, was not homogeneous across the burned plot. Especially around thickets of *C. farinosa* and *L. europaeum*, the grass was still fresh and green. The result of these variations in fire intensity was uneven burns in the range with some shrubs and grasses left unburned.

Most of the *A. drepanolobium* trees <2 -m tall had burnt canopies (Table 2) while most of the larger *A. drepanolobium* tree canopies escaped the fire. This may be because the average fire height (1.5 m) was lower than the base of most canopies and because fire temperatures decreased with height (Fig. 1). Most trees that showed severe burn effects were <1.5 m in height, where the average temperatures were 250°C .

We found no evidence of short-term fire-related mortality of *A. drepanolobium* trees, and even those trees that showed a high degree of fire damage soon coppiced. Although temperatures of over 500°C were attained at the ground level, even the smallest *A. drepanolobium* coppiced after being top-killed. This result suggests that *A. drepanolobium* is adapted to fire (Higgins *et al.*, 2000; Bond & Midgley, 2001).

Acacia drepanolobium seeds that were recovered from below the soil surface germinated at ten times the rate of those recovered from the surface. We previously showed that *A. drepanolobium* seeds exposed to fire do not germinate (Okello & Young, 2000). The high germination rate of buried seeds versus low rates at the surface indicates that lethal temperatures for germination were not reached below the soil surface, but may well have been exceeded at the surface (c.f. Tozer & Auld, 2006). Most of the surface seeds were charred beyond recognition, and recovery rate was low (34%). In contrast, about 70% of buried seeds were recovered. The 30% loss suggests that another agent, possibly rodents, removed them (c.f., Miller, 1994; Walters *et al.*, 2005). Our results suggest that fire may not only reduce densities of living trees, but also reduce their ability to recruit via seeds after a fire. However, the effects of fire on seeds are probably species-specific and related to the duration of fire exposure (Sabiiti & Wein, 1987; Mucunguzi & Oryemoriga, 1996; Radford, Nicholas & Brown, 2001).

In stark contrast to the high survival of *A. drepanolobium* trees in the months after the fire, there was a

dramatic long-term reduction in larger *A. drepanolobium* trees (Fig. 2). It is striking that this effect was mainly concentrated on the larger size classes, which had experienced the least apparent fire damage (see also Meyer *et al.*, 2005). One possible explanation for this delayed mortality is that large mammalian herbivores prefer to visit burnt areas or to feed upon individual trees that have experienced a burn, perhaps either because of higher quality grass forage or because of increased visibility (Ryan Sensenig, pers. comm.). In our study area, there is evidence that herbivore preferences for burned areas persist for at least 2 years after a fire (Zavala & Holdo, 2005). The study area has experienced a steady increase in the presence of elephants over the last 10 years (I. Douglas-Hamilton and N. Georgiadis, unpubl. data) that parallels a 4–5% annual increase in the adjacent Samburu ecosystem (Wittemyer *et al.*, 2005). This may explain why differences between burnt area and unburnt area were initially muted, and only later dramatic (as well as in unexpectedly affecting tall trees more strongly). This may also account for the lower densities of *A. drepanolobium* trees in 2006 compared to 1998, even in the control areas (see also Birkett & Stevens-Wood, 2005; Goheen *et al.*, 2007; Pringle *et al.*, 2007). In other words, elephants (and their effects) have been increasing locally, and their effects may have been particularly concentrated in previously burnt areas.

Repeated burning can have profound impacts on savanna structure (Bond & Archibald, 2003; Nangendo *et al.*, 2005; Govender *et al.*, 2006). Our results show the potential of even a single fire to reverse woody encroachment in this ecosystem, at least when large herbivores are present. In addition to the mortality of adult *A. drepanolobium*, the fact that few surface seeds of *A. drepanolobium* germinated also suggests that fire may also reduce recruitment, although even shallow burial appears to provides considerable protection from fire in this fire-adapted species. In the past, mechanical and chemical control of *A. drepanolobium* had mixed results and are both labour-intensive and expensive (Pratt & Gwynne, 1977). Harvesting for fuelwood and charcoal offers a source of alternative income, but can clear the range of shrubs only in the short term (Okello *et al.*, 2001; Smit, 2004), and may even allow greater recruitment of woody individuals. Fire may offer a useful option to open the woody layer, but perhaps mostly in the presence of large native browsers (see also Mills & Fey, 2005).

Acknowledgements

We especially appreciate the comments of Katrin Meyer, Ryan Sensenig, and Kari Veblen. This research was supported by the University of California at Davis, the Mpala Research Centre and Mpala Farm, the U.S. Fish and Wildlife Service African Elephant Conservation Fund (98210-0-G563), the Smithsonian Institution (James Smithson grant to the late Alan P. Smith); the National Geographic Society (4691-91), NSF grants BSR 97-07477 and 03-16402 (to Young), Leslie Scott and a Citibank Mpala Fellowship (to Okello). Field assistance was provided by F. Erii and D. Kinyua. Special thanks to George Small, Nick Georgiadis, and John and Ken Wreford-Smith. This research was carried out under the auspices of the Ministry of Education, Science, and Technology of the Republic of Kenya (MOEST 13/001/34 17).

References

- AHN, P.M. & GEIGER, L.C. (1987) *Soils of Laikipia District*. Kenya Soil Survey, National Agricultural Laboratories, Kabete, Kenya.
- BIRKETT, A. & STEVENS-WOOD, B. (2005) Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. *Afr. J. Ecol.* **43**, 123–130.
- BOND, W.J. & ARCHIBALD, S. (2003) Confronting complexity: fire policy choices in South African savanna parks. *Int. J. Wildland Fire* **12**, 381–389.
- BOND, W.J. & MIDGLEY, J.J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* **16**, 45–51.
- DALL, G., MAASS, B.L. & ISSELSTEIN, J. (2006) Encroachment of woody plants and its impact on pastoral livestock production in the Borana lowlands, southern Oromia, Ethiopia. *Afr. J. Ecol.* **44**, 237–246.
- GOHEEN, J.R., YOUNG, T.P., KEESING, F. & PALMER, T.M. (2007) Consequences of herbivory by native ungulates for reproduction of a savanna tree. *J. Ecol.* **95**, 129–138.
- GOVENDER, N., TROLLOPE, W.S.W. & VAN WILGEN, B.W. (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *J. Appl. Ecol.* **43**, 748–758.
- HEADY, H.F. (1960) *Range Management in East Africa*. Government Printer, Nairobi.
- HIGGINS, S.L., BOND, W.J. & TROLLOPE, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *J. Ecol.* **88**, 213–229.
- LEICA GEOSYSTEMS (2002) *ERDAS Imagine 8.6*. Leica Geosystems GIS & Mapping, LLC Atlanta, GA, U.S.A.
- MEYER, K.M., WARD, D., MOUSTAKAS, A. & WIEGAND, K. (2005) Big is not better: small *Acacia mellifera* shrubs are more vital after fire. *Afr. J. Ecol.* **43**, 131–136.

- MILLER, M.F. (1994) The fate of mature African *Acacia* pods and seeds during their passage from the tree to the soil. *J. Trop. Ecol.* **10**, 183–196.
- MILLS, A.J. & FEY, M.V. (2005) Interactive response of herbivores, soils and vegetation to annual burning in a South African savanna. *Austral Ecol.* **30**, 435–444.
- MUCUNGUZI, P. & ORYEMORIGA, H. (1996) Effects of heat and fire on the germination of *Acacia sieberiana* DC and *Acacia gerrardii* Benth in Uganda. *J. Trop. Ecol.* **12**, 1–10.
- NANGENDO, G., STEIN, A., TER STEEGE, H. & BONGERS, F. (2005) Changes in woody plant composition of three vegetation types exposed to a similar fire regime for over 46 years. *For. Ecol. Manage.* **217**, 351–364.
- O'CONNOR, T.G. (1985) A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa. In: *South African National Scientific Programmes Report No 114*. Foundation for Research Development, CSIR, Pretoria.
- OKELLO, B.D. & YOUNG, T.P. (2000) Effects of fire, bruchid beetles and soil type on the germination and seedling establishment of *Acacia drepanolobium*. *Afr. J. Range Forage Sci.* **17**, 46–51.
- OKELLO, B.D., O'CONNOR, T.G. & YOUNG, T.P. (2001) Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. *For. Ecol. Manage.* **142**, 143–153.
- PRATT, D.J. & GWYNNE, M.D. (1977) *Rangeland Management and Ecology in East Africa*. Hodder & Stoughton, London.
- PRINGLE, R.M., YOUNG, T.P., RUBENSTEIN, D.I. & MCCAULEY, D.J. (2007) Primary productivity and the strength of herbivore-initiated interaction cascades. *Proc. Natl Acad. Sci. U. S. A.* **104**, 193–197.
- RADFORD, I.J., NICHOLAS, D.M. & BROWN, J.R. (2001) Impact of prescribed burning on *Acacia nilotica* seed banks and seedlings in the *Astrebla* grasslands of northern Australia. *J. Arid Environ.* **49**, 795–807.
- ROQUES, K. G., O'CONNOR, T.G. & WATKINSON, A.R.R. (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.* **38**, 268–280.
- SABIITI, E.N. & WEIN, R.W. (1987) Fire and acacia seeds: a hypothesis of colonization success. *J. Ecol.* **75**, 937–946.
- SABIITI, E.N., WEIN, R.W. & EDROMA, E.L. (1991) Fire and browsing effects on the biology of East African *Acacia* species: a review. In: *African Wildlife: Research and Management* (Eds F. I. B. KAYANJA and E. L. EDROMA). International Council of Scientific Unions, Paris.
- SMIT, G.N. (2004) An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *J. Environ. Manage.* **71**, 179–191.
- TOZER, M.G. & AULD, T.D. (2006) Soil heating and germination: investigations using leaf scorch on graminoids and experimental seed burial. *Int. J. Wildland Fire* **15**, 509–516.
- WALLY, A.L., MENGES, E.S. & WEEKLEY, C.W. (2006) Comparison of three devices for estimating fire temperatures in ecological studies. *Appl. Veg. Sci.* **9**, 97–108.
- WALTERS, M., MILTON, S.J., SOMERS, M.J. & MIDGLEY, J.J. (2005) Post-dispersal fate of *Acacia* seeds in an African savanna. *S. Afr. J. Wildl. Res.* **35**, 191–199.
- WEIN, R.W. & EDROMA, E.L. (1986) *Fire in Tropical Savannas with Emphasis on East Africa: A Bibliography*. International Development Research Centre Canada, Ottawa, ON.
- WHELAN, R.J. (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge, U.K.
- WITTEMYER, G., DABELLEN, D., RASMUSSEN, H., KAHINDI, O. & DOUGLAS-HAMILTON, I. (2005) Demographic status of elephants in the Samburu and Buffalo Springs National Reserves, Kenya. *Afr. J. Ecol.* **43**, 44–47.
- YOUNG, T.P., OKELLO, B., KINYUA, D. & PALMER, T.P. (1998) KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *Afr. J. Range Forage Sci.* **14**, 94–102.
- ZAVALA, M.A. & HOLDO, R.M. (2005) Delayed effects of fire on habitat use by large herbivores in *Acacia drepanolobium* savanna. *Afr. J. Ecol.* **43**, 155–157.

(Manuscript accepted 24 September 2007)

doi: 10.1111/j.1365-2028.2007.00872.x