Establishment of Broad-leaved Thickets in Serengeti, Tanzania: The Influence of Fire, Browsers, Grass Competition, and Elephants

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ABSTRACT

The role of Euclea divinorum in the establishment of broad-leaved thickets was investigated in Serengeti National Park, Tanzania. Thickets are declining due to frequent fires, but have not reestablished when fires have been removed. Seedlings of E. divinorum, a fire-resistant tree, were found in grassland adjacent to thickets and as thicket canopy trees and may function to facilitate thicket establishment. Seedlings of thicket species were abundant under E. divinorum canopy trees but not in the grassland, indicating that E. divinorum can facilitate forest establishment. We examined E. divinorum establishment in grassland by measuring survival and growth of seedlings with respect to fire, browsers, elephants, and competition with grass. Seedling survival was reduced by fire (50%), browsers (70%), and competition with grass (50%), but not by elephants. Seedling growth rate was negative unless both fire and browsers, or grass was removed. Establishment of thickets via E. divinorum is not occurring under the current conditions in Serengeti of frequent fires, abundant browsers, and dense grass in riparian areas. Conditions that allowed establishment may have occurred in 1890–1920s during a rinderpest epizootic, and measurements of thicket canopy trees suggest they established at that time.

Key words: browsing; Croton dichogamus; elephant; Euclea divinorum; fire; recruitment; savanna; Tanzania; thicket.

SAVANNA ECOSYSTEMS ARE GENERALLY COMPOSED OF A combination of open grasslands, woodlands of dispersed trees, and closed thickets of broad-leaved shrubs and trees. Thickets occur particularly in riparian and hilltop areas and are composed of dense patches of shrubs, interspersed with taller emergent trees. In Africa, thickets are important for fauna such as birds, small browsers, and larger animals such as rhinoceros (Ceratotherium simum and Diceros bicornis), particularly in dry areas where they represent the only closed-canopy habitat (Medley & Hughes 1996). Despite their widespread distribution and importance for wildlife, the dynamics of thickets are not entirely understood, particularly the processes that lead to their establishment.

Typically, the establishment of woodlands and Acacia thickets are controlled by fire, including thickets composed of common species such as Dichrostachys cinerea (L., Wight & Arn.) (Toibler et al. 2003), Acacia tortilis (Forsk., Hayne), Grewia flava (DC.), and Terminalia sericea (Burch., Ex. DC.) which establish when fire is removed (Moleele et al. 2002). This process is often facilitated by grazing, which removes grass biomass, reducing fire intensity, and increasing shrub establishment. In Serengeti, Acacia woodlands underwent a dramatic pulse of establishment when fires were reduced during the late 1970s and early 1980s after an increase in wildebeest (Connochaetes taurinus) numbers in the 1960s and 1970s (Dublin 1995).

The most common broad-leaved (non-Acacia) thicket type in East Africa is the Croton thicket (Dale & Greenway 1961), composed of the fire-tolerant shrubs Croton dichogamus (Pax.) and Teclea trichocarpa (Engl.) and an additional 8–12 species of emergent trees (Sharam 2005). Croton thickets compose most of the closed-canopy hilltop thickets and riparian forests in Serengeti National Park, Tanzania and have declined 78–80 percent since the 1950s due to frequent fires (Norton-Griffiths 1979, Dublin 1986) but have not reestablished when fire was reduced during the 1970s–1980s, or suppressed by fire-breaks (G. Sharam, pers obs.).

Grassland savannas are high disturbance systems, of which fire is the only one component. Acacia establishment in grassland is also reduced by browsers (Prins & van der Jeugd 1993) and elephant (Loxodonta africana) disturbance (Dublin 1995). Antelope reduces Acacia growth and survival in Manyara National Park (NP; Prins & van der Jeugd 1993), Serengeti NP, Tanzania (Belsky 1984), and Chobe NP, Botswana (Barnes 2001). Elephants at high densities in Masai Mara Game Reserve consumed sufficient Acacia seedlings to limit woodland regeneration (Dublin 1995). Forest tree establishment is also limited by fire and by competition with grass (Chapman et al. 1999). Grass competes with tree seedlings for water, light, and nutrients (Hoffmann et al. 2004). High buffalo numbers in Serengeti may have removed grass competitors and facilitated thicket establishment historically (Sinclair 1977). Understanding the role of these factors in the establishment of Croton thickets in grasslands is essential for future conservation.

When tropical forests and thickets establish in grassland, they can follow one of two patterns. First, many Acacia woodlands and thickets establish in a pulse when several species recruit simultaneously when conditions allow, as occurred in Serengeti (Packer et al. 2005). Second, species composition can follow a successional pattern. In South African Transvaal, thickets of Acacia senegal (L., Willd.) were succeeded by broad-leaved thickets of Euclea divinorum (Hiern) (Ben-Shahar 1991). In Serengeti, stands of Acacia polyacantha (Willd.) facilitated the establishment of whole...
communities of riparian forest trees (Sharam 2005), also reported in West Africa (Favier et al. 2004) and India (Puyravaud et al. 2003).

We examined the pattern and process of broad-leaved thicket establishment in grassland. We tested the alternative hypotheses that either thicket species simultaneously establish into grassland or a pioneer species establishes and facilitates forest succession. These hypotheses predicted that either all tree seedlings (trees <30 cm) will be found in similar abundance in the grassland, or a single species of seedlings will be found in grassland areas and this species will facilitate the establishment of other tree species. We also predicted that pioneer species will be limited by: (a) competition from grass; (b) fire; and (c) browsing by herbivores (antelope and elephant) or some combination of these.

METHODS

STUDY SITE.—The Serengeti Ecosystem is a mosaic of open grasslands and woodlands covering 25,000 km² of northwestern Tanzania and southwestern Kenya (Fig. 1). Croton thickets and forests occur within Serengeti in the tributary valleys of the Mara River and on hillsops south of the Mara River.

Serengeti has a semiarid climate with mean maximum temperatures of 27–28 °C in Seronera (Fig. 1). Minimum temperatures vary from 16 °C in the wet season (November–April), to 13 °C in the dry season (May–September). Rainfall occurs bimodally with “short rains” occurring in November–December and the “long rains” in February–April. Rainfall follows an altitudinal gradient across the park, with the highest altitude and annual rains in the north of the park near the Mara River (1950 m, 1200 mm/year) and lowest in the south (1800 m, 500 mm/year; Sinclair 1995b).

The most common herbivore in the ecosystem is the wildebeest with a population of approximately 1.4 million (Mduma et al. 1999). Other grazers in Serengeti include zebra (Equus burchelli) (200,000) and Thomson’s gazelles (Gazella thomsonii) (440,000; Sinclair 1995b). Where this study was carried out in northern Serengeti (2715 km²) elephants are common (3270 ± 1380), as are impala (Aepyceros melampus; 11,250 ± 2500; Anonymous 2003) and smaller numbers of bushbuck (Tragelaphus scriptus), redbuck (Redunca arundinum), and dikdik (Madoqua kirkii).

Fires in Serengeti are common. Many are lit by park rangers and managers who attempt “early burns” at the beginning of each dry season to prevent or reduce the severity of larger scale fires lit by poachers or cattle thieves later in the dry season. Many riparian areas burn every 2–4 yr; however, some burn every year due to poaching and close proximity to roads (G. Sharam, pers obs.).

CROTON THICKETS AND RIPARIAN FORESTS.—Hilltop thickets cover areas from 1–5 ha on hilltops south of the Mara River in northern Serengeti. They consist of a dense matrix of 2–3 m C. dichogamus and T. trichocarpa shrubs with interspersed emergent (6–15 m) E. divinorum trees and smaller numbers of Diospyros abyssinica (Hiern) F. White (Maba abyssinica (Hiern)) and Olea africana Mill. (Olea europaea L., Olea chrysophylla Lam.). Riparian forests have a similar structure and extend 50–100 m from and 100–500 m along Mara river tributaries. The core of riparian thickets sits adjacent to the river and contains a dense area of closed-canopy forest with increased species richness, including the canopy trees D. abyssinica, Drypetes gerrardii Hutch. [Drypetes battiscombei Hutch.], Ekebergia capensis Sparrm. [Ekebergia meyeri Presl ex C. DC.], O. africana and Ficus spp., with an understory of C. dichogamus, T. trichocarpa and Strychnos spp. All species studied are bird-dispersed (Beentje 1994).

STUDY SPECIES.—Euclca divinorum, Hiern subsp. keniensis (R. E. Fries) de Wit, is common in thorn scrub in riparian areas and on termite mounds in south and south east Africa (Coates Palgrave 1983) and in rocky areas and hilltops in Kenya and Tanzania (Dale & Greenway 1961). Euclca divinorum occurs in both Mara hilltop and riparian thickets and as seedlings and stunted rootstocks in the adjacent grassland. This species has two features characteristic of pioneer species: it is fire resistant by way of its thick bark and reproduces via root-coppicing following fires (Beentje 1994). This species is defended against herbivory with a variety of emetic compounds (Mebe et al. 1998).

SEEDLING ABUNDANCE IN GRASSLAND AND THICKETS.—All observations and experiments were conducted in six hilltop thickets and six riparian forests, termed focal study patches. We surveyed grassland areas for seedlings of thicket trees by searching 12 0.25 ha plots adjacent to both hilltop and riparian focal patches. Seedlings were surveyed inside thickets and forests along a 50 × 150 m belt.
transect extending from the forest edge to center. When seedlings were found, we recorded the seedling species and the distance to and identity of the nearest canopy tree.

GRASS REMOVAL AROUND SEEDLINGS.—Forty *E. divinorum* seedlings (0.05–0.75 m) were chosen in grassland sites adjacent to each of the six focal riparian forests. In March 2000 each seedling was tagged, flagged, measured for height, and a statement of its initial condition (clipped by browsers, attacked by insects, etc.) was recorded. We removed the grass from around half of the seedlings at each focal thicket to a distance of 1.5 m using a C-4 herbicide (Ornamec, Phi/Gordon Corp, Kansas City, Missouri, U.S.A.) applied at a concentration of 7.5 ml Ornamec/liter water and rate of approximately 15 ml/m², until grass was coated but there was no runoff. The seedlings were protected during spraying with a plastic shield. Seedling survival, height, and condition were monitored every 2 mo for 2 yr.

EXPERIMENTS WITH HERBIVORES AND FIRE.—An additional 150 *E. divinorum* seedlings were tagged in grassland adjacent to the 12 focal patches in May 2000. Due to the low density of seedlings and high animal traffic, we built small thorn fences (approximately 1 m per side) around and above 75 individual seedlings in each focal site to protect them from browsers. We used branches of *D. cinerea* (L.) Wigt & Arn. that were arranged upside down into a dense fence, effective at excluding all small browsing antelope (i.e., impala, bushbuck, reedbuck, and dikdik). Fences allowed more light to reach seedlings than grass neighbors and did not appreciably alter site conditions beyond excluding browsers (Sharam 2005). At each focal patch, grassland areas were divided into two 200 × 200 m areas using fire-breaks burned in early May; each containing an equal number of control and herbivore exclusion *E. divinorum* seedlings. One of these paired areas at each site was then burned during the middle of dry season (June 2000 and 2001) producing an intense grassland fire, similar to natural fires in rate of spread, fraction of grass removed, and effect on standing dead wood. Seedlings were monitored before and after fires for survival, height, and browsing every 2 mo for 2 yr.

To study the effects of elephants, we could not exclude elephants from areas, so instead we monitored natural elephant damage to tagged *E. divinorum* seedlings. Elephant damage is very characteristic to seedlings (tearing marks and uprooting) and we marked seedling locations with wires and flagging tape to ensure resighting and an accurate measure of elephant damage. We also monitored seedlings for clip-marks on the stem apices indicative of antelope browsing.

PULSE ESTABLISHMENT MEASUREMENTS.—Trees we studied in the riparian sites did not display growth rings, so we estimated age from diameter at breast height (DBH). We measured the DBH of 200 canopy trees in each of the six hilltops and riparian focal patches: *E. divinorum* and *D. abyssinica* in hilltop thickets and *E. divinorum*, *D. abyssinica*, *D. gerrardii*, and *E. capensis* in riparian forests. *Euclea divinorum* trees are often composed of multiple trunks, so an average value per tree was used instead of a single measurement.

**STATISTICAL ANALYSES.**—Seedling densities were compared using Analysis of Variance (ANOVA) with forest type (hilltop–riparian), habitat (grassland–forest), and species as variables. Seedling distribution inside forests was compared using the variables of canopy species (*E. divinorum* vs. “other”) and distance from the forest center with the data split into species occurring in thickets and hilltops. Experiments with fire, grass, and browsers were analyzed using focal forests as blocks and individual seedlings at each forest as replicates. The effect of grass removal on seedling survival was tested using Kaplan–Meier survival curves and the log-rank results were reported (Zar 1974). The effect of grass on growth rate was tested using ANOVA. The effects of fire and browsers on *E. divinorum* seedling survival were tested using Cox regressions on Kaplan–Meier survival curves and the log-rank results were reported. The effects of fire and browsers on seedling growth rate were tested using a 2-factor ANOVA. The interactions between fire and browsers on seedling survival and growth rate were assessed using Likelihood-ratio tests. Seedling growth rates before and after fires were compared using ANOVA. Canopy tree DBH measures were compared between species and forest type using ANOVA and Tukey’s tests.

**RESULTS**

**PATTERN OF SEEDLING ABUNDANCE.**—Seedlings of *E. divinorum* were found in grassland areas at a low density of 14.1 ± 4.3/ha (±SD), while other species were not. Within thickets and forests, we found seedlings of all 12 canopy tree species. Seedlings were more abundant in riparian forests than hilltop thickets (*P* = 0.03, ANOVA) and seedling density was higher inside hilltop thickets than *E. divinorum* seedling density in the grassland (*P* = 0.001, ANOVA) (Table 1).

Of the seedlings found inside thickets and forests, five species occurred under *E. divinorum* canopy trees. These species included a high density of two shrub species (*C. dichogamus* and *T. trichocarpa*)

**TABLE 1.** Seedling density/ha (±SD) of canopy tree species in grassland, hilltop thickets, and riparian forests in northern Serengeti. Seedlings were surveyed in grassland in 50 × 50 m plots. Thicket and forest estimates were made along a 50 × 150 m belt transect in each of six hilltop thickets and six riparian forests.

<table>
<thead>
<tr>
<th>Species</th>
<th>Grasslands</th>
<th>Hilltop thickets</th>
<th>Riparian forests</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Euclea divinorum</em></td>
<td>14.1 ± 4.3</td>
<td>56 ± 23</td>
<td>126 ± 75</td>
</tr>
<tr>
<td><em>Croton dichogamus</em></td>
<td>0.0 ± 0</td>
<td>29 ± 11</td>
<td>31 ± 20</td>
</tr>
<tr>
<td><em>Tecla trichocarpa</em></td>
<td>0.0 ± 0</td>
<td>44 ± 21</td>
<td>68 ± 31</td>
</tr>
<tr>
<td><em>Diospyros abyssinica</em></td>
<td>0.0 ± 0</td>
<td>16 ± 8</td>
<td>112 ± 59</td>
</tr>
<tr>
<td><em>Drypetes gerrardii</em></td>
<td>0.0 ± 0</td>
<td>18 ± 12</td>
<td>49 ± 38</td>
</tr>
<tr>
<td><em>Ekebergia capensis</em></td>
<td>0.0 ± 0</td>
<td>48 ± 37</td>
<td>45 ± 41</td>
</tr>
<tr>
<td><em>Ficus spp.</em></td>
<td>0.0 ± 0</td>
<td>3 ± 2.5</td>
<td>12 ± 7</td>
</tr>
<tr>
<td><em>Olea africana</em></td>
<td>0.0 ± 0</td>
<td>0.0 ± 0</td>
<td>2.0 ± 0</td>
</tr>
<tr>
<td><em>Strychnus spp.</em></td>
<td>0.0 ± 0</td>
<td>40 ± 23</td>
<td>24 ± 11</td>
</tr>
</tbody>
</table>
and a lower density of three canopy tree species (D. gerrardii, E. buchananii, and D. abyssinica; Table 2). Both shrub species were found at higher densities under *E. divinorum* trees than in the forest in general (*P* = 0.03, ANOVA), while the three tree species were at lower densities under *E. divinorum* than the rest of the forest (*P* = 0.041, ANOVA). Those species not found under *E. divinorum* canopy were found at higher density within 10 m of a stream or river than >10 m (*P* = 0.01, ANOVA) and are thus likely riparian obligate species and unlikely to establish at greater distances from the river.

**GRASS REMOVAL AND *E. DIVINORUM* SEEDLINGS.—** In grassland sites, survival of *E. divinorum* seedlings increased by 100 percent from 0.13 to 0.27/yr when grass was removed (*P* = 0.047, log-rank; Fig. 2). These seedlings were protected from fire, but not from browsers. Growth rate of seedlings was positive when grass was removed (17 ± 11.9 cm/yr) (±SD) and negative when grass was present (−5.2 ± 5.7 cm/yr; *P* = 0.038, ANOVA; Fig. 3). In both cases, forest blocks were not different from each other (*P* = 0.57, log rank) and (*P* = 0.39, ANOVA), respectively.

**TABLE 2.** Seedling density/ha (±SD) under the canopy of *Euclea divinorum* in hilltop thickets and riparian forests in northern Serengeti.

<table>
<thead>
<tr>
<th>Species</th>
<th>Hilltop thickets</th>
<th>Riparian forests</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Euclea divinorum</em></td>
<td>154 ± 42</td>
<td>186 ± 55</td>
</tr>
<tr>
<td><em>Croton dichogamus</em></td>
<td>129 ± 49</td>
<td>164 ± 23</td>
</tr>
<tr>
<td><em>Teclea trichocarpa</em></td>
<td>156 ± 63</td>
<td>138 ± 59</td>
</tr>
<tr>
<td><em>Diospyros abyssinica</em></td>
<td>17 ± 9</td>
<td>58 ± 17</td>
</tr>
<tr>
<td><em>Drypetes gerrardii</em></td>
<td>9 ± 4</td>
<td>32 ± 11</td>
</tr>
<tr>
<td><em>Ekebergia capensis</em></td>
<td>18 ± 11</td>
<td>36 ± 28</td>
</tr>
</tbody>
</table>

**FIGURE 2.** Survival of *Euclea divinorum* seedlings in riparian areas of the Mara River: with and without fire and browsing and with and without grass present. The grass present treatment is equivalent to the unburned, with browsers’ treatment. (Error bars = 1 SD)

**FIGURE 3.** Growth rate of *Euclea divinorum* seedlings in riparian areas of the Mara River with and without fire and browsing and with and without grass present. The grass present treatment is equivalent to the unburned, with browsers’ treatment.

**EFFECTS OF FIRE, ANTELOPE, AND ELEPHANTS ON *E. DIVINORUM* SEEDLINGS.—** Removal of fire increased seedling survival by 100 percent from 0.074 to 0.15/yr where seedlings were exposed to browsers and from 0.25 to 0.56/yr with browsers removed (*P* = 0.039, log rank; Fig. 2). Removing browsers also increased survival by 70 percent compared to seedlings exposed to browsers (*P* = 0.022, log rank). However, we found no interaction between fire and browsing on seedling survival (*P* = 0.93, Likelihood-ratio test).

Seedling growth rate was positive only when both burning and browsing were removed. Burning decreased growth rate (*P* = 0.019, ANOVA), as did browsing (*P* = 0.03, ANOVA; Fig. 3). Again, there was no interaction effect between browsers and fire on seedling growth, rather their effects were additive (*P* = 0.15, Likelihood-ratio test). When growth rates of individual seedlings were examined, there was no increase in growth rate following fires that removed grass competitors (*P* = 0.54, ANOVA). Again, forest blocks were not different from each other (*P* = 0.39, ANOVA), respectively.

**CANOPY TREE DBH.—** Canopy trees showed evidence of a pulse establishment event. There was no difference in canopy tree DBH within forest patches (*P* = 0.15, ANOVA), but there was a trend for *E. divinorum* trees to be larger than other species in hilltop and riparian thickets (*P* = 0.07 and *P* = 0.09, Tukey’s test; Table 3). There was a difference in DBH between forest type, where riparian trees were larger than those in hilltop thickets (*P* = 0.02, ANOVA).
**Table 3. Diameter breast height (±SD) of canopy trees in hilltop and riparian forests, northern Serengeti (N = 1200 trees/species-forest type).**

<table>
<thead>
<tr>
<th>Species</th>
<th>Hilltop thicket</th>
<th>Riparian forest</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Drypetes gerrardii</em></td>
<td>N/A</td>
<td>25 ± 4.5</td>
</tr>
<tr>
<td><em>Euclea divinorum</em></td>
<td>32 ± 7.9</td>
<td>44 ± 6.1</td>
</tr>
<tr>
<td><em>Dimorphocarpa abyssinica</em></td>
<td>25 ± 3.6</td>
<td>29 ± 3.2</td>
</tr>
<tr>
<td><em>Fimbristylis capensis</em></td>
<td>N/A</td>
<td>25 ± 7.8</td>
</tr>
</tbody>
</table>

**DISCUSSION**

*Euclea divinorum* has attributes of a pioneer species that can facilitate the establishment of hilltop thickets and riparian forests in Serengeti: it establishes into grassland areas and when mature, other tree species can establish beneath it. However, under the present conditions of frequent fires and abundant browsers and grass, seedling survival is low and yearly growth rates are negative. Only when both browsers are excluded and burning stopped are seedling growth rates positive. Removal of grass also allows for positive growth, even in the presence of browsers. Thus, establishment of new thickets and forests in East Africa via *E. divinorum* establishment may depend on reducing browsing and fire, or removing grass.

**Fire.**—Fire reduced both seedling survival and growth rate. Seedlings were scorched and burned when the surrounding grassland burned. We did not observe compensatory growth or survival of seedlings following fires, and saw no positive effect of fire in removing competitors, or increasing growth rates. In contrast, Kellman (1997) reported that periodic fires inside riparian forests in Belize removed competitive herbs and increased subsequent survival of seedlings. Removal of fire may be insufficient, however, to allow *E. divinorum* to establish in grasslands as seedling growth rates were negative when fires were removed, but browsers remained (Fig. 3). In South Africa, *Acacia nilotica* established in grasslands when fires were removed, followed by establishment of *E. divinorum* under the canopy (Smith & Goodman 1987, Ben-Shahar 1991). Thus, reduction in fire frequency alone does not permit *E. divinorum* to establish in grasslands of Serengeti or South Africa. Successful establishment in Serengeti likely requires removal of browsing or grass competition.

**Browsers.**—Browsers (principally impala) decreased seedling survival by 70 percent, but their principal effect was to reduce seedling growth to negative rates. Browsers clipped the apical bud and youngest shoots from seedlings. Recruitment limitation by browsers is reported in both temperate zones with deer (Husheer et al. 2003, Potvin et al. 2003, Tsujino & Yumoto 2004) and in the tropics with impala and *Acacia* trees in savanna (Belsky 1994, Prins & van der Jeugd 1993). Browsers (likely impala) limited the height of *Acacia* seedlings to below 32 cm in Serengeti, but did not affect survival (Belsky 1984). In nearby Manyara NP, Tanzania, anthrax sufficiently reduced impala populations to allow *A. tortilis* trees to establish in a pulse in the early 1980s (Prins & van der Jeugd 1993). The timing of the *Acacia* recruitment in Manyara NP provided evidence that *Acacia* seedlings are controlled by impala and not by fire (Prins & van der Jeugd 1993). Impala were also reported to limit *Acacia erioloba* (E. Meyer) recruitment in Chobe NP, Botswana (Barnes 2001). Moreover, no thicket or forest establishment was observed when fires were reduced in Serengeti in the late 1970s and early 1980s due to wildebeest grazing and higher dry season rainfall (Sinclair 1995a), but browser numbers remained high (Campbell & Borner 1995).

In order for browsers to successfully limit thicket regeneration, they must maintain both high and constant browsing pressure on seedlings. Impala numbers do decline periodically due to diseases, such as anthrax in Manyara NP, Tanzania (Boshe & Malima 1986) and both brucellosis (Madsen & Anderson 1995) and foot and mouth disease (Bengis et al. 1994) in Kruger NP, South Africa (Keet et al. 1996). Thus, conditions necessary for *E. divinorum* establishment could occur naturally if increased dry season rainfall reduced fire frequency and disease reduced browser abundance.

We were surprised that elephants were not observed to consume *E. divinorum* seedlings. We expected them to do so because we observed them consuming *Acacia* seedlings in nearby savanna areas and elephants appear to prefer seedlings to larger trees. Dublin (1986) reported that elephants prefer *Acacia* seedlings that are 0.5–2 m tall. Elephants may avoid feeding on *E. divinorum* due to chemical defenses (Mebe et al. 1998) and prefer seedlings that are not chemically defended. *Acacia* seedlings are physically defended, but not heavily chemically defended (Gowda 1997).

Despite evidence that browsers can limit growth in unburned areas (Belsky 1984), several *Acacia* spp. established in a pulse during the late 1970s and early 1980s in Serengeti when fires were reduced by increasing wildebeest numbers, which removed grass fuel (Packer et al. 2005) and by higher than average dry season rainfall (Stronach 1989). Frequent fires can remove seeds from the seed bank (Williams 2000), such that insufficient seedlings are present to take full advantage of favorable growing conditions. Dry season rainfall of at least once every 30 d is considered essential for *Acacia* seedling establishment in South Africa (Higgins et al. 2000). Thus, while *E. divinorum* must have both fire and browsing removed for growth to occur on the time scale of this study, establishment may be possible if fire is reduced for longer periods of time (*i.e.*, more than 3–4 yr), or by increasing dry season rainfall.

**Competition with Grass.**—Competition with grass decreased seedling survival by 50 percent and produced negative growth rates. Seedlings follow a pattern of rapid growth following germination (Sharam 2005), which may be followed by repeated browsing and a slow decrease in height. We did not observe rapid growth of young *E. divinorum* seedlings in grassland, but it was observed inside forest areas where seedling abundance was higher (Sharam 2005). Regardless of the cause of negative growth, the highest growth rates found in the study occurred when grass was removed.

Poor seedling recruitment has been attributed to grass competition in similar grasslands of Belize (Kellman & Miyaniishi 1982), Costa Rica (Holl et al. 2000), Australia (Bowman & Panton 1993),
and Uganda (Chapman et al. 1999). Tall grass in riparian areas competes with seedlings for light, water, and soil nutrients (Kellman 1984).

**Forest establishment.**—Thicket and forest establishment in grasslands via a facilitating species has been reported in West Africa (Favier et al. 2004), South Africa (Dean et al. 1999), South America (Kellman & Miyanishi 1982), and India (Puyravaud et al. 2003). Typically, the trees that establish first are fire-resistant savanna trees, around which rain forest species establish via increased seed rain (Dean et al. 1999, Holl et al. 2000, Puyravaud et al. 2003), higher nutrients and reduced competition with grasses (Holl et al. 2000, Holl 2002) and consequently reduced fires (Sharam 2005).

Our results suggest that *E. divinorum* functions as a pioneer species when conditions are suitable, establishing in grassland, and facilitating the establishment of other forest trees. Such conditions existed during the period 1890–1920s when ungulates and fires were reduced in Serengeti (Sinclair 1995b). Beginning in the early 1890s, the cattle disease rinderpest removed ungulates in the park and severely reduced the cattle and thus human pastoralist population outside the park (Sinclair 1995b). Most fires are lit by pastoralists to increase forage quality in the dry season. Thus, fewer cows and people led to fewer fires for a 20-yr period beginning about 1900 (Sinclair 1995b). With reduced browsing and fires, *E. divinorum* likely established on hilltops and in riparian areas and facilitated thicket and forest establishment. These results also suggest that grass removal by buffalo is not the mechanism by which forests establish in grasslands. First, buffalo were present in Serengeti in high numbers 1950–1970s, a period during which no thicket or forest establishment was observed (Norton-Griffiths 1979). Second, long periods with high buffalo numbers and low grass would not result in a pulse of establishment but rather a long period of establishment and greater variance in canopy tree DBH.

Demographic evidence from riparian forests supports the hypothesis that forests established via a pulse of recruitment. Diameter measurements of canopy tree trunks indicate that trees are of similar age. Trees in riparian areas of Zambia attained 30 cm DBH after 100 yr (Chitondo 1996), a size similar to those found in Serengeti. These data suggest a pulse of establishment in Serengeti about 1900. Most DBH growth models in Africa are based on arid or semiarid sites with slow growth rates (Geldenhuys 1998), which may not be applicable to riparian areas, as trees in riparian and hilltop areas grow faster and are taller than trees elsewhere (Beentje 1994). In this study, DBH measures were not different within and between species suggesting that all trees are of a common age class. There was also a trend for *E. divinorum* DBH to be higher, though variable between species and sites (Geldenhuys 1998). Moreover, DBH–age relationships are poorly known for African species in general and for African riparian areas in particular, so this data must be treated cautiously.

In addition to DBH data, community composition also suggests a pulsed recruitment event. First, individual forest patches have different dominant canopy trees in addition to *E. divinorum* (Sharam 2005), suggesting a founder-effect. Second, islands within streams contain a higher number of tree species and those trees are larger and are likely older than forests in comparable riparian habitats (Sharam 2005). We propose that during the period 1890–1920s, reduced browsers and fire allowed *E. divinorum* to establish in grassland areas. Existing trees on islands then provided seeds of the other thicket and forest species, which established under the *E. divinorum* canopy and formed the current thicket and forest communities.

Our results suggest that the tree *E. divinorum* can establish in grasslands when either fire and antelope, or grass are removed, and provide conditions for the establishment of hilltop thickets and riparian forest trees. However, under the current conditions of frequent fires, abundant browsers, and grass in Serengeti, *E. divinorum* growth and survival are very poor and thicket and forest regeneration is not occurring. Current thickets likely established during the 1890–1920s period following the rinderpest epizootic, but did not establish in the 1970s when only fire was reduced. Thus, *E. divinorum* is a less aggressive pioneer species than *Acacia* species such as *A. tortilis* and *A. robusta*, which were able to establish in the 1970s. The lack of an aggressive pioneer species that can facilitate establishment of thickets may help to explain their rapid decline during the last 35 yr. Future conservation efforts need to consider the interacting roles of fire and grazing pressure against a backdrop of likely climatic change and characteristics of the pioneer tree species found in a particular region.

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**Literature Cited**


