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The Impact of Fire on the Soil Seed Bank and Regeneration of Harenna Forest, Southeastern Ethiopia

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The composition and density of soil seed banks was studied at Harenna Forest after a major fire in the year 2000. Soil samples were collected from burned and unburned portions of the forest using quadrants 15 × 15 cm and

9 cm deep, laid along line transects. Forest recovery was also monitored on burned sites using permanent plots of 0.1 ha. One hundred fifty-five seedlings germinated from the soil samples, of which 140 and 15 were from the unburned and burned sites, respectively. The proportion of woody species found on the unburned site was 47%, while on the burned site only one woody species was recorded. Overall mean densities were 621 ± 15 and 66 ± 2 seeds per m^2 on the unburned and burned sites, respectively. The greatest diversity was found in the upper soil layer, followed by the middle, litter, and lower soil layers collected from the unburned site. Eighteen months after the fire, the burned site was covered with 32 species of dense vegetation, which attained a height of 3.5 m. Our results revealed that although the fire exhausted the soil seed bank, the vegetation could regenerate quickly with pioneer species, which differed in composition from the neighboring unburned stand. This implies that most species in Harenna Forest are sensitive to fire and could be eliminated easily from the area unless they are properly protected. Therefore, an appropriate management plan should be developed and implemented for the remaining forest, including protection from fire.

Keywords: Disturbance; diversity; seed bank; forest regrowth; post-fire regeneration; Ethiopia.

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Introduction

Soil seed banks play a crucial role in determining plant communities after disturbances (Whitmore 1983; Granström 1986; Keeley and Keeley 1987; Leck et al 1989; Grime and Hillier 1992; Jerry 1992; Bazzaz 1998). They allow plant species to co-exist by providing spatial and temporal heterogeneity over time (Garwood 1989; Thompson 1992) and by ensuring regeneration in degraded ecosystems (Uhl et al 1981; Keeley and Keeley 1987). Therefore, knowledge about the composition and densities of soil seed banks provides clues about the natural dynamics, regeneration and restoration of

degraded forest ecosystems after disturbance (Gerhardt and Hytteborn 1992).

Information about different aspects of soil seed banks for various vegetation types around the globe (Leck et al 1989), including tropical plant communities (Garwood 1989), has been accumulating over the years. Studies done on soil seed banks in Ethiopia have so far focused on seed bank composition, densities and regeneration following disturbance in dry Afromontane forests in Ethiopia (Demel and Granström 1995; Demel 1997; Kebrom and Tesfaye 2000), degraded hillslopes (Kebrom 1998; Tesfaye 2000), *Acacia* woodland (Mekuria et al 1999; Eriksson et al 2002), savanna woodland and grassland (Menassie 2000), and abandoned arable fields (Demel 1998). The results of these studies indicate that herbaceous species dominate the soil seed banks while only a few woody species were capable of accumulating long-lived seeds in the soil. This implies that herbaceous species have better chances of recovery than woody species from the soil seed banks in the event of disturbance.

Only a few studies have focused on the impact of fire on soil seed banks and their potential contribution to regeneration in tropical forests (Booyesen and Tainton 1984; Garwood 1989; Eriksson et al 2002). For instance, some studies (Uhl et al 1982; Enright and Lamont 1989) have investigated the impact of slash-and-burn agriculture, forest clearing, and fire disturbances in tropical forests. Putz (1983) and Swaine (1992) reported that fire killed a significant proportion of seed banks in tropical forests. Recovery of forests to their original condition was very slow after fire had removed or destroyed a considerable proportion of the soil seed bank, and regrowth depended on seeds dispersed after the disturbance (Whitmore 1983; Swaine and Whitmore 1988; Janzen and Vazquez-Yanes 1991).

Although valuable information was generated on soil seed banks exposed to experimental fire in an Afromontane forest and *Acacia* woodland (Eriksson et al 2002), information on soil seed banks in forests subjected to large-scale natural or human-induced fire is lacking in Ethiopia and elsewhere in Eastern Africa. The objectives of the present study were, therefore, to: 1) determine the impact of fire on the species composition and densities of soil seed banks in an Afromontane forest that suffered from severe human-induced fire; 2) monitor post-fire regeneration in the forest; and 3) draw relevant lessons and formulate recommendations that contribute to the sustainable management and conservation of such forest resources.

Materials and methods

Study site

The study was carried out in Harenna Forest, about 480 km southeast of Addis Abeba, at 6°40′–7°10′ N and

39°30'–40°E. This is one of the largest remaining tracts of Afromontane forest in Ethiopia, on the southern slopes of the Bale Mountains (Lisanework and Mesfin 1989; Miede and Miede 1994). The forest covers an area of nearly 7000 km², of which 14% is part of the Bale Mountains National Park (Getachew et al 2002), known for its spectacular landscape, diverse flora and fauna, and endemism (Friis 1986; Hedberg 1986; Hillman 1988; Lisanework and Mesfin 1989). The dominant overstorey tree species include *Podocarpus falcatus*, *Pouteria adolfi-friedericii*, *Olea europaea* subsp. *cuspidata*, *Warburgia ugandensis*, *Croton macrostachyus*, and *Syzygium guineense* subsp. *guineense*.

The area is characterized by 8 rainy months from March to October, and 4 dry months from November to February, with average annual rainfall of 987 mm (EMA 1999). It experiences mean monthly minimum and maximum temperatures of 19.9°C and 25.4°C, respectively. A detailed description of the study site has been reported elsewhere (Getachew et al 2002).

Haremma Forest has been subjected to encroachment through clearing of the vegetation—usually involving fire—for settlement expansion, crop cultivation and animal grazing (Getachew et al 2002). For instance, the Bale Zone, in which Haremma Forest is located, and the adjacent Borena Zone were among the areas in the country that suffered significant damage by fire in the year 2000, when more than 150,000 ha of natural forestland, including wild populations of coffee, were destroyed (Demel 2000).

The present study was conducted in the central portion of the forest, estimated at 40 ha, and located between 1650 and 1760 m. This portion of the forest is part of the above-mentioned 150,000 ha of burned forestland. All of the previously standing vegetation at the study site was completely destroyed by the fire. The unburned surrounding vegetation was used as control.

Soil sampling and incubation

For the soil seed bank study, 2 parallel line transects were established in the North to South direction, one through the burned and the other through the unburned portions immediately after the fire, ie in April 2000. The transect lines were 1 km each. Twenty rectangular quadrats, ie 10 quadrats each in the burned and unburned portions, measuring 15 x 15 cm and 9 cm deep, were established every 100 m along the 2 transect lines. Soil samples were collected from 4 layers—the litter, upper (0–3 cm), middle (3–6 cm), and lower (6–9 cm) layers—and kept separately in plastic bags (Figure 1). Immediately after the samples were collected, they were transported to a glass house in the Department of Biology of Addis Abeba University.

The soil samples were spread on perforated plastic trays with cotton cloths at the bottom to keep seeds and soil particles from getting washed away during watering.

FIGURE 1 Collection of samples from a permanent plot on the burned site in the Haremma Forest study area. (Photo by Getachew Tesfaye)



FIGURE 2 Regeneration on one of the permanent plots on the burned site, after 18 months. (Photo by Getachew Tesfaye)

Watering of the samples was done every morning until the incubation was terminated. Seedling germination was checked every 7 days and seedlings readily identified were recorded and discarded. Seedlings that were difficult to identify were counted, recorded, tagged and grown separately until they were identified. The incubation of soil samples was terminated after 9 months.

Post-fire regeneration

Regeneration of plants on the burned site was monitored on 10 permanent plots measuring 10 x 10 m (100 m²). These were laid down along the line transects at intervals of 100 m. The study site was visited 18 months after the fire (Figure 2), and inventories were taken of all plants that had regenerated.

TABLE 1 Total number of seedlings, and corresponding soil seed bank densities per m², of species that germinated in the 4 soil layers, in samples collected at the unburned and burned sites at Harena Forest. Soil layers: 1 = litter, 2 = 0–3 cm, 3 = 3–6 cm, and 4 = 6–9 cm.

Species	Family	Unburned site					Burned site				
		Soil layer				Density (N=10)	Soil layer				Density (N=10)
		1	2	3	4		1	2	3	4	
A) Woody species											
<i>Albizia gummifera</i>	Fabaceae	2	1	0	0	13	0	0	0	0	0
<i>Ehretia cymosa</i>	Boraginaceae	0	3	0	0	13	0	0	0	0	0
<i>Ekebergia capensis</i>	Meliaceae	2	1	0	0	13	0	0	0	0	0
<i>Ficus sur</i>	Moraceae	5	40	5	2	231	0	2	3	0	22
<i>Ilex mitis</i>	Aquifoliaceae	2	1	0	0	13	0	0	0	0	0
<i>Millettia ferruginea</i>	Fabaceae	2	0	0	0	9	0	0	0	0	0
<i>Rubus apetalus</i>	Rosaceae	3	10	2	1	67	0	0	0	0	0
<i>Trema orientalis</i>	Ulmaceae	0	1	2	1	18	0	0	0	0	0
Subtotal		16	57	9	3	377	0	2	3	0	22
B) Herbaceous species											
<i>Dichrocephala chrysanthemifolia</i>	Asteraceae	1	3	3	0	31	0	0	0	0	0
<i>Dichrocephala integrifolia</i>	Asteraceae	2	4	5	0	49	1	0	5	3	40
<i>Impatiens rothii</i>	Balsaminaceae	0	2	0	1	13	0	0	0	0	0
<i>Lactuca oleracea</i>	Brassicaceae	1	0	2	0	13	0	0	0	0	0
<i>Laggera crispata</i>	Asteraceae	3	3	1	1	36	0	0	0	0	0
<i>Kalanchoe petitiiana</i>	Crassulaceae	0	0	1	1	9	0	0	0	0	0
<i>Veronica javanica</i>	Scrophulariaceae	0	1	1	0	9	0	0	0	0	0
Subtotal		7	13	13	3	160	1	0	5	3	40
C) Climbers											
<i>Urera hypselodendron</i>	Urticaceae	1	1	1	0	13	0	0	0	0	0
<i>Zehneria scabra</i>	Cucurbitaceae	2	0	1	2	22	0	0	0	0	0
Subtotal		3	1	2	2	35	0	0	0	0	0
D) Unidentified											
	–	0	6	3	2	49	0	1	0	0	4
Overall total		26	77	27	10	621	1	3	8	3	66

Data analysis

To determine the statistical differences in seed banks between the soil collected from the burned and unburned sites and their corresponding soil layers, one-way ANOVA (Zar 1984) was carried out. The Shannon-Wiener Diversity Index (Magurran 1988) was used to determine species diversity and evenness (H' max). Seed densities for the burned and unburned sites and their corresponding soil layers were compared to evalu-

ate the extent of fire damage on seed banks in the soil. Plant nomenclature used here follows that of Hedberg and Edwards (1989, 1995), Friis (1992), Edwards et al (1995, 1997) and Hedberg et al (2003).

Results

Species composition and density of soil seed banks

A total of 155 seedlings germinated from the soil sam-

ples collected at both unburned and burned sites. Of these, 140 were recorded from the unburned site while only 15 seedlings were recorded from the burned site. Twelve of the seedlings—11 from the unburned and 1 from the burned sites—died before being identified. The remaining 143 seedlings belonged to 17 different plant species and 14 flowering plant families. The proportions of woody, herbaceous and climber species recorded from the soil samples collected at the unburned site were 47, 41, and 12%, respectively. From soils collected at the burned site, only 1 woody and 1 herbaceous species were recorded.

The overall mean densities down to 9 cm of soil were 621 ± 15 and 66 ± 2 seeds per m^2 on the unburned and burned sites, respectively (Table 1). At the unburned site, the contributions of woody, herbaceous, climber and unidentified species to the overall soil seed density were 61, 26, 5 and 8%, respectively. Species exhibited differences in the densities of their soil seed banks at the unburned sites, with ranges from 9–231 seeds per m^2 for all the species and for woody species, and 9–49 and 13–22 seeds per m^2 for herbaceous and climber species, respectively (Table 1). The 5 species with the highest soil seed bank densities at the unburned site were *Ficus sur* (37%), *Rubus apetalus* (11%), *Dichrocephala integrifolia* (9%), *Laggera crispata* (6%), and *Dichrocephala chrysanthemifolia* (5%). At the unburned site, 2 species—*C. integrifolia* and *F. sur*—contributed 61 and 33%, respectively, to the total soil seed bank density, the rest being from unidentified species.

Spatial distribution of the soil seed banks

Depth distribution of species and densities of the soil seed banks showed variations at both the unburned and burned sites (Figures 3 and 4). At the unburned site, the highest soil seed density occurred in the upper soil layer and decreased with increasing depth. A relatively high seed density was also recorded in the litter layer. Unlike the unburned soil samples, there was a gradual increase in the soil seed densities with increasing depth at the burned site. There was a distinct variation in the depth distribution of species across the soil layers on the unburned site (Table 1). For instance, seeds of *Milletia ferruginea* occurred only in the litter layer, while those of *Ehretia cymosa* occurred only in the upper soil layer. Seeds of *Albizia gummifera*, *Ilex mitis* and *Ekebergia capensis* were distributed at both the litter and upper soil layers. *Dichrocephala chrysanthemifolia*, *Dichrocephala integrifolia*, *Rubus apetalus*, and *Urera hypselodendron* were found at both the litter and the upper 2 soil layers. *Trema orientalis* and *Kalanchoe petitiiana* were recorded from all the 3 and the lower 2 soil layers, respectively, while *Ficus sur* and *Laggera crispata* were found across all 4 soil layers.

FIGURE 3 Number of species found in each soil layer sample at the unburned and burned sites. Soil layers: 1 = litter, 2 = 0–3 cm, 3 = 3–6 cm, and 4 = 6–9 cm.

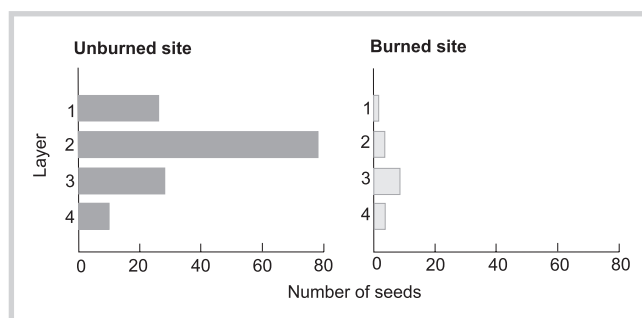
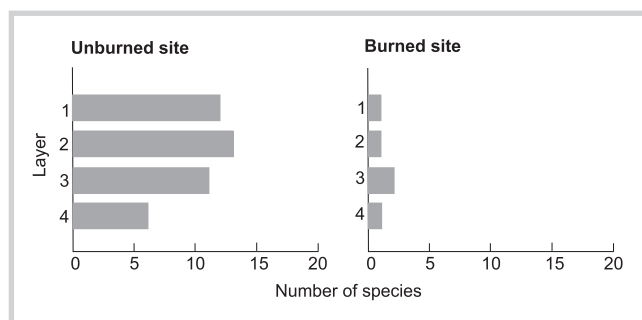


FIGURE 4 Number of seeds found in each soil layer sample at the unburned and burned sites. Soil layers: 1 = litter, 2 = 0–3 cm, 3 = 3–6 cm, and 4 = 6–9 cm.

Horizontal distribution of the species composition (Figure 5) and densities of the soil seed banks (Figure 6) also exhibited considerable variations within and between the unburned and burned sites. For example, seeds germinated from all the soil samples collected at the unburned site, although variations existed both in

FIGURE 5 Number of species recorded per quadrat at the unburned and burned sites.

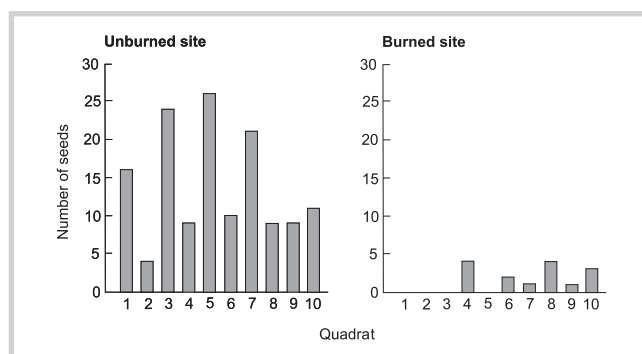
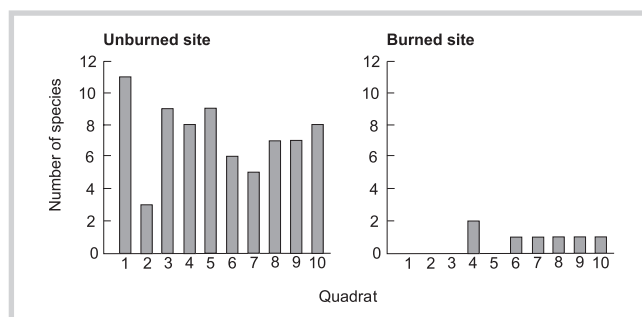


FIGURE 6 Number of seeds recorded per quadrat at the unburned and burned sites.

TABLE 2 Species Richness, Shannon-Wiener Diversity (H') and Evenness (H' max) of the soil seed bank in the soil layers of the unburned and burned sites.

Site and soil layer	Species richness	H'	H' max
Unburned site			
Litter layer	12	3.55	0.95
0–3 cm layer	14	4.17	0.65
3–6 cm layer	12	3.9	0.92
6–9 cm layer	6	3	0.97
Burned site			
Litter layer	1	0	0
0–3 cm layer	1	1	0.91
3–6 cm layer	2	1	0.95
6–9 cm layer	1	0	0

numbers of species and seedlings recorded. On the other hand, there was no germination of seeds in 40% of the soil samples collected at the burned site. The number of species recorded ranged between 3 and 11 on the unburned and between zero and 2 on the burned sites. Similarly, the number of seeds that were recovered ranged between 4 and 26 on the unburned and between zero and 4 on the burned sites. The frequency of species occurrence, defined here as the number of plots in which a species occurred, in soil samples collected at the unburned site, varied between 20 and 80%. The species with the highest frequency of occurrence was *Ficus sur* (80%), followed by *Rubus apetalus* (70%), *Dichrocephala integrifolia* (60%), and *Laggetera crispata* (60%).

Diversity and evenness of the soil seed banks

The Shannon-Wiener index showed greatest diversity in the upper (4.17) soil layer, followed by the middle (3.90), litter (3.55), and lower (3.00) soil layers collected from the unburned site (Table 2). Species richness had a similar pattern of species diversity. On the other hand, the Shannon-Weiner evenness (H' max) index had the highest value in the lower soil layers, followed by the litter, middle, and upper soil layers at the unburned site. In contrast, the burned site had 1 or 2 species only at all layers, and had the lowest species richness and diversity.

Impact of fire

Of the 18 seed bank species recorded, only 2—*Ficus sur* and *Dichrocephala integrifolia*—germinated from the soil samples collected at the burned site. The remaining 16 species (Table 1) may have been eliminated from the soil seed bank by fire. Analysis of variance showed signif-

icant differences in the number of seeds ($P = 0.001$) and species ($P = 0.04$) between the unburned and burned sites. The number of seeds also exhibited significant variation in the litter ($P = 0.001$), upper ($P = 0.001$), and middle ($P = 0.038$) soil layers, while there was no significant variation ($P = 0.11$) in the number of seeds in the lower layers of the two sites. *F. sur* showed significantly lower numbers of seeds ($P < 0.001$) on the burned than on the unburned site (Table 1).

Post-fire regeneration

Eighteen months after the fire, the bare ground at the burned site was completely covered with dense vegetation and hence recovering from injury. Thirty-two plant species representing 21 families were recorded (Table 3). The most dominant families were the Asteraceae (22%), Fabaceae (9%) and Solanaceae (9%). The most dominant groups were herbaceous plants, which accounted for 56.25% of the species, followed by shrubs (25%), trees (12.5%) and climbers (6.25%) (Table 3). The dominant tree species was *Croton macrostachyus* with a density of 1–2 plants per m^2 and 50% of the canopy cover. Common tree species in the recovering forest were *Celtis gomphophylla*, *Ficus sur*, *Millettia ferruginea*, *Vernonia hochstetteri*. Common shrubs included *Acanthus eminens*, *Calpurnia aurea*, *Senecio gigas*, and *Senna petersiana*. The common herbaceous species included *Achyranthes aspera*, *Ageratum conyzoides*, *Carduus leptacanthus*, *Laggetera crispata*, *Solanum incanum*, *Tagetes minuta*, and *Urtica* sp. The regrowth forest on the burned site attained a height of 3–3.5 m within 18 months.

Comparison of the species composition of the germinated seeds from the soil seed banks collected at the unburned site and the actual post-fire regeneration showed that 19% (6 out of 32) species occurred in common. These included *Impatiens rothii*, *Laggetera crispata*, *Millettia ferruginea*, *Rubus apetalus*, and *Vernonia hochstetteri*. *Ficus sur* occurred both in the soil seed banks collected at unburned and burned sites, and in the post-fire recovering forest.

Discussion

The results of soil seed banks collected from the unburned site in Harenna Forest showed fairly considerable quantities of buried viable seeds in the soil represented by several plant species. Soil seed banks reflect vegetation cover that existed in the past at the site and/or the standing vegetation (Garwood 1989; Demel and Granström 1995). They are considered potential sources of regrowth in the event of disturbance (Thompson 1992) and their contribution to future regeneration is highly variable (Uhl et al 1982).

The mean density of seeds at the unburned site at Harenna Afromontane forest (622 ± 15 seeds per m^2)

was considerably lower than in other Afromontane forests of Menagesha (12,300 seeds per m²), Munessa (13,700 seeds per m²), Gara-Ades (20,100 seeds per m²), and Wof-Washa (24,000 seeds per m²) (Demel and Granström 1995). The low seed density could be attributed to factors such as sample size, spatial and temporal heterogeneity of soil seed banks, successional stages of the forest, and the techniques employed. The less common seed bank strategy in moist tropical forests can also be due to high mortality risks through predation and pathogens, in addition to the adaptation of seedling bank strategy as a major regeneration route (Swaine and Whitmore 1988; Whitmore 1993; Demel 1996). A large number of species in Hareenna Forest are known to possess young seedlings in the understorey (Getachew et al 2002). Studies in other tropical forests (for example Keay 1960; Liew 1973; Hall and Swaine 1980; Young et al 1987) reported results comparable to those in Hareenna Forest, and according to Garwood (1989) the average seed density of mature tropical forest is 384 seeds per m².

The total number of species recorded in the soil seed banks at the unburned site in Hareenna Forest (18 species) was also lower than in other dry Afromontane forests of Ethiopia (Demel and Granström 1995). In secondary forests where human disturbance is high (such as the dry Afromontane forests in Ethiopia), soil seed banks are usually more diverse than in mature forests. On the other hand, tropical mature forests tend to have 4–79 species in their soil seed banks (Garwood 1989). The seed bank at Hareenna Forest was dominated by woody species (52%). Similar studies in tropical wet forests show that woody species constitute up to 90% of the soil seed bank (Garwood 1989). Dominance of woody species in the seed banks of mature forests can be attributed to the predominance of mature trees in the standing vegetation. In general, Hareenna is a humid Afromontane forest (Friis 1986; Lisanework and Mesfin 1989) more closely related to other tropical moist forests than the dry Afromontane forests of Ethiopia.

Most of the species observed in the soil seed banks collected at the unburned site in Hareenna Forest were either pioneer or ruderal species, namely *Dichrocephala chrysanthemifolia*, *Dichrocephala integrifolia*, *Ficus sur*, *Rubus apetalus*, *Urera hypselodendron*, and *Veronica javanica*. The unburned site at Hareenna Forest showed a general decrease both in seed densities and numbers of species with increasing depth. The upper soil layer accounted for 55% of the total seed banks, while only 6% was contained in the lower layer. This finding concurs with results reported from previous studies where seed densities and number of species in soil seed banks of mature tropical forests were shown to decrease with increasing depth, and the upper 3-cm layer to account for more than 33% of the soil seed banks (Garwood 1989).

TABLE 3 List of plant species growing on the burned site (after 18 months) and corresponding plant height (only highest shoots measured).

Species	Family	Life form	Height (m)
<i>Acanthus eminens</i>	Acanthaceae	Shrub	1
<i>Achyranthes aspera</i>	Amaranthaceae	Herb	<1
<i>Ageratum conyzoides</i>	Asteraceae	Herb	2.5
<i>Amaranthus spinosus</i>	Amaranthaceae	Herb	<1
<i>Asplenium aethiopicum</i>	Aspleniaceae	Herb	<1
<i>Calpurnia aurea</i>	Fabaceae	Shrub	2
<i>Canthium oligocarpum</i>	Rubiaceae	Shrub	0.5
<i>Carduus leptacanthus</i>	Asteraceae	Herb	2
<i>Celtis gomphophylla</i>	Ulmaceae	Tree	3
<i>Croton macrostachyus</i>	Euphorbiaceae	Tree	3
<i>Cyperus sp.</i>	Cyperaceae	Herb	<1
<i>Ethulia sp.</i>	Asteraceae	Herb	<1
<i>Ficus sur</i>	Moraceae	Tree	1
<i>Geranium arabicum</i>	Geraniaceae	Climber	2
<i>Hypoestes sp.</i>	Acanthaceae	Herb	<1
<i>Impatiens rothii</i>	Balsaminaceae	Herb	<1
<i>Lagenaria siceraria</i>	Cucurbitaceae	Climber	3
<i>Laggera crispata</i>	Asteraceae	Herb	3
<i>Leucas martinicensis</i>	Lamiaceae	Herb	<1
<i>Milletia ferruginea</i>	Fabaceae	Tree	1.5
<i>Oplismenus compositus</i>	Poaceae	Herb	<1
<i>Physalis peruviana</i>	Solanaceae	Herb	<1
<i>Ricinus communis</i>	Asteraceae	Shrub	3
<i>Rubus steudneri</i>	Rosaceae	Shrub	1.5
<i>Senecio gigas</i>	Solanaceae	Shrub	3
<i>Senna petersiana</i>	Fabaceae	Shrub	1
<i>Sida oligocarpum</i>	Malvaceae	Herb	1
<i>Solanum incanum</i>	Solanaceae	Herb	2
<i>Solanum sp.</i>	Solanaceae	Herb	<1
<i>Tagetes minuta</i>	Asteraceae	Herb	2.5
<i>Urtica sp.</i>	Urticaceae	Herb	2
<i>Vernonia hochstetteri</i>	Asteraceae	Shrub	3

The fire that occurred at Harenna Forest in 2000 consumed a significant proportion of the soil seed bank population and species, as could be seen from the record of soil seed banks of only 2 species. When forests are burned, the temperature often exceeds 100°C at 1 cm below the surface (Ewel et al 1981), and seeds of many species are killed (Gartner et al 1983; Putz 1983; Marrs 1985). Some species remain unaffected or are even stimulated to germinate by the high temperature (Janzen and Vazquez-Yanes 1991). In the present study, the 2 species that survived fire injuries and were recorded in the soil samples collected from the burned site were *Ficus sur* and *Dichrocephala integrifolia*. *Ficus sur* had the highest seed densities (231 seeds per m²) in the soil samples collected at the unburned site, and had also been reported to have relatively high seed density (498 seeds per m²) in other dry Afromontane forests (Demel and Granström 1995). It accounted for 37% of the total soil seed bank population of Harenna Forest. Such single species dominance (up to 49%) is common in mature tropical forests (Garwood 1989).

Fire damaged a significant proportion of seeds found in the litter, upper, and middle soil layers of the burned site at Harenna Forest, compared with the unburned site. This indicates that the temperature was lethal to the seeds up to about 6 centimeters in the soil layers. On the other hand, whether the buried seeds that survived the fire—6 and more centimeters below the surface—can contribute to future regeneration depends on several factors, such as the rate at which they can be brought up to the surface, seed size, and species (Garwood 1989). In general, the ability of seeds to germinate decreases with increasing soil depth. Nonetheless, the statistically insignificant variation in the number of seeds of *Dichrocephala integrifolia* between the soil samples collected at the unburned and burned sites suggests the presence of large quantities of seeds buried below 6 cm of the soil layer, which are likely to escape fire injury.

The vegetation at the burned site was evidently different in species composition from the neighboring undisturbed mature forest. The undisturbed forest stand was occupied by, among others, *Pouteria adolfi-friedericii*, *Diospyros abyssinica*, *Millettia ferruginea*, *Mimosa kummel*, *Olea capensis* subsp. *macrocarpa*, *Podocarpus falcatus*, *Polyscias fulva*, *Strychnos mitis*, and *Teclea nobilis*.

Observation of the burned site after 18 months at Harenna Forest showed that trees and shrubs were damaged by the fire and had disappeared, and dense vegetation of both herbs and woody species had recolonized the site. Forest regrowth at the burned site was dominated by a single species, *Croton macrostachyus*, which indicates that the species is an early successional species. This has also been demonstrated by results of previous studies (Demel 1996; Demel and Granström 1997b). The high plant density, together with dense canopy cover, revealed that conditions at the burned site were favorable and preferred for establishment by the species. The removal of vegetation and probably the increased soil temperature might also have triggered germination of buried seeds of *C. macrostachyus*, which have already been shown to remain viable for several years in the soil (Demel 1996; Demel and Granström 1997a). Post-fire microclimate in tropical forests has a strong impact on the recruitment of plant populations (Whitmore 1998). An even-sized population of *C. macrostachyus*, *Celtis gomphophylla*, *Ficus sur*, and *Vernonia hochstetteri* occupied the upper stratum of the developing vegetation.

Our results revealed that Harenna Forest possesses soil seed banks of woody and herbaceous species, although the mean density of seeds and the number of species were considerably lower than those recorded in other dry Afromontane forests. However, the fire that occurred in 2000 exhausted the soil seed bank. It was also observed that Harenna Forest could regenerate quickly from disturbance that destroyed most constituents of its soil seed banks. The regrowth forest was mainly composed of pioneer species, which differ in composition from the neighboring unburned stand, and develop into secondary forest. This implies that most species in the standing vegetation of Harenna Forest are sensitive to fire and might be easily eliminated from the area unless they are properly protected. Hence it is recommended that an appropriate management plan—which includes protection of the forests from fire in the Bale Mountains National Park and a similar agro-ecological set up—should be developed and implemented with the active participation of relevant stakeholders, especially the farming community living adjacent to the forests.

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