

Soil seed banks in plantations and adjacent natural dry Afromontane forests of central and southern Ethiopia

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Abstract: The soil seed bank was investigated in plantation stands and adjacent natural forests at Menagesha-Suba and Munessa-Shashemene forest sites in central and southern Ethiopia, respectively. The total numbers of species identified in the 0-9 cm soil layer were 58 at Menagesha-Suba and 52 at Munessa-Shashemene with the corresponding soil seed bank densities ranging between 27,200 and 82,600, and 4,500 and 36,900 seeds m⁻², respectively. Herbs dominated both in the number of species and densities of seeds while the contribution of woody species was generally low. The horizontal distribution of seeds in the soil exhibited considerable variation at both sites. However, the overall vertical distribution of seeds in the soil was similar in all stands with the highest densities occurring in the upper three centimeters of soil with gradually decreasing densities with increasing depth. The similarities in species composition of the soil seed bank was generally low in stands both within and between the two sites. In general, the results provide further evidence that consolidate the conclusions of previous studies on soil seed banks in Ethiopia. The dry Afromontane region, in which the two study sites are located, can be characterized as possessing large numbers of buried seeds of forbs, grasses and sedges. Only a few woody plants are represented, and these by few seeds, in the soil seed bank, suggesting that most woody plants rather use the seed rain, seedling banks or coppicing from stumps as alternative regeneration routes. These results imply that the herbaceous flora has a better chance of natural recovery in the event of disturbances owing to the diverse soil seed banks while the regeneration of woody species, particularly trees and shrubs, would be prevented by removal of mature individuals and their seedlings on the forest floor since most of them lack seed reserves in the soil. This, in turn, indicates that future existence of the woody flora characteristic of dry Afromontane areas in Ethiopia depends on the conservation and sustainable utilization of the few remnant natural forests.

Resumen: Se estudió el banco de semillas en el suelo en plantaciones y en rodales forestales naturales adyacentes en Menagesha-Suba y Munessa-Shashemene, en el centro y sur de Etiopía, respectivamente. En la franja de suelo de 0-9 cm se identificaron en total 58 especies en Menagesha-Suba y 52 en Munessa-Shashemene; las correspondientes densidades de semillas variaron de 27,200 a 82,600, y de 4,500 a 36,900 semillas m⁻², respectivamente. La distribución horizontal de las semillas en el suelo varió considerablemente en ambos sitios. Sin embargo, la distribución vertical general de las semillas fue similar en todos los rodales: las densidades más altas se presentaron en los tres centímetros superiores del suelo y decrecieron gradualmente hacia mayores profundidades. La similitud en la composición de especies en el banco de semillas del suelo fue en general baja en los rodales, tanto dentro de los sitios como entre ellos. En general, la evidencia proporcionada por los resultados apoya las conclusiones de estudios previos sobre bancos de semillas en el suelo en Etiopía. La región Afromontana seca, donde se localizan los dos sitios de estudio, se caracteriza por poseer grandes números de semillas enterradas de subarbustos, pastos y ciperáceas. Sólo unas cuantas plantas leñosas están representadas, y éstas a su vez por pocas semillas, lo que sugiere que la mayoría de las plantas

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leñosas usan más bien la lluvia de semillas, los bancos de plántulas o el rebrote a partir de tocones como rutas alternativas de regeneración. Los resultados implican que la flora herbácea tiene mayores posibilidades de recuperación natural después de disturbios debido a sus bancos de semillas tan diversos, mientras que la regeneración de especies leñosas, particularmente de árboles y arbustos, estaría siendo impedida por la remoción de individuos maduros y de sus plántulas presentes en el piso del bosque, ya que la mayoría de ellas carecen de reservas de semillas en el suelo. A su vez, esto indica que la existencia futura de la flora leñosa característica de las áreas Afromontanas secas en Etiopía depende de la conservación y el uso sostenible de los pocos bosques naturales que aún persisten.

Resumo: O banco seminal no solo foi investigado em parcelas plantadas e em estações florestais naturais adjacentes em Menagesha-Suba e Munessa-Shashemene na zona central e sul da Etiópia, respectivamente. O número total de espécies identificadas na camada dos 0-9 cm no solo foi de 58 em Menagesha-Suba e de 52 em Munessa-Shashemene com a correspondente densidade do banco seminal no intervalo de 27 200 e 82 600 e 4 500 e 36 900 sementes m⁻², respectivamente. As ervas dominavam quer em número de espécies e densidade de sementes, enquanto que a contribuição das espécies arbóreas era relativamente pequena. A distribuição horizontal das sementes no solo exibiu uma variação considerável em ambas as estações. Contudo, a distribuição vertical global das sementes no solo era semelhante em todas as parcelas com as maiores densidades a ocorrer nos três centímetros da camada superior do solo e decrescendo gradualmente com o aumento da profundidade. As semelhanças na composição das espécies do banco seminal no solo eram geralmente baixas nas parcelas, quer dentro quer entre as duas estações. Em geral, os resultados foram convergentes com estudos anteriores quanto aos bancos seminais na Etiópia. A região Afromontana seca, onde se localizaram as duas estações de estudo, pode ser caracterizada como possuindo um grande número de sementes enterradas de herbáceas altas de folhas largas, ervas e junças. Só um número reduzido de espécies lenhosas se encontram representadas, e estas por poucas sementes no banco seminal, sugerindo que a maior parte das plantas arbóreas antes usem as sementes de produção corrente, bancos de plântulas ou rebentos de toíça com alternativas às vias de regeneração. Estes resultados implicam que a flora herbácea tem uma maior chance de recuperação natural na hipótese de distúrbios ocorrendo nos vários bancos seminais no solo enquanto que a regeneração das espécies lenhosas, particularmente árvores e arbustos, ficará obstaculizada pelo corte dos indivíduos adultos e das suas plântulas dada a ausência de sementes na reserva de sementes no solo. Este facto, por seu lado, indica que a existência futura de flora lenhosa nas áreas Afromontanas da Etiópia depende da conservação e utilização sustentada das poucas florestas naturais remanescentes.

Key words: Density of seeds, horizontal and vertical distribution, Menagesha-Suba, Munessa-Shashemene, similarity of species composition.

Introduction

The soil seed bank refers to all viable seeds and fruits present on or in the soil and associated litter/humus. Soil seed banks can be either transient, with seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil more than one year (Simpson *et al.* 1989; Thompson & Grime 1979). They exhibit

variations in space as well as time and display both horizontal and vertical dispersion, reflecting initial dispersal onto the soil and subsequent movement (Simpson *et al.* 1989). Soil seed banks partly reflect history of the vegetation and can play an important role in its regeneration or restoration after disturbances. They have been exploited in two contexts: to manage the composition and structure of existing vegetation and to restore

or establish native vegetation (van der Valk & Pederson 1989).

Natural forests in the tropics have been and continue to be subjected to natural and human-induced disturbances, which have resulted in their degradation or complete destruction. The fates of these forest sites vary from place to place. In places where the sites are left without further interference, the processes of succession that will ultimately lead to re-vegetation of the sites may be initiated. Here, the soil seed banks serve as one of the major sources of plant re-growth. In most tropical areas, however, the degraded or completely destroyed forest sites are changed either to other land uses, e.g. establishment of monoculture plantations of fast growing trees (Feyera 1998; Feyera & Demel 2001), or permanent arable lands, which is a common practice in the tropics, e.g. in Ethiopia (Demel 1997a). In these cases, although the soil seed banks have the potential to initiate re-vegetation of the sites, they are continuously eliminated through weeding practices and ultimately completely exhausted (Demel 1997a). A third scenario could be the conversion of the destroyed forest sites to permanent arable lands followed by their abandonment. Here, some of the persistent seeds in the soil and the seed rain (if any) may lead to restoration of the vegetation (Demel 1998).

Considerable information/knowledge has been generated over the past several decades on the concepts of soil seed banks, seed bank processes, and role of seed banks in different vegetation types on the globe. The vegetation types include arctic and alpine plant communities, coniferous forests, temperate deciduous forests, tropical plant communities, grassland communities, Mediterranean climate shrublands as well as plant communities in deserts and wetlands. In addition, the management of soil seed banks for the restoration and conservation of natural vegetation and in arable lands has been studied (Leck *et al.* 1989, chapters and references therein).

In Ethiopia, only a few studies have been conducted on soil seed banks. These studies focused on species composition, density, spatial and temporal heterogeneity and longevity of seeds in the soil as well as their potential in the regeneration of dry Afromontane forests (Demel & Granström 1995, 1997; Demel Teketay 1996). The effects of clearing and conversion of dry Afromontane forests into arable lands (Demel 1997a) and their aban-

donment (Demel 1998) on various attributes of the soil seed banks have been investigated. Soil seed banks have also been investigated in an acacia woodland in the Rift Valley (Mekuria *et al.* 1999) and highly degraded sites (Kebrom & Tesfaye 2000). In addition, a comparative study has been carried out on species composition, density and depth distribution of soil seed banks before and after an experimental fire in an acacia woodland in the Rift Valley and a dry Afromontane forest (Eriksson 2000).

Despite proliferating studies on various aspects of soil seed banks, investigations on their role in enhancing the regeneration of native species under the canopies of monoculture plantations established by clearing tropical forest sites are lacking. The objective of this study was, therefore, to investigate the different plantation stands and the adjacent natural forests at two sites located in the dry Afromontane region.

Materials and methods

Study sites

The study was conducted in two dry Afromontane forest sites, namely Menagesha-Suba and Munessa-Shashemene forests.

Menagesha-Suba forest

Menagesha-Suba forest is located 50 km Southwest of Addis Ababa at 9°00' N and 38°35' E (Friis 1992). The topography of the area is extremely dissected, with alternating ridges and valleys dominating the landscape (von Breitenbach & Koukol 1962). The area consists of an isolated mountain surrounded by low-lying plains. The soils are light brown to reddish brown and shallow at the higher altitudes, but deeper at the lower altitudes. The altitudinal range of the site is between 2300 m and 3000 m. The eastern slope has been converted into farmland (Demel 1997b). The annual rainfall in the area is estimated to be around 1225 mm and the mean monthly temperatures range from 12 to 16°C (Tamrat 1993).

Prior to human disturbance, the natural forest communities were: *Hypericum* belts, *Hagenia-Juniperus* forest, *Juniperus* forest, *Juniperus-Podocarpus* and *Podocarpus* forest. The destruction of Menagesha-Suba natural forest started when a sawmill was established at the site in the early 20th century to exploit timber (von Breiten-

bach & Koukol 1962). In addition, the natural forest has been cleared by the local people for agricultural expansion.

Establishment of monoculture tree plantations was initiated in the middle of the 20th century with some indigenous and exotic species including *Cupressus lusitanica* Miller, *Eucalyptus globulus* Labill., *Juniperus procera* Endl. (indigenous sp.), *Pinus patula* Schlechtendal & Chamisso and *Pinus radiata* D. Donn. Most of these plantations were established on deforested areas and cover an area of 800 ha while the natural forest covers about 2720 ha (Forest Rangers, personal communication).

At this study site, six monoculture plantation compartments comprised of *C. lusitanica*, *E. globulus*, *J. procera*, *P. patula*, *P. radiata* and the adjacent natural forest were used for the study (Table 1). Description and other relevant information about these species can be found in the works of von Breitenbach (1961), Fichtl & Admasu (1994) and Friis (1995).

Munessa-Shashemene forest

Munessa-Shashemene forest is located about 240 km away from Addis Abeba in southern Ethiopia at 7°13' N and 38°37' E, and covers an altitudinal range between 2100 and 2700 m. It stretches along the eastern escarpment of the Great Rift Valley in Ethiopia. The soils at the site are reddish, freely draining and of medium to heavy texture (Lundgren 1971). The area experiences two rainy seasons, the main rainy season extending from July to October and the small one occurring between March and June. The mean annual rainfall of the area is about 1250 mm while the mean annual temperature is 20°C depending on the alti-

tude (Chaffey 1980). The study area originally supported deciduous natural forest dominated by *Podocarpus falcatus* (Thunb.) Mirb. (Chaffey 1980).

Subsistence farmers and saw-millers exploited the forest extensively for many years, and subsequently some of the area has been converted to forest tree plantations. Plantation establishment in this area began in the late 1950s and early 1960s (Lundgren & Lundgren 1969). Most of the plantations were established on disturbed Afromontane forest areas, which had been selectively logged at various intervals over the last 50 to 60 years. Remnant natural forest areas were cleared and burned prior to the establishment of the plantation (personal observation).

At this study site, different monoculture plantation stands composed of four exotic evergreen tree species, namely *C. lusitanica*, *E. globulus*, *E. saligna*, *P. patula* and the adjacent natural forest were selected for the study (Table 2). Description and other relevant information about these species can be found in the works of von Breitenbach (1961), Fichtl & Admasu (1994) and Friis (1995).

Methods

To analyze the composition and density, as well as the horizontal and vertical distribution, of the soil seed banks in the different plantation stands, soil samples were collected from quadrats measuring 10 cm x 10 cm (100 cm²) and nine centimetres deep. The quadrats were laid out at 100 m intervals along line transects spaced 100 m apart from each other. From each quadrat, four layers consisting of the litter layer and three successively deeper mineral soil layers (each three centimetres thick) were carefully removed with a

Table 1. Characteristics of the plantation stands sampled at Menagesha-Suba forest.

Stand	Area (ha)	Distance to Natural Forest (m)	Age (yr)	Rotation	Mean Basal Area (m ² ha ⁻¹)	Mean DBH (cm)	Mean Height (m)	Stems ha ⁻¹	Crown cover (%)
<i>C. lusitanica</i>	18	2000	14	1	20	16	11	980	71
<i>C. lusitanica</i>	32	200	24	1	31	22	20	820	76
<i>E. globulus</i>	25	250	17	2	5	9	12	790	25
<i>J. procera</i>	8	200	42	1	22	20	21	710	65
<i>P. patula</i>	49	300	24	1	27	22	24	790	72
<i>P. radiata</i>	30	300	24	1	45	26	25	860	60
Natural forest*	2500		500+		124	30	21	1760	80

* Only upperstorey trees ≥ 10 cm diameter.

Table 2. Characteristics of the plantation stands sampled at Munessa-Shashemene forest.

Stand	Area (ha)	Distance to Natural Forest (m)	Age (yr)	Rotation	Mean Basal Area (m ² ha ⁻¹)	Mean DBH (cm)	Mean Height (m)	Stems ha ⁻¹	Crown cover (%)
<i>C. lusitanica</i>	7	200	9	1	14	13	10	900	75
<i>C. lusitanica</i>	15	250	17	1	40	29	23	575	80
<i>C. lusitanica</i>	9	300	25	1	35	30	26	475	65
<i>E. globulus</i>	6	100	13	1	21	29	31	275	50
<i>E. globulus</i>	8	200	16	1	28	19	26	900	65
<i>E. globulus</i>	6	350	22	2	25	20	27	625	60
<i>E. saligna</i>	6	250	11	1	16	23	28	450	55
<i>E. saligna</i>	6	350	22	2	24	18	21	900	65
<i>E. saligna</i>	2	1000	27	3	4	21	17	100	10
<i>P. patula</i>	4	200	10	1	20	18	15	750	80
<i>P. patula</i>	11	500	21	1	29	27	25	500	85
<i>P. patula</i>	6	100	28	1	50	35	31	475	70
Natural forest*					28	59	26	142	30

* Refers to only upperstorey trees ≥ 10 cm diameter.

field knife and placed in plastic bags separately. At Menagesha-Suba site, a total of 10 soil samples composed of 40 different layers were taken from each stand. Accordingly, a total of 70 soil samples and 280 different layers were collected from the seven stands at the site, including the adjacent natural forest. In the case of Munessa-Shashemene, four soil samples were collected in each plantation stand, owing to the large number of stands, composed of 16 different layers. Hence, a total of 52 soil samples and 208 layers were collected from the 13 plantation stands. In addition, 12 soil samples composed of 48 different layers were collected from the adjacent natural forest. Therefore, the total numbers of soil samples and different layers taken from Munessa-Shashemene site were 64 and 256, respectively. The adjacent natural forests were included in the study for comparison.

The soil samples were first sieved using a mesh size of 0.5 mm to recover seeds of the different plant species. The seeds recovered by sieving were collected into paper bags and identified using local reference material. The viability of seeds was determined by cutting/dissection, and seeds were considered viable when the content of each seed was white and firm (Demel & Granström 1995).

Soil samples were spread in small plastic trays and incubated for seed germination in the glass-

house for six months. The minimum daily temperature in the glasshouse ranged between 19 and 32°C, and the maximum daily temperature ranged between 29 and 39°C. The emerging seedlings were identified, recorded and discarded once or twice a week. The soil samples were stirred continuously to bring seeds located deeply in the soil samples to the surface thereby stimulating them to germinate. Seedlings that were difficult to identify were transplanted for future identification.

In this paper the term “tree” refers to a woody plant with a single main stem (a trunk or hole) and a distinct upper crown; “shrub” refers to a woody plant usually with two or more perennial woody stems originating near the ground; “herb” refers to a plant with non woody stem, excluding grasses, persisting only for one growing season or a year (Hedberg & Edwards 1989). Nomenclature follows Cufodontis (1953-1972), Hedberg & Edwards (1989) and Friis (1992).

Data analysis

To compare similarities in terms of species composition between the plantations and adjacent natural forest stands as well as among plantation stands at each study site, data from the litter and top nine centimetres layers were analysed using Jaccard's Coefficient of Similarity (JCS) (Krebs 1989).

Results

Species composition of soil seed banks

A total of at least 86 plant species (data from sieving and germination trials combined) of four life forms were recovered from the litter and the top nine centimetres of soil samples collected beneath the different plantation stands and adjacent natural forests at both sites (Appendix 1 and 2). Generally, herbs were dominant, represented by 64 species (74%), trees by eight species (9%) and shrubs and grasses by seven species each (8%). Out of the total number of species recorded at both

sites, 58 plant species (excluding those that could not be identified at family level) were recovered from the soil samples collected at the Menagesha-Suba forest (Table 3) and 52 plant species (excluding those that could not be identified at family level) from those collected at Munessa-Shashemene forest (Table 4).

Among the different plantation stands at Menagesha-Suba forest, the soil samples collected under the canopies of the 14-year-old stand of *C. lusitanica* had the highest number of plant species while the lowest number of species was recorded from soil samples collected under the canopies of *P. patula*. In the case of Munessa-Shashemene for-

Table 3. Total number of species recorded from the soil samples collected in the different plantation stands and the adjacent natural forest at Menagesha-Suba forest.

Stand	Age (year)	Species in Life Forms				Total
		Trees	Shrubs	Herbs	Grasses	
Natural forest	> 500	2	2	22	1	23
<i>J. procera</i>	42	1	1	29	–	31
<i>C. lusitanica</i>	24	1	1	21	–	23
<i>P. patula</i>	24	–	1	18	–	19
<i>P. radiata</i>	24	–	–	20	–	20
<i>E. globulus</i>	17	–	1	27	1	29
<i>C. lusitanica</i>	14	–	–	27	6	33
Total		3	4	45	6	58

Table 4. Total number of species recorded from the soil samples collected in the different plantation stands and the adjacent natural forest at Munessa-Shashemene forest.

Stand	Age (year)	Species in Life Forms				Total
		Trees	Shrubs	Herbs	Grasses	
Natural forest	> 500	4	1	17	1	23
<i>P. patula</i>	28	1	2	9	–	12
<i>E. saligna</i>	27	2	–	15	–	17
<i>C. africana</i>	25	2	–	20	1	23
<i>C. lusitanica</i>	25	1	–	17	1	19
<i>E. globulus</i>	22	2	–	15	–	17
<i>E. saligna</i>	22	1	–	21	1	23
<i>P. patula</i>	21	1	2	18	–	21
<i>C. lusitanica</i>	17	1	1	12	–	14
<i>E. globulus</i>	16	2	1	16	–	19
<i>E. globulus</i>	13	3	–	17	–	20
<i>E. saligna</i>	11	1	1	25	–	27
<i>P. patula</i>	10	–	–	13	–	13
<i>C. lusitanica</i>	9	–	–	5	–	5
Total		6	5	39	2	52

est, the highest number of plant species was recorded from soil samples collected under the canopies of the 11-year-old stand of *E. saligna* while the soil samples collected under the canopies of 9-year-old stand of *C. lusitanica* showed the lowest number of species (Tables 3 & 4).

At both sites, very few species of trees were recorded from the soil samples, i.e. only three and six species at Menagesha-Suba and Munessa-Shashemene forests, respectively. Most of these species were also recorded from soil samples collected in the adjacent forests.

Density of seeds in the soil

The mean densities of viable seeds in the soil seed bank (including both sieving and germination) ranged from 27,200 seeds m⁻² in the adjacent natural forest to 82,600 seeds m⁻² in the 17-year-old stand of *E. globulus* at Menagesha-Suba (Table 5). Similarly, there was variation in the mean densities of viable seeds at Munessa-Shashemene forest, ranging from 4,500 seeds m⁻² in the 9-year-old stand of *C. lusitanica* to 36,900 seeds m⁻² in the 21-year-old stand of *P. patula* stand (Table 6). At both forests, the soil seed banks were dominated by a

Table 5. The densities of seeds (number of seeds m⁻²) recovered from the four different layers of the samples collected in the different plantation stands and the adjacent natural forest at Menagesha-Suba forest.

Stand	Age (year)	Soils Layers				Total
		Litter	0 – 3 cm	3 – 6 cm	6 – 9 cm	
Natural forest	>500	2100	10400	10500	4200	27200
<i>J. procera</i>	42	8800	19600	14600	8100	51100
<i>C. lusitanica</i>	24	900	16100	17800	9300	44100
<i>P. patula</i>	24	8900	36300	19100	7700	72000
<i>P. radiata</i>	24	7900	38600	11000	6400	63900
<i>E. globulus</i>	17	3500	44700	24400	10000	82600
<i>C. lusitanica</i>	14	300	38400	16300	4600	59600
Total		32400	204100	113700	50300	400500

Table 6. The densities of seeds (number of seeds m⁻²) recovered from the four different layers of the samples collected in the different plantation stands and the adjacent natural forest at Munessa-Shashemene forest.

Stand	Age (year)	Soil Layers				Total
		Litter	0 – 3 cm	3 – 6 cm	6 – 9 cm	
Natural forest	>500	2750	4250	1480	720	9200
<i>P. patula</i>	28	2000	6250	6500	1300	16050
<i>E. saligna</i>	27	1500	8000	7250	1500	18250
<i>C. africana</i>	25	2500	15000	6250	800	24550
<i>C. lusitanica</i>	25	3000	7750	2550	2250	15550
<i>E. globulus</i>	22	6250	5500	1500	1300	14550
<i>E. saligna</i>	22	80	12600	6000	3000	21680
<i>P. patula</i>	21	1850	22000	8300	4750	36900
<i>C. lusitanica</i>	17	2100	13500	5750	1220	22570
<i>E. globulus</i>	16	3000	8750	2750	1300	15800
<i>E. globulus</i>	13	550	8750	5250	1550	16100
<i>E. saligna</i>	11	250	18200	6000	4250	28700
<i>P. patula</i>	10	1350	5000	1750	4500	12600
<i>C. lusitanica</i>	9	0	1000	3000	500	4500
Total		27180	136550	64330	28940	257000

few species. For instance, the five plant species with the highest number of seeds in the Menagesha-Suba forest site included (in descending number of seeds): *Cyperus rotundus*, *Laggera crispata*, *Persicaria nepalense*, *Veronica javanica* and *Cerastium afromontanum* (Appendix 1). Similarly, in Munessa-Shashemene forest site, *Celtis africana*, *Veronica javanica*, *Cynodon dactylon*, *Veronica abyssinica* and *Crassula alsinoides* were the five species that had the highest number of seeds in the soil (Appendix 2). It is very interesting to note that *C. africana*, one of the relatively big trees common in dry Afromontane forests, had the highest seed density in the site.

Spatial distribution of seeds in the soil

There were great differences in the spatial, horizontal and vertical, distribution in both the number of species and seeds in the soil.

Horizontal distribution

The horizontal distribution of species and seeds in the soil exhibited considerable variation as can be verified by comparing the various stands studied at both sites (Tables 3-6). For example, the total number of species ranged between 19 and 33 (Table 3) and between 5 and 27 (Table 4) at Menagesha-Suba and Munessa-Shashemene forest sites, respectively. Similarly, the total density of seeds (per square meter) ranged between 27,200 and 82,600 (Table 5) and between 4,500 and 36,900 (Table 6) at Menagesha-Suba and Munessa-Shashemene forest sites, respectively.

Vertical distribution

The number of seeds in the soil showed similar vertical distribution in almost all plantation stands and the adjacent forests, with the highest

number of species and densities of seeds in the upper three centimetres of soil and a gradually decreasing number of species and densities of seeds with increasing soil depth (Tables 5 & 6). There were no differences among different plantation species, different ages of plantation stands and the adjacent natural forests with respect to the pattern of depth distribution of seeds in the soil. In all stands, the litter layers had lower number of species and densities of seeds compared with the top three centimetres of soil. Most of the species recorded in the soil seed banks had seeds in the different soil layers. On the other hand, there was variation in the depth distribution of seeds among different plant species. For instance, seeds of some species were recovered only from the upper three centimetres soil layers.

Similarity of species composition of soil seed banks

The similarity in species composition of the soil seed bank was generally low both in stands within sites and between sites (Tables 7-9). The highest (JCS = 0.57) and lowest (JCS = 0.22) similarities in species composition were recorded between the *J. procera* stand and the natural forest and the two *Cupressus* stands respectively in the Menagesha-Suba forest site (Table 7). In the Munessa-Shashemene forest site, the similarities of both the 22-year-old stand of *E. globulus* as well as the 27-year-old stand of *E. saligna* with the adjacent natural forest scored the highest (JCS = 0.63) while the 21-year-old and 28-year-old stands of *P. patula* exhibited no similarity (JCS = 0) at all (Table 8). Comparison of similarities in species composition among the adjacent natural forests and all plantation stands (pooled data) at the two sites revealed that the similarity between the two natural forests was the highest (JCS = 0.69). On the

Table 7. Jaccard's Coefficients of Similarity in species composition of the soil seed banks between plantation stands and the adjacent forest at Menagesha-Suba forest.

Stand	CL14	CL24	EG	JP	PP	PR	NF
<i>C. lusitanica</i> (CL14)	–	0.22	0.51	0.39	0.24	0.33	0.28
<i>C. lusitanica</i> (CL24)		–	0.33	0.50	0.45	0.39	0.52
<i>E. globulus</i> (EG)			–	0.54	0.30	0.40	0.40
<i>J. procera</i> (JP)				–	0.47	0.55	0.57
<i>P. patula</i> (PP)					–	0.34	0.44
<i>P. radiata</i> (PR)						–	0.38
Natural forest (NF)							–

Table 8. Jaccard's Coefficients of Similarity (JCS) in species composition of the soil seed banks between plantation stands and the adjacent forest at Munessa-Shashemene forest.

Stands	CL9	CL17	CL25	EG13	EG16	EG22	ES11	ES22	ES27	PP10	PP21	PP28	NF
<i>C. lusitânica</i> (CL9)	–	0.26	0.21	0.17	0.18	0.23	0.20	0.21	0.23	0.28	0.19	0.29	0.19
<i>C. lusitânica</i> (CL17)		–	0.06	0.31	0.48	0.19	0.28	0.19	0.29	0.17	0.13	0.18	0.24
<i>C. lusitânica</i> (CL25)			–	0.26	0.27	0.29	0.31	0.45	0.29	0.10	0.11	0.19	0.28
<i>E. globulus</i> (EG13)				–	0.15	0.19	0.38	0.26	0.23	0.19	0.28	0.15	0.20
<i>E. globulus</i> (EG16)					–	0.06	0.35	0.27	0.13	0.23	0.25	0.11	0.14
<i>E. globulus</i> (EG22)						–	0.22	0.29	0.79	0.20	0.12	0.38	0.63
<i>E. saligna</i> (ES11)							–	0.25	0.26	0.18	0.30	0.05	0.29
<i>E. saligna</i> (ES22)								–	0.29	0.13	0.22	0.25	0.29
<i>E. saligna</i> (ES27)									–	0.17	0.19	0.32	0.63
<i>P. patula</i> (PP10)										–	0.10	0.32	0.21
<i>P. patula</i> (PP21)											–	0.00	0.13
<i>P. patula</i> (PP28)												–	0.31
Natural Forests (NF)													–

Table 9. Jaccard's Coefficients of Similarity (JCS) in species composition of the soil seed banks between plantation stands of exotic* and indigenous species as well as the adjacent forests at both sites.

Stand	MESP	MES-JPS	MES-NF	MUSP	MUS-NF
Menagesha-Suba (MES) Plantations (MESP)	–	0.51	0.39	0.47	0.29
MES- <i>Juniperus procera</i> Stand (MES-JPS)		–	0.57	0.17	0.61
MES-Natural Forest (MES-NF)			–	0.23	0.69
Munessa-Shashemene (MUS) Plantations (MUSP)				–	0.37
MUS-Natural Forest (MUS-NF)					–

*Data from all stands pooled together.

other hand, the similarity between the *J. procera* stand at Menagesha-Suba and the plantation stands of exotic species at Munessa-Shashemene forest site was the lowest (JCS = 0.17) (Table 9).

Discussion

The soil seed banks of plantations and natural forests were dominated by herbaceous species at both sites, and most of them had already been reported to exhibit persistent soil seed banks in dry Afromontane forests (Demel & Granström 1995), arable lands (Demel 1997a) and abandoned arable lands (Demel 1998) in Ethiopia. On the other hand, with the exception of *Celtis africana*, which exhibited high number of seeds, other woody species had very few or no seeds in the soil samples. The woody species represented in the soil seed bank were only seven in Menagesha-Suba forest site and 11 in Munessa-Shashemene forest site.

Previous studies in dry Afromontane forests (Demel & Granström 1995; Demel 1997a, 1998) had also shown that few woody species are represented in the soil seed banks.

Densities of seeds in the samples collected from the different stands varied greatly within and between the two sites (Tables 5 & 6). Likewise, the similarities in species composition of the soil seed banks in the stands within each site and between the two sites were not only quite low but also very variant (Tables 7 & 8). The species composition and density of the soil seed banks in each stand generally depend on the type of vegetation that existed and the history of the site before the establishment of the stands. The factors that are responsible for the disparity in densities of seeds and composition of species within and between sites require further investigation.

The number of species represented in the soil seed banks of the various stands, including the

adjacent forests, at both sites were much lower than those previously reported (Demel & Granström 1995). In contrast, soil seed bank densities in the soil samples from all stands in Menagesha-Suba were invariably much higher than the previous studies (Demel & Granström 1995).

In general, our results provide further evidence that consolidate the conclusions of previous studies on soil seed banks in Ethiopia. The dry Afromontane region, in which the two study sites are located, can be characterized as possessing large numbers of buried seeds of forbs, grasses and sedges. Only a few woody plants are represented in the soil seed bank, and these by few seeds, suggesting that most woody plants rather use the seed rain, seedling banks or coppicing from stumps as alternative regeneration routes (Demel & Granström 1995; Demel 1996, 1997b). These results imply that the herbaceous flora has a better chance of natural recovery in the event of disturbances owing to the diverse soil seed banks while the regeneration of woody species, particularly trees and shrubs, would be prevented by removal of mature individuals and their seedlings on the forest floor since most of them lack seed reserves in the soil. This, in turn, indicates that future existence of the woody flora characteristic of dry Afromontane areas in Ethiopia depends on the conservation and sustainable utilization of the few remnant natural forests.

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Appendix 1. List of species and total number of seeds recovered from soil samples collected in the plantation stands and adjacent natural forest at Menagesha-Suba forest (sieving and germination combined).

Species	Life Form*	CL14**	CL24	PP	PR	JP	EG	NF	Total
<i>Abutilon longicapse</i>	S	–	–	–	–	–	109	1	110
<i>Achyranthus aspera</i>	H	8	–	–	1	–	–	–	9
<i>Acmella caulirhiza</i>	H	1	–	–	–	–	1	–	2
<i>Alchemilla abyssinica</i>	H	20	1	–	14	34	23	8	100
<i>Bidens pilosa</i>	H	–	–	–	–	–	–	3	3
<i>Carduus nyassanus</i>	H	18	33	26	18	9	1	13	118
<i>Cerastium afromontanum</i>	H	66	–	–	1	–	75	–	142
<i>Chenopodium ambroides</i>	H	2	–	–	–	1	22	–	25
<i>Clitoria ternate</i>	H	–	–	21	–	–	–	–	21
<i>Conyza steudelli</i>	H	1	–	–	2	6	–	–	9
<i>Crassula alsinoides</i>	H	20	1	4	–	7	1	23	56
<i>Cuperssus lusitanica</i>	T	–	6	–	–	–	–	–	6
<i>Cyperus rotundus</i>	H	–	246	578	366	85	14	57	1376
<i>Dichrocephala integrifolia</i>	H	2	–	–	–	–	–	–	2
<i>Discopodim penninervium</i>	S	–	1	–	–	1	–	–	2
<i>Drouguetia iners</i>	H	6	–	–	–	–	11	–	17
<i>Ficus sur</i>	T	–	–	–	–	–	–	3	3
<i>Erica arborea</i>	T	–	–	1	–	–	–	–	1
<i>Galium simense</i>	H	–	–	–	1	3	–	2	6
<i>Geranium arabicum</i>	H	–	16	11	23	24	2	3	79
<i>Girardinia diversifolia</i>	H	–	1	7	2	1	–	8	19
<i>Helichrysum foetidum</i>	H	7	21	12	12	12	14	12	90
<i>Hydrocotyle</i> sp.	H	–	6	1	–	1	25	1	34
<i>Hypericum peplidifolium</i>	H	–	–	2	–	1	–	–	3
<i>Hypoestes</i> sp.	H	–	–	–	119	49	3	–	171

contd...

Appendix 1. *contd.*

Species	Life Form*	CL14**	CL24	PP	PR	JP	EG	NF	Total
<i>Juncus</i> sp.	H	6	–	1	–	–	–	–	7
<i>Juniperus procera</i>	T	–	–	–	–	1	–	3	4
<i>Kalanchoe</i> sp.	H	–	18	–	–	6	–	3	27
<i>Lactuca oleracea</i>	H	1	–	3	–	1	–	1	6
<i>Laggera crispata</i>	H	186	1	6	–	5	206	1	405
<i>Lippia abyssinica</i>	S	1	–	–	–	–	–	–	1
<i>Medicago polymorpha</i>	H	1	1	–	–	1	1	–	4
<i>Monopsis stellarioides</i>	H	43	2	–	14	3	5	2	69
<i>Oldenlandia monanthos</i>	H	54	–	–	1	5	23	–	83
<i>Oxalis corniculata</i>	H	11	40	1	1	34	10	13	110
<i>Persicaria nepalense</i>	H	10	14	39	5	85	2	23	178
<i>Phyllanthus fischeri</i>	H	–	–	–	2	21	59	4	86
<i>Physalis peruviana</i>	H	–	1	–	–	–	–	–	1
<i>Plantago lanceolata</i>	H	13	–	–	–	34	71	–	118
<i>Poa leptodada</i>	G	3	–	–	–	–	–	–	3
<i>Rubus apetalus</i>	S	–	–	–	–	–	–	1	1
<i>Scleranthus annuus</i>	H	1	–	–	–	–	–	1	2
<i>Solanum indicum</i>	H	8	–	–	–	–	21	–	29
<i>Solanum nigrum</i>	H	–	1	–	–	–	–	–	1
<i>Solanum</i> sp.	H	–	3	8	9	9	–	2	31
<i>Stellaria media</i>	H	2	–	–	–	1	43	–	46
<i>Tagetes minuta</i>	H	–	1	–	–	–	–	–	1
<i>Trifolium</i> sp.	H	–	–	–	–	–	1	–	1
<i>Urera hypselodendron</i>	S	–	–	1	–	6	–	4	11
<i>Vernonia leopoldi</i>	S	–	–	–	–	–	3	–	3
<i>Veronica abyssinica</i>	H	2	4	4	32	15	14	10	81
<i>Veronica javanica</i>	H	3	6	8	29	31	22	44	143
Unidentified sp. 1 (Poaceae)	G	7	5	–	–	–	1	1	14
Unidentified sp. 2 (Poaceae)	G	5	–	–	–	–	–	–	5
Unidentified sp. 3 (Poaceae)	G	14	–	–	–	–	–	–	14
Unidentified sp. 4 (Poaceae)	G	2	–	–	–	–	–	–	2
Unidentified sp. 5 (Poaceae)	G	1	–	–	–	–	–	–	1
Unidentified sp. 6 (Rubiaceae)	H	26	–	–	1	16	4	–	47

* Life Forms: T = Tree; S = Shrub; H = Herb; and G = Grass; ** For abbreviations refer to Table 7

