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Changes in soil seed bank composition and density following deforestation and subsequent cultivation of a tropical dry Afromontane forest in Ethiopia

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Abstract: Changes in the species composition and density of viable seeds in the soil seed banks (SSB) following deforestation and subsequent cultivation of a tropical dry Afromontane forest were assessed in the southern highlands of Ethiopia. Soil samples for the study were collected from a chronosequence of six farm fields having ages of 7, 10, 14, 26, 34 and 53 years since conversion and from an adjacent relatively undisturbed natural forest. A total of 66 plant species (54 identified and 12 unidentified) germinated from all the soil samples collected for the investigation. Herbs dominated the SSB, representing nearly 78% of the identified species. Composition and density of the SSB varied significantly between sites and with soil depth, but did not follow a pattern with cultivation period. However, there was a general tendency of disappearance of native woody species from the SSB with increasing period of soil cultivation as evidenced by the declining contribution of woody species to the SSB, i.e., from 5.7% after seven years to 0% after 53 years of continuous cultivation following deforestation. There was relatively high similarity in species composition of the SSB between sites including the natural forest, while the similarity in species composition of the SSB with the standing vegetation in the adjacent natural forest was very low. This implies that reliance on the SSB for the recovery of native woody flora on farm fields abandoned after certain years of continuous cultivation may not be successful. Therefore, future planning for rapid forest vegetation restoration on degraded abandoned farm fields should not be designed based on strategies that rely only on SSB.

Resumen: Se evaluaron los cambios en la composición de especies y la densidad de semillas viables en los bancos de semillas del suelo (BSS) posteriores a la deforestación y el cultivo subsecuente de un bosque tropical seco afromontano en las tierras altas del sur de Etiopía. Las muestras de suelo para el estudio fueron recolectadas en una cronosecuencia de seis campos agrícolas con edades de 7, 10, 14, 26, 34 y 53 años desde su conversión, y en un bosque natural adyacente relativamente no perturbado. Un total de 66 especies de plantas (54 determinadas y 12 no determinadas) germinaron en las muestras de suelo recolectadas para la investigación. El BSS estuvo dominado por las hierbas, las que representaron cerca de 78% de las especies de identidad conocida. La composición y la densidad del BSS varió significativamente entre sitios y con la profundidad del suelo, pero no mostró un patrón relacionado con el tiempo de cultivo. Sin embargo, hubo una tendencia general de desaparición de las especies leñosas nativas del BSS conforme aumentó el tiempo

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de cultivo de suelo, tal como fue evidenciado por la contribución decreciente de especies leñosas al BSS, i.e. de 5.7% después de siete años a 0% después de 53 años de cultivo continuo después de la deforestación. La similitud en la composición de especies del BSS entre sitios fue relativamente alta incluyendo el bosque natural, mientras que la similitud en la composición de especies del BSS con la vegetación en pie en el bosque natural adyacente fue muy baja. Esto implica que si se depende del BSS para la recuperación de la flora leñosa nativa en campos agrícolas abandonados después de un cierto número de años de cultivo continuo uno podría no tener éxito. Por lo tanto, la planeación futura para la rápida restauración de la vegetación forestal en campos agrícolas abandonados no debería estar diseñada con base en estrategias que sólo dependen del BSS.

Resumo: As mudanças na composição das espécies e densidade das sementes viáveis nos bancos seminais no solo (SSB) na sequências da desflorestação e subsequente cultivo de uma floresta tropical seca Afromontana foram avaliadas nas terras altas a sul da Etiópia. As amostras de solo para o estudo foram colectadas de uma cronosequência de 6 campos agrícolas com idades de 7, 10, 14, 26, 34 e 53 anos após conversão e de uma floresta adjacente relativamente não disturbada. Um total de 66 espécies de plantas (54 identificadas e 12 não identificadas) germinaram de todas as amostras de solo colectadas para a investigação. Nos SSB dominavam as ervas, representando aproximadamente 78% das espécies identificadas. A composição e densidade dos SSB variou significativamente entre estações e com a profundidade do solo, mas não apresentou um padrão com o período de cultivo., Evidenciou-se, contudo, uma tendência geral para o desaparecimento das espécies lenhosas nativas dos SSB com o aumento do período de cultivo do solo, tal como é evidenciado pelo declínio da contribuição das espécies lenhosas nos SSB, i.e. de 5,7% depois de sete anos para 0% depois de 53 anos de cultivo contínuo pós desflorestação. Verificou-se um alto valor de semelhança na composição relativa em espécies nos SSB entre estações incluindo a floresta natural, enquanto que a semelhança na composição de espécies nos SSB com a vegetação corrente na floresta natural adjacente era muito baixa. Isto implica que a confiança nos SSB para recuperação da flora lenhosa nativa nos campos de cultivo abandonados depois de um certo número de anos de cultivo contínuo pode não ter sucesso. Por isso, o planeamento futuro para a rápida restauração da vegetação florestal em campos agrícolas abandonados e degradados, não deve ser delineado com base em estratégias que se baseiam só nos SSB

Key words: Biodiversity, chronosequence, native woody species, regeneration restoration, seed dispersal, seed rain.

Introduction

Ethiopia has diverse geography that has given rise to the development of wide diversities of flora and fauna rich with endemic elements. Between 6,500-7,000 species of higher plants, 240 species of mammals and 845 species of birds are estimated to exist in the country, of which about 780-840 plant species, 22 mammalian species, and 16 bird species are endemic (Demel 2001; Taye *et al.* 1999). The floral resource is the fifth largest in tropical Africa (Eshetu 2001), and the avifauna is the richest in Africa (Demel 2001). Consequently, Ethiopia is recognized as an important regional center of biodiversity (Edwards & Ensermu 1999; Sayer *et al.* 1992; Shibru & Martha 1998). However, these biologically rich resources of Ethiopia are vanishing at an alarming rate due to extensive deforestation.

Although several factors drive natural forest destruction in Ethiopia, agricultural land expansion triggered by increasing human population is probably the dominant force. In fact, deforestation and conversion to farm land are the primary causes for dwindling tropical biodiversity, and in Ethiopia these practices have already threatened a number of plant species, including the gene pool of wild populations of *Coffee arabica* L. (Ensermu *et al.* 1992; Tadesse *et al.* 2001, 2002; Tewolde 1989, 1990). Due to increasing human pressure, traditional land management practices, such as shifting cultivation, have been replaced by permanent farming systems in most parts of the country. Such continuous cultivations are associated with decline or loss of biodiversity not only through the outright loss of habitat but also through the deterioration of the soil seed banks (SSB) (Demel 1997, 1998).

Soil seed banks, which are the aggregations of viable seeds in the soil potentially capable of replacing adult plants (Baker 1989; Leck *et al.* 1989; Thompson & Grime 1979), play a critical role in vegetation maintenance, succession, ecosystem restoration, differential species management and conservation of genetic variability (Harper 1977; Hills & Morris 1992; Leck *et al.* 1989; McGraw *et al.* 1991; van der Valk & Pederson 1989). Use of SSB in vegetation succession management is acknowledged as a low cost restoration technique since it disposes of many of the problems associated with collecting, storing and sowing seeds as well as transplanting individual seedlings raised in a nursery (van der Valk & Pederson 1989). Therefore, knowledge about soil seed bank dynamics has practical advantages in vegetation succession management (Grime 1989; Leck *et al.* 1989; Onaindia & Amezaga 2000). However, the potential in using SSB to assist post-disturbance succession management heavily depends on the nature and degree of disturbance inflicted on a site (Granström 1986). It is very important to understand the potential effects of different disturbances, especially deforestation and subsequent cultivation, on the composition of SSB as these could be a potential threat to biodiversity. An understanding of the functions of SSB requires not just knowledge of the number of seeds present at one time but also knowledge of SSB dynamics (Fenner 1985; Thompson 1992).

Recently, a number of investigations of SSB have been made in different ecosystems in the highlands of Ethiopia (e.g. Demel 1996, 1997; Kebrom & Tesfaye 2000). However, few of these studies examined how long seeds of the native forest flora can survive when previously forested sites are cleared and subjected to continuous cul-tivation (Demel 1997). Studies on the changes in the composition and density of soil seed flora with time following clearance of natural forests and subsequent cultivation in the highlands of Ethiopia have not been available until now. As a result, it may not be possible to predict whether abandonment of farm fields, after different years and intensities of cultivation, could potentially result in restoration of the natural plant communities with the assistance of SSB. Such knowledge could also (i) provide understanding of the responses of tropical dry Afromontane forest communities to different ecosystem disturbances, (ii) assist in predicting the point at which re-vegetation from the SSB may become a problem or benefit; and (iii) provide clues to the kind of strategies to be followed, i.e., passive or active, for the restoration of the vast degraded agricultural landscapes in the country.

The objective of this study was to investigate changes in composition and density of the soil seed flora following deforestation and continuous cultivation of farm fields of different ages formed by clearing portions of a dry Afromontane forest in Ethiopia. The emphasis was to investigate effects of cultivation period on composition and density of SSB with the help of a farm field chronosequence. We hypothesized that SSB of recently converted farm fields might have greater species richness and seed densities, particularly of woody species, than older farm fields.

Materials and methods

Study site

The study was undertaken at Lepis near the Gambo district of the Shashemene Forest Industry Enterprise (SFIE) situated at 7^{0}20′N and 38^{0}45′E. The natural forest around Lepis is a tropical dry Afromontane evergreen forest (Lundgren 1971), and belongs to the Munessa-Shashemene Forest that covers the eastern escarpment of the Central Ethiopian Rift Valley. Although Munessa-Shashemene Forest covers a wider altitudinal range (from 1500 m at the Rift Valley plain to over 3000m on the fringe of the Rift Valley escarpment), the farm fields and the adjacent natural forest sampled for this study lie at the bottom of the Rift Valley escarpment at about 2300 m elevation. Mean annual rainfall and temperature are 1200 mm and 20^0 C, respectively. The soils are Mollic Andosols, which developed from volcanic lava and ash from quaternary volcanic activities in the Rift Valley and its surroundings (Mesfin 1998).

Munessa-Shashemene forest is one of the floristically diverse remnant Afromontane natural forests existing in Ethiopia today. However, pressure for more land to cultivate crops and graze animals has resulted in heavy deforestation of large portions of the original forest of the site (Chaffey 1980; Kebede 1998; Mooney 1954; Russ 1944). Based on satellite images and GIS analysis, Kebede (1998) estimated that arable land increased at the rate of 2.8% annually, while grasslands, natural forests and woodlands declined at the rate of 6.4%, 1.7%, and 2.6%, respectively, each year in the area.

For the present study, six farm fields 7, 10, 14, 26, 34, and 53 years of age since conversion and the adjacent natural forest were selected. The period of forest clearance and subsequent cultivation of each farm field was determined from aerial photographs taken in 1967, 1972 and 1987, and by interviewing the farm owners and village elders. The farm fields, on the average 0.5 ha in size, were all cleared with slash and burn techniques using simple local tools such as axes.

Farming system and cropping

The agriculture in Lepis is dominantly subsistence farming based on a mixed crop-livestock (mostly cattle) production system. As a tradition, a few trees, mainly *Croton macrostachyus* Del., *Podocarpus falcatus* Thunb., *Celtis africana* Burm f., *Milittia ferruginea* (Hochst.) Baker and *Prunus africana* (Hook. f.) Kalkam, are deliberately preserved as on-farm scattered trees (parkland agroforestry) from the original forest. The average density of the on-farm trees was about 8 stems per hectare.

Crop cultivation involves plowing the fields with oxen-driven simple plows. Before plowing, grasses and any leftover residues from the previous crops are burnt. Then, the fields are plowed two to three times and sown. Major crops grown in the area are maize and sorghum, with only one harvest each year. Fertilizers used on the farm fields in the area are diammonium phosphate (DAP) in combination with urea at the average rate of 50:50 kg ha^{-1} yr^{-1} each.

Soil sampling

To investigate the SSB, five randomly located plots of one square meter area each were selected and marked, both in each selected farm field and adjacent natural forest. At the centre of each plot, three sub-plots, 15 x 15 cm, were marked in a triangular shape. Soil samples were removed from three separate soil layers, each three centimeters thick (0-3 cm, 3-6 cm and 6-9 cm) using a knife and a spoon. The rationale for taking the soil samples at the three soil layers was to examine if there is any variation in the depth distribution of seeds within and among the croplands and the adjacent natural forest in the soil. Soil samples from identical layers of the three sub-plots were mixed and put in one plastic bag to form composite samples. The intention was to capture the spatial heterogeneity of seed distribution in the soil. Later on, the composite samples were divided into three equal parts out of which one was randomly chosen as the working sample for the study. Accordingly, a total of 105 samples were collected. The soil samples were transported to the Forestry Research Center (FRC) of the Ethiopian Agricultural Research Organization (EARO) in Addis Abeba.

Vegetation sampling

To compare the soil seed flora with the flora of the standing vegetation in the adjacent natural forest, 10 plots of 314 m^2 area each were randomly selected in the adjacent natural forest. All woody species found in these plots were first identified. Then, sub-plots of 2.5 m x 2.5 m, marked at the centre of each plot, were used to identify all herbaceous species, including grasses and sedges.

Incubation of soil samples

In this study, the seedling emergency method of SSB assessment was employed (Roberts 1981). All the samples were taken to a glasshouse on the premises of EARO Headquarters where they were incubated to stimulate germination of seeds. The soil samples were spread to a thickness of about two centimetres on cotton cloth placed in plastic trays of four centimetres thickness and kept continuously moist. Seedlings started to emerge after one week, and those that were readily identifiable were counted, recorded and discarded. Those difficult to identify at the seedling stage were counted, transplanted and grown separately until they could be identified. Every month, the soil samples were stirred to stimulate seed germination. The number of seedlings emerging declined considerably after approaching a year since the incubation experiment began. Thus, the experiment was terminated after being monitored for a year. Plant nomenclature in this paper follows Hedberg & Edwards (1989, 1995), Friis (1992), Edwards *et al.* (1995), Edwards *et al.* (1997), Edwards *et al.* (2000) and Hedberg *et al.* (2003).

Data analyses

Species composition (number of species germinated per sample) and density (number of germinated seeds per sample) of the soil seed banks among the study sites and between soil depths were compared using two-way Analysis of Variance (ANOVA). Similarities of soil seed flora among study sites and with the standing vegetation in the adjacent natural forest were also compared using Jaccard's Coefficient of Similarity (JCS) (Krebs 1989). Compared with other similarity indices, this coefficient has been recognized as robust and unbiased even with small sample sizes (Ludwig & Reynolds 1988).

Results

Species composition of the soil seed flora

Excluding those seedlings that died before identification, a total of 66 plant species (54 identified and 12 unidentified) were recovered (Appendix 1). Of these, only six (11.1%) were woody species: four trees, one shrub and one climber. Herbs dominated the SSB flora, represented by 42 species (77.8%), and grasses by five species (9.2%). Of the four tree species recovered from the SSB, one was *Eucalyptus* sp., an exotic tree planted commonly along farm boundaries in the study area. Only one tree species, *Croton macrostachyus*, belonging to the upperstory species in the adjacent natural forest was recovered from the soil samples collected from the farm fields. In fact, *Croton macrostachyus*, is also a common on-farm tree species observed to exist on most of the sampled farm fields. The other two native tree species recovered, *Vernonia amygdalina* and *V. auriculifera*, are pioneer species common to open landscapes.

Species composition (mean number of species per sample) of the SSB differed significantly between sites and between soil layers (Two-way ANOVA: $F_{(6,104)} = 16.7$, $P < 0.001$ and $F_{(2,104)} = 13.7$, $P < 0.001$, respectively). Neither total number of species recovered from the SSB samples nor species number by growth forms (tree, shrub, herb or grass) fitted to the original hypothesis, i.e., ecline with increasing years of cultivation after deforestation. The highest species composition was recorded in the SSB taken from the 7and 34 years old farm fields, while the soil samples collected from the natural forest exhibited the least number of species in all the soil layers (Tables 1 & 2). It is interesting to note that the only upperstory species recovered from the SSB samples was encountered in samples taken from both the natural forest and the seven

Table 1. Mean (± SD) species richness (number of germinated species plot^{-1}) recorded from the soil seed bank samples collected from a chronosequence of six farm fields converted from tropical dry Afromontane forest and an adjacent natural forest (NF) in southern Ethiopia.

Soil layers (cm)	NF	Years of cultivation since conversion					
		7	10	14	26	34	53
0 - 3	16.0 ± 2.0	17.4 ± 7.6	13.2 ± 2.3	9.8 ± 2.3	16.2 ± 1.3	22.2 ± 1.5	14.8 ± 2.3
3 - 6	11.0 ± 3.4	15.4 ± 4.5	11.8 ± 1.3	8.6 ± 3.2	12.8 ± 2.6	19.8 ± 2.4	12.2 ± 0.45
6 - 9	7.4 ± 1.7	13.2 ± 8.0	9.8 ± 1.6	8.0 ± 2.8	12.0 ± 2.0	16.8 ± 2.5	11.6 ± 2.3
Distance from the adjacent forest (m)	-	108	162	183	87	108	162

Table 2. Number of species (excluding exotic species) by growth form recorded from soil seed banks of the upper 9 cm soil depth collected from a chronosequence of six farm fields (FL) and an adjacent natural forest (NFSSB) including the above ground vegetation in the adjacent natural forest (NFAGF) in southern Ethiopia.

Site	Species in growth forms						
	Tree	Shrubs	Herbs/Sedges	Climber	Grasses	Unidentified	Total
7 yr FL	3	1	30	0	3	7	43
10 yr FL	2	0	15	1	3	5	26
14 yr FL	1	0	20	0	3	4	27
26 yr FL	1	0	20	0	4	3	27
34 yr Fl	1	0	24	0	3	3	31
53 yr FL	0	0	18	0	3	3	24
NFSSB	2	1	25	0	3	3	34
NFAGF	22	6	16	3	4	2	53

years old farm field. No native woody species were recovered from the oldest, i.e., 53 years old farm field.

Density of seeds in the soil seed banks

Mean seed density (number of germinated seeds m^{-2}) of the SSB in the upper nine-centimetre soil layer ranged from 1,425 seeds in the adjacent natural forest to 13,298 in the 34 years old farm field (Table 3). The highest density of seeds in the farm fields is due to a very few species of herbs; *Galinsoga quadriradiata*, *Crassula alsinoides*, *Geranium arabicum* and *Pilea tetraphylla* contributed 79% and 78% of the seed densities in the 7 and 53 years old farm fields, respectively. Generally, the soil seed densities differed significantly between the sites and soil layers (Two way ANOVA: $F_{(6,104)} = 25.6$, $P < 0.001$ and $F_{(2,104)} = 64.7$, $P < 0.001$, respectively). The density of seeds recorded from all sampled soil layers taken from the natural forest was much lower than those collected from the farm fields. Despite the large differences in the cultivation time between the farm fields sampled, changes in soil seed density did not show any trend with cultivation time, contrary to our original hypothesis.

Spatial heterogeneity of soil seed flora

Species richness and densities of the SSB varied considerably in a spatial dimension, both horizontally and vertically. For instance, species richness of the SSB varied from the minimum of 9 to the maximum of 25 among samples of the 0-3 cm soil layer on the 7 years old farm field. There was also a declining trend of species richness with increasing soil depth in all the sites, the upper three centimetres of soil layer exhibiting the highest species richness (Table 1). Herbs and grasses were deeply distributed, while woody species were mostly limited to the surface. However, the interaction among study sites and soil layers with respect to species richness of the SSB did not show a significant difference (Two-way ANOVA: $F_{(12,104)} = 0.67$, $P > 0.05$). Similarly, the soil seed densities varied considerably within a site. For instance, seed density varied from 3,126 to 9,970 seeds m^{-2} among the samples of the 0-3 cm soil layer within a site on the 53 year old farm field. There was also significant variation in soil seed densities among the soil layers in all sites, and the top layers (0-3 cm) exhibited the highest soil seed densities consistently while densities declined gradually with increasing soil depth in all sites (Table 3).

Similarity of soil seed banks

The similarity in species composition of the SSB among the different aged farm fields and the natural forest was relatively high (JCS = 0.32 – 0.41) compared with the similarity of SSB species composition and the standing vegetation in the natural forest, which was very low (JCS = 0.032 – 0.06) (Table 4). There was only one tree species, an exotic species of *Eucalyptus*, which was recorded from the SSB on four of the farm field sites (Appendix 1) that was not recorded both in the SSB and standing vegetation of the adjacent natural forest. Generally, major differences in species composition of the SSB among sites were due to the number of herbaceous species recovered.

Table 3. Mean (± SD) density of seeds (number of regenerated seeds m^{-2}) recovered from the soil seed bank samples collected from a chronosequence of six farm fields and the adjacent natural forest (NF) in southern Ethiopia.

Years of cultivation since conversion	Soil depth (cm)		
	0 - 3	3 - 6	6 - 9
NF	912 ± 238	278 ± 224	163 ± 40
7	6254 ± 2250	2640 ± 1470	1678 ± 957
10	5277 ± 1714	2743 ± 377	2124 ± 416
14	1644 ± 709	1093 ± 341	779 ± 130
26	3605 ± 960	1665 ± 385	1309 ± 502
34	6915 ± 1847	2927 ± 712	2080 ± 561
53	58689 ± 2567	2871 ± 879	2130 ± 387

Table 4. Jaccard's Coefficient of Similarity in the species composition of soil seed banks between farm fields (FL), the natural forest (NFSSB) and the above ground flora (NFAGF) in the adjacent natural forest.

	NFSSB	Years of cultivation					
		7	10	14	26	34	53
NFAGF	0.038	0.039	0.06	0.043	0.047	0.056	0.032
NFSSB	–	0.46	0.43	0.46	0.34	0.39	0.32
7 yr FL	–	–	0.33	0.32	0.54	0.50	0.39
10 yr FL	–	–	–	0.49	0.50	0.44	0.33
14 yr FL	–	–	–	–	0.43	0.51	0.37
26 yr FL	–	–	–	–	–	0.59	0.57
34 yr FL	–	–	–	–	–	–	0.50

Discussion

Our initial hypothesis was that relict seeds of woody species in the SSB from the original forest might play a role in succession of native woody vegetation following abandonment of farm fields originally carved out of natural forests, although the utility of the seeds might diminish with increasing cultivation periods. However, the results indicated that viable seeds of native woody species are generally rare in the SSB of the farm fields regardless of the length of cultivation period. The rarity of viable seeds of woody species was also true for the SSB taken under the natural forest. Despite the general low contributions to the SSB, the number of viable seeds of woody species also declined with cultivation period from about 5.7% contribution at 7 years to nil after 53 years of continuous cultivation.

These dynamics of the SSB composition were probably influenced by woody species seed outputs (losses) from and inputs to the SSB of the farm fields. The lack of viable seeds of woody species in the SSB of the farm fields could be attributed to several factors. Seeds of some native woody species common to the natural forest of the study site, e.g. *Bersama abyssinica* Fresen. and *Ekebergia capensis* Sparrm. are large, fleshy and recalcitrant and, hence, are short-lived (Demel 1996, Demel & Granström 1995, 1997; Kebrom & Tesfaye 2000). Although other species, e.g. *Croton macrostachyus,* have the capacity to accumulate in the SSB, it is likely that their seeds could be lost due to predation or exhausted due to the impacts of subsequent farm practices such as tillage, burning and weeding as has been shown in previous studies in the highlands of Ethiopia (Demel 1996, 1997, 1998). Plowing affects the SSB by damaging or breaking seeds directly or by bringing buried seeds to the surface and exposing them to predators, desiccating winds, high temperature and direct solar radiation or inducing them to germinate and die.

Such environmental factors as high temperature and direct solar radiation on the bare soils of the farm fields may induce rapid loss of seed viability and consequently reduce woody species composition in the SSB of the farm fields. Furthermore, germinating seeds of the woody species on the farm fields either from the SSB and/or newly dispersed seeds are continuously removed during site preparation and successive weeding. Stumps from cut/damaged woody plants are split into pieces or dug out for fuelwood preventing effective sprouting. Domestic animals that graze freely on the farm fields throughout the dry season following crop harvest damage seedlings that might have escaped other detrimental factors. These processes may result not only in exhaustion of woody species from farm fields but also lead, eventually, to domination of the SSB by opportunistic herbaceous weedy species, including grasses and sedges (Demel 1997, 1998; Demel & Granström 1995).

On the other hand, seed inputs of woody species to the SSB of farm fields, other than those seeds that remained from the original forest before clearance for agriculture, can probably occur through seed rains from the adjacent natural forest or from the selectively preserved on-farm trees. The contributions from the adjacent natural forest, in turn, depend on the distance of the natural forests to the farm fields and on the mode of seed dispersal of the native woody species. Seed dispersal behaviour of native woody species in the Afromontane forests of Ethiopia is generally not well studied. However, the fact that most native woody species of the Afromontane forests of Ethiopia possess large seeds has been mentioned as a potential limitation for their long-distance dispersal (Demel & Granström 1995).

Experiences from other tropical sites have also shown that seed dispersal of dry tropical woody species, like the forests of Ethiopia, are limited to very short distances from forest edges when their sizes are large enough to limit dispersability (Cubina & Aide 2001). Thus, seed inputs from woody species to the SSB of the farm fields through seed rain from adjacent natural forest are expected to be minimal. On the other hand, some tree species such as *Podocarpus falcatus, Prunus africana, Croton macrostachyus* and *Celtis africana* are traditionally preserved as scattered on-farm trees in the study area. However, *Croton macrostachyus* was the only species recovered from the SSB of the farm fields studied. These selectively preserved on-farm trees may or may not produce viable seeds due to age, isolation, which affects seed production associated with their reproductive habit (e.g. monoecious or dioecious habit) and/or tree management activities such as continuous lopping. These processes imply that deforestation followed by permanent cultivation could hamper the recovery of native woody species through the exhaustion of viable seeds of forest flora from the soil seed reserves with negative effect on the biodiversity resources of the country.

Previous studies of SSB of various ecosystems in the highlands of Ethiopia have also shown that seeds of woody species are relatively scarce in the SSB of most ecosystems including natural forests (Demel 1996; Demel & Granström 1995; Feyera & Demel 2001; Feyera *et al.* 2002). These studies have indicated that most woody species in the dry Afromontane forests depend on seed rain and formation of seedling banks under the shades of mature forest canopy as strategies for regeneration (Demel 1996; Feyera & Demel 2001; Feyera *et al.* 2002; Mulugeta *et al.* 2004; Pohjonen 1989). In spite of these facts, most farm fields that are acutely degraded by cultivation in the Ethiopian highlands are abandoned for nature to take its own course. Active restoration practices are very rare. In natural succession of such degraded sites, regeneration is expected to originate mainly from the seed reserves in the soil while seed rain might also be expected to contribute. However, as has been clearly demonstrated by results from this study and similar other works discussed above, the chances for getting woody regeneration from the SSB and seed rains from adjacent forests are very unlikely and the rate and extent of natural succession would at best be very slow.

Furthermore, the remnant patches of dry Afromontane forests in Ethiopia are still under continuous threat from deforestation associated with the need for more land to produce food. Historical records show that forests used to cover large areas of the Ethiopian highlands. Although there are controversies about the extent of the former forest cover in Ethiopia, based on “climatic-climax”, natural forests are assumed to have covered 37% of the Afromontane region of Ethiopia in the past, which declined to only 4.4% by 1960 (von Breitenbach 1962), to 3% in the 1980s (Anonymous 1988) and to about 2.7% by 1990 (Anonymous 1994). Destruction of the remnant high forests continues at an estimated rate of 150,000 - 200,000 ha per year (Anonymous 1994; Reusing 1998).

Disappearance and/or fragmentation of the remnant natural forests will further restrict contributions through seed rain from these forests to the re-vegetation of abandoned degraded lands. Furthermore, the disparity in species composition between the SSB of farm field sites and the standing vegetation in the adjacent natural forest, which is consistent with results from similar previous works (Demel 1996; Tesfaye 2000), suggests that preservation of plant diversity in the dry Afromontane forests of Ethiopia mainly depends on the conservation and sustainable utilization of the remnant forests. In addition, effective vegetation restoration on degraded lands and abandoned farm fields in the dry Afromontane regions of the country needs to be based on active management strategies rather than just relying on natural succession originating from the SSB and/or seed rain.

Conclusions

Our results showed that clearance of Afromontane natural forest followed by subsequent cropping alters the composition and density of viable seeds in SSB. Deforestation followed by subsequent cultivation resulted in a more or less continuous exhaustion of seeds of woody species from the SSB. This shows that deforestation, driven mainly by the need for more land for permanent agriculture, is a threat to the diversity of the tropical dry Afromontane forest in the highlands of Ethiopia, not only through direct removal of the above ground forest vegetation but also through gradual exhaustion of viable seed reserves of the woody species in the SSB.

Since fresh dispersal of seeds will be needed for the restoration of native woody species on abandoned agricultural sites in the future, there is a desperate need for urgent interventions, backed by appropriate policy and legislation instruments, which could prevent or reduce deforestation and enhance development, conservation and sustainable utilization of the remnant dry Afromontane forests. Furthermore, future planning for rapid forest vegetation restoration on degraded abandoned farm fields should be designed based on strategies that include measures other than relying only on SSB.

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Appendix 1. List of identified plant species recovered through germination from the soil samples collected from a chronosequence of six farm fields and the adjacent natural forest (NFSSB = Natural Forest Seed Bank; + (present) and – (absent) in southern Ethiopia).

Species	NFSSB	Time since conversion to arable land					
		7	10	14	26	34	53
				TREES			
Croton macrostachyus	+	+	–	–	–	–	–
Eucalyptsu saligna	–	–	+	–	+	+	+
Vernonia amygdalina	–	+	–	+	+	–	–
Vernonia auriculifera	+	+	+	–	–	+	–
				SHRUB			
Sida ternata	+	+	–	–	–	–	–
				HERBS			
Achmella caulirhiza	–	+	–	+	+	+	+
Alchemilla sp.	–	–	+	+	–	–	–
Amaranthus sp.	–	–	–	+	+	–	+
Asterolinum adoënse	–	+	–	–	+	+	+
Bidens pilosa	–	+	–	–	+	+	+
Brassica carinata	–	–	–	–	–	+	–

Contd...

Appendix 1. continued.

Centella asiatica	+	–	–	–	–	–	–
Ceraastum sp.	+	+	–	–	–	–	–
Chenopodium album	+	–	–	–	–	–	–
Chrysanthemum sp.	+	–	–	–	–	+	–
Cotula abyssinica	–	+	–	–	–	–	+
Crassula alsinoides	+	+	+	+	+	+	+
Cyperus sp.	+	+	+	–	–	+	–
Datura stramonium	–	+	–	–	–	–	–
Dichondra repens	+	–	–	+	+	+	–
Dichrocephala integrifolia	–	+	–	–	–	+	–
Erucastrum arabicum	–	+	–	+	+	+	–
Falkia oblonga	+	+	–	+	–	–	–
Galinsoga parviflora	+	+	+	+	+	+	+
Galinsoga quadriradiata	+	+	+	+	+	+	+
Geranium arabicum	+	+	+	+	+	+	+
Girardenia diversifolia	+	+	+	+	+	+	+
Gossypium sp.	–	+	–	–	+	–	–
Guizotia schmperiana	–	–	+	–	+	+	–
Hypoestes trifolia	+	–	–	–	–	–	–
Laggera crispata	+	–	–	–	–	+	–
Monopsis stellarioides	–	+	–	–	–	+	+
Nicandra physaloides	–	–	–	+	–	–	–
Oxalis corniculata	+	+	+	+	–	–	–
Pavonia schimperiana	+	+	–	–	+	+	+
Periscaria nepalensis	+	+	+	+	+	+	+
Pilea tetraphylla	+	+	+	+	+	+	+
Plectranthus sp.	+	+	–	–	–	–	–
Scadoxus multiflorus	+	–	–	+	–	–	–
Scleranthus annus	–	+	–	+	+	+	–
Sida sp.	–	+	–	–	–	–	–
Solanium indicum	+	+	+	–	–	–	–
Solanum nigrum	+	+	+	+	+	+	+
Sonchus oleraceus	–	+	–	–	–	–	–
Spilanthus mauritiana	–	+	+	–	–	–	+
Veronica abyssinca	+	+	+	+	+	+	+
Veronica javanica	+	+	+	+	+	+	+
				CLIMBER (HERB)			
Zehneria scabra	–	–	+	–	–	–	–
				GRASSES AND SEDGE			
Cyperus sp.	–	+	+	–	–	+	–
Eleusine indica	+	+	+	+	+	+	–
Eragrostis schweinfurthii	–	+	–	+	–	–	–
Poa leptoclada	+	+	+	+	+	+	+
Snowdenia polystachya	–	–	+	–	+	+	+
Poaceae sp.	+	–	–	–	+	–	+

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