

OPEN

Study of Soil Seed Banks in Ex-closures for Restoration of Degraded Lands in the Central Rift Valley of Ethiopia

Shemsedin Ahmed Mohammed^{1,2*} & Mekuria Argaw Denboba²

Soil seed banks (SSB) can be important components in the process of rehabilitating degraded lands. Thus, this study was aimed to evaluate the role of SSB to the restoration of degraded lands in six, fifteen and twenty-five year's ex-closures and adjacent degraded open grazing land (DOGL). Totally, 160 samples of SSB from four soil layers (litter, 0–3 cm, 3–6 cm & 6–9 cm), four sites and ten in a composite of 5 (15 × 15 cm) were collected and tested for seed viability through seed extraction and seedling emergence methods. Species richness and diversity showed a significant difference between the SSB of the ex-closures and DOGL ($P = 0.0148$ and $P = 0.0218$ respectively). Seed densities also showed significant differences between the vertical layers of the soils in the ex-closures and DOGL ($P = 0.0112$) and the interaction effect of the land use type and the vertical soil layers ($P = 0.0174$). Ex-closures and DOGL scored highest seed densities in their litter and bottom layers of the soils respectively. Most of the woody species in the SSB of older ex-closures were represented in the aboveground flora. Thus, this study has verified that SSB has played a vital role in the restoration of woody species in degraded land through ex-closure practices.

Large areas of the world's land have been degraded and landscapes everywhere are being simplified by different land-use practices¹ and it became one of the most challenging concerns of environmentalists. Land degradation in Ethiopia through deforestation, agricultural land expansion, overgrazing, cutting of trees for fuelwood and construction materials is one of the national and local environmental challenges^{2–4}. Avoiding the stress and allowing the degraded land to recover readily by itself had perceived as the most important tool next to the preservation of the original habitats and it has been widely recognized as a means of preventing the continual loss of biodiversity and receiving considerable attention. Hence, counteracting the degradation of vegetation to rehabilitate degraded lands had been one of the central concerns of the government and non-government organizations in Ethiopia⁵.

Therefore, government and non-government organizations have been promoted and started rehabilitation practices on the degraded lands of the country using a set of passive rehabilitation measures particularly ex-closures were dominantly practiced^{2,4,5}. Thus, ex-closures are rehabilitation techniques where, degraded land areas are closed off from the interference of human and domestic animals to lessen land degradation of formerly degraded open grazing lands, promoting natural regeneration of plants and replenish biodiversity and restore soil fertility^{5–7}. In ex-closures practices, it is believed that a degraded ecosystem recovers readily by itself in the absence of stress or disturbance through what is termed as “passive restoration”⁸.

In the passive restoration of degraded lands, the presence of viable soil seed banks and changes in environmental conditions such as moisture, light regime, and temperature fluctuations are very essential which may bring about the germination of dormant seeds that have remained viable in the soil for several years⁹. This implied that species overcome periods of unfavourable weather conditions by building up large seed stock in the soil, which is known as “soil seed banks”. This strategy protects plant species diversity against local extinction of the species during the disturbance and provides information on the past population dynamics and structure and future regeneration potential of degraded land¹⁰. Thus the “soil seed banks” are defined as an aggregation of viable seeds in the soil and the upper litter of the soil which are capable of replacing adult plants in a degraded ecosystem and

¹Department of Environmental Science, College of Natural and Computational Science, Wolaita Sodo University, Wolaita Sodo, Ethiopia. ²Center for Environmental Science, College of Natural and Computational Science, Addis Ababa University, Addis Ababa, Ethiopia. *email: shemsu1985@gmail.com

Land-use type	mean (\pm SE) richness	mean (\pm SE) diversity	Shannon-Wiener diversity index (H')
Degraded open grazing land	3.7 \pm 0.49	0.94 \pm 0.18	2.03
Six years ex-closure	2.9 \pm 0.35	0.74 \pm 0.13	1.84
Fifteen years ex-closure	4.3 \pm 0.25	1.15 \pm 0.07	1.78
Twenty-five years ex-closure	4.7 \pm 0.34	1.28 \pm 0.07	2.01

Table 1. Mean (\pm SE) Shannon-Weiner diversity, richness, and index of woody species in the soil seed banks.

a key factor for ecosystem reclamation^{11–14}. Therefore, for a good result to be noted in the restoration process, gathering information on the presence and absence of persistent soil seed banks or sources of re-growth after disturbances are very crucial¹⁵.

Nowadays, area ex-closure is one of the most widespread forms of restoration practices in Ethiopia and as many studies in the northern part of Ethiopia have confirmed that the biophysical conditions of degraded open grazing lands had been recovered and made socioeconomic benefits to the local communities^{4,16–19}. However, studies on the contribution of soil seed banks to the rehabilitation of degraded lands, particularly in area ex-closure practices were lacking. Thus, there were no documented studies on the status of soil seed banks in the degraded lands before the establishment of ex-closures and after the establishment of ex-closures thereby its role in the restoration process. However, research-based knowledge on such matters is very essential in planning the restoration of degraded land through ex-closure practices, and this study was designed to reduce the knowledge gap on the status of woody species in the soil seed banks of degraded open grazing land and ex-closures of different ages so the role of soil seed banks to a restoration process. Therefore, in Alaba district in the central rift valley of southern Ethiopia, ex-closures with six years, fifteen years and twenty-five years duration from their establishments in Choroko-1, Hebibo and Asore peasant associations respectively were selected for this study. Besides, adjacent to the ex-closures degraded open grazing land (DOGL) in Keranso was selected. Thus, the degradation status of DOGL in Keranso was with the assumption of in a similar status of degradation with the above-mentioned ex-closures before the establishment of the ex-closures.

Thus, the general objective of this study was to investigate the role of soil seed banks in the restoration of degraded lands through ex-closure practices in the central rift valley, southern Ethiopia. The emphasis was to: (1) Determine the composition, density, diversity and richness of woody species in the soil seed banks of six, fifteen, twenty-five years ex-closures and DOGL, (2) Investigate the soil seed bank distribution of woody species in the vertical layers of the soils in the six, fifteen, twenty-five years ex-closures and DOGL, (3) Examine and compare the similarities between woody species richness and diversity in the soil seed banks and their respective aboveground standing woody species in the six, fifteen, twenty-five years ex-closures and DOGL thereby to determine the role of soil seed banks to the restoration of woody species in the ex-closures.

Results

Species composition of soil seed banks. A total of 16 woody species in 12 families were recovered from the litter and the top nine centimetres of the soil samples collected from all the ex-closures and DOGL (Supplementary Table S1). From this total eight, seven, twelve and ten species were recovered from DOGL, six, fifteen and twenty-five years ex-closures respectively. While, six, seventeen, twenty-four and thirty-three aboveground standing woody species were recorded from the aboveground sample vegetation inventory of the DOGL, six, fifteen and twenty-five years ex-closures respectively. Fabaceae was represented by four species (25%) of all woody species in the soil seed banks of ex-closure and DOGL. The remaining 11 families were represented by only one species each. The higher proportion (75%) of the total species were trees and shrubs constitute only 25% of the life forms of the woody species in the soil seed banks. *Acacia torotolis* (Forssk.) Hayne, *Calpurnia aurea* (Ait.) Benth and *Dodonaea angustifolia* L.f were the only species detected in all the sampling sites.

Planted woody species during the establishment of the ex-closures as enrichment planting constitutes 24%, 16% and 15% of the total sample standing woody species in the six, fifteen, twenty-five years ex-closures respectively. The rest larger proportion 76%, 84% and 85% of the sample standing woody species in the six, fifteen, twenty-five years ex-closures respectively were not planted which were regenerated indigenous species (Supplementary Table S1).

Woody species richness and diversity in the soil seed banks. The land-use type had shown a significant difference in the woody species richness and diversity in the soil seed banks ($P = 0.0148$) and ($P = 0.0218$) respectively. Thus, the mean \pm standard error (SE) woody species richness was (3.7 \pm 0.49), (2.9 \pm 0.35), (4.3 \pm 0.25) and (4.7 \pm 0.34) for DOGL, six, fifteen and twenty-five years ex-closures respectively. While, the mean (\pm SE) woody species diversity was (0.94 \pm 0.18), (0.74 \pm 0.13), (1.15 \pm 0.07) and (1.28 \pm 0.07) for DOGL, six, fifteen and twenty five years ex-closures respectively (Table 1). The result through Eq.(1) showed the highest overall Shannon-Wiener diversity index of the soil seed bank was recorded in the DOGL ($H' = 2.03$) (Table 1) and the least Shannon-Wiener diversity index was recorded in fifteen years ex-closure.

The density of seeds in the soil. The overall total seed densities (D) per square metre (m^{-2}) were 155 m^{-2} , 107 m^{-2} , 265 m^{-2} and 275 m^{-2} for DOGL, six, fifteen and twenty-five years ex-closures respectively (Supplementary Table S1). The mean (\pm SE) seed densities (m^{-2}) of soil seeds down to 9 cm of soils were (15.5 \pm 3.2), (10.7 \pm 3.0), (26.5 \pm 12.3) and (27.5 \pm 7.7) for DOGL, six, fifteen and twenty five years ex-closures

Land-use type	mean (\pm SE) seeds densities	Layers of soil			
		Litter	0–3 cm	3–6 cm	6–9 cm
Degraded open grazing land	15.5 \pm 3.2	1.8 \pm 1.2	3.9 \pm 1.5	3.9 \pm 1.2	5.7 \pm 2.0
Six years ex-closure	10.7 \pm 3.0	2.1 \pm 1.3	2.6 \pm 1.2	3.4 \pm 1.1	2.1 \pm 1.0
Fifteen years ex-closure	26.5 \pm 12.3	15.4 \pm 7.8	6.2 \pm 3.0	3.0 \pm 1.7	1.8 \pm 1.2
Twenty-five years ex-closure	27.5 \pm 7.7	17.3 \pm 6.6	3.5 \pm 1.6	6.1 \pm 2.5	0.4 \pm 0.4

Table 2. Mean (\pm SE) seeds densities m^{-2} recovered from the soil seed banks.

Source of variations	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Land-use type	3	531	176.8	2.0177	0.1141
Soil Layer	3	1007	335.7	3.830	0.0112*
Soil layer*land-use type	9	1842	204.7	2.336	0.0174*
Residuals	144	12622	87.7		

Table 3. Results of two way ANOVA test to soil seed bank density across soil layers and each land use type. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘.’ 1.

respectively (Table 2). The overall mean densities of the soil seeds did not show significant variation between the land use types ($P = 0.1141$) (Table 3).

Carissa edulis (Forssk.) Vahl exhibited the highest seed density (31 seeds m^{-2}) and it accounts for 20% of the total seed density in the DOGL. While the highest density of seeds was scored by *Dodonaea angustifolia* L.f in all ex-closure sites with 27 seeds m^{-2} , 133 seeds m^{-2} and 84 seeds m^{-2} in six, fifteen and twenty-five years ex-closures respectively.

Vertical distribution of seeds in the soil layers. Seeds of woody species in the soil seed banks showed different distributions between the vertical layers of the soil. For instance, the mean (\pm SE) seeds densities (m^{-2}) recovered from the soil seed banks showed the highest (5.7 \pm 2.0) in the bottom (6–9 cm) layer and the least (1.8 \pm 1.2) in the top (litter) layer of the DOGL (Table 2). In contrary to this, the highest and the least mean (\pm SE) seed densities (m^{-2}) recovered from the soil seed banks of twenty-five years ex-closure was (17.3 \pm 6.6) and (0.4 \pm 0.4) in the top (litter) layer and in the bottom (6–9 cm) layer respectively. As it is shown in Table 3, the seed densities of the soil seed banks between the land use types did not show a significant difference ($P = 0.1141$). However, there were significant differences in the seed densities of the soil seed banks between vertical layers of the soil samples ($P = 0.0112$) and the interaction effect of the land use types and the vertical soil layers ($P = 0.0174$) (Table 3).

The pattern of seed density from the top (litter) layer to bottom (6–9 cm) layer of soil samples showed various trends in the land use types (Fig. 1a–d). The highest seed density was scored in the litter layers of ex-closures showing an increasing trend of seed densities in the litter layers of the soil from the youngest ex-closure to the oldest ex-closure (Fig. 1c,d). On contrary to this, as the age of ex-closures increases, seed densities in the mineral (0–9 cm) layers of the soils decreased. However, the litter layer of the soil samples from the DOGL scored the lowest seed density and elevated automatically in deep mineral soil layers resulted in highest seed density in the bottom (6–9 cm) layer of the soil (Fig. 1a).

Similarities between species compositions of soil seed banks and aboveground woody species. The similarities between the soil seed banks and aboveground vegetation had Jaccard’s Coefficient of similarities (JCS) value of 0.4, 0.2, 0.44 and 0.27 in DOGL, six, fifteen and twenty-five years ex-closures respectively (Table 4). Thus, the lowest JCS was scored in the six years ex-closure and the highest JCS was in twenty-five years.

The number of woody species in the aboveground standing vegetation was much higher than the number of woody species in the soil seed banks of ex-closures. Thus, the proportion of woody species in the soil seed banks which were represented in the aboveground standing vegetation showed substantial variation across the age of ex-closures. For instance, 50%, 57%, 92%, and 90% of all the woody species of the soil seed banks in the DOGL, six, fifteen and twenty-five years ex-closure respectively had represented in the aboveground flora of each site (Fig. 2 and Supplementary Table S2).

Discussions

The highest overall Shannon-Wiener diversity index of the soil seed bank was recorded in the DOGL ($H' = 2.03$) (Table 1) that indicating relatively highest abundance and evenness of woody species was scored in the soil seed banks of DOGL²⁰. The overall highest seed density was scored in the fifteen and twenty-five years ex-closures which could be the result of the presence of matured woody species in the old ex-closures that could produce new seeds to the soil. However, the six years ex-closure scored the lowest seed density of all the land use types. This could happen when regeneration of seedlings from the soil seed banks triggered by the establishment of ex-closure is damaged or eaten by livestock which is entered into the ex-closed area illegally. That is, once the seeds in the soil emerged following the conducive environments created due to the establishment of the

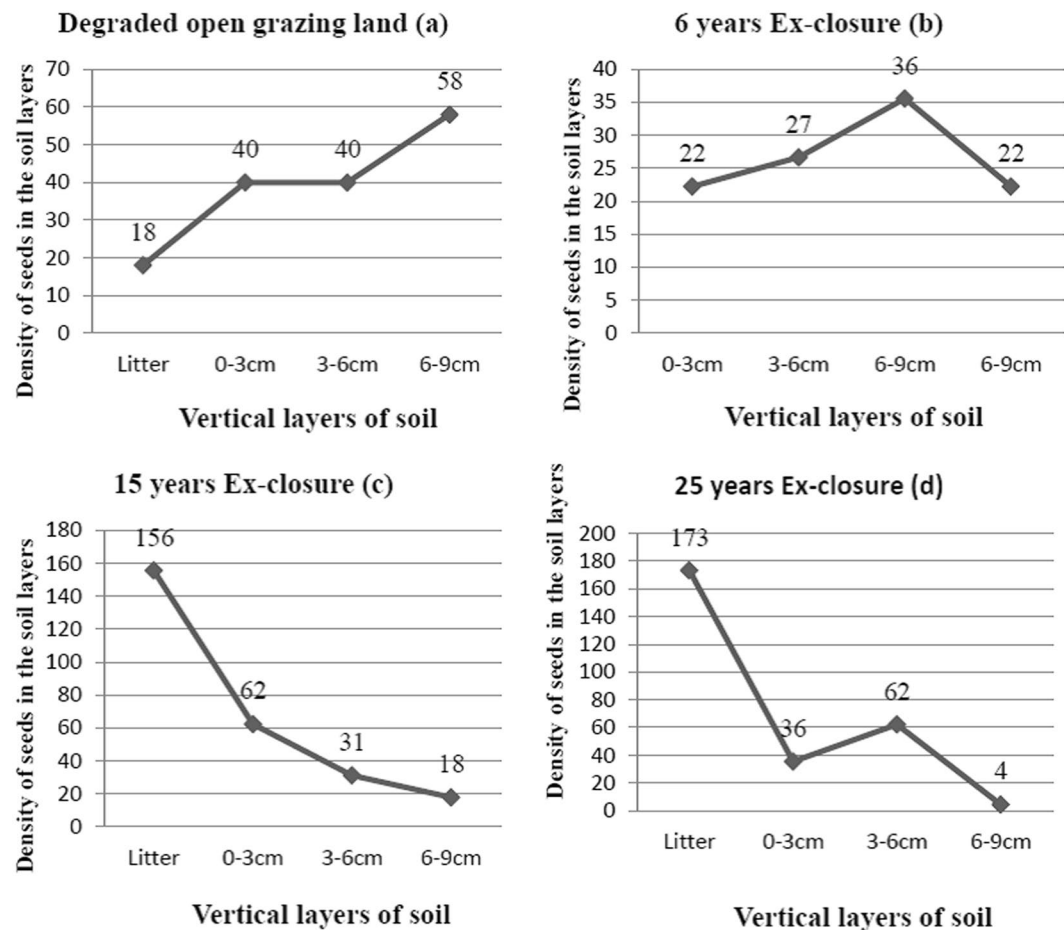


Figure 1. The density of total seeds in the vertical layers of soil in each land-use type.

Land-use type	Jaccard's similarity index
Degraded open grazing land	0.4
Six years ex-closure	0.2
Fifteen years ex-closure	0.44
Twenty-five years ex-closure	0.27

Table 4. Jaccard's Coefficient of Similarities of woody species composition in the soil seed banks and aboveground woody species.

ex-closures, no more those seeds in the soil seed banks would be available unless other matured trees produce and supply it which is rare in degraded lands.

The number of woody species in the soil seed banks of all ex-closures was lower than the number of their respective aboveground woody species and most of the woody species in the soil seed banks were represented in their respective aboveground woody species. Besides, a larger proportion of the sample standing woody species in the ex-closures were indigenous species regenerated from the soil seed banks following the establishment of the ex-closures. Most of the soil seed bank species were germinated in ex-closures by using the advantages of encouraging environmental conditions like increased soil moisture, organic matter, and other soil nutrients generated following the removal of the external stress by the ex-closure practices^{2,18}.

However, the number of woody species in the soil seed banks of DOGL was higher than the number of its respective aboveground woody species and only half of the soil seed bank species in the DOGL were represented in their respective aboveground woody species and the rest kept as viable in the soil seed banks until the surrounding edaphic and climatic conditions improved. Thus, these explicitly verified that soil seed banks well kept up seeds of woody species for the period of unfavourable environmental conditions and played a foremost role in woody species restoration in the degraded lands through ex-closure practices. Information about the past vegetation composition and the structure of a future population can provide by soil seed banks. Similarly, many previous studies agreed that the composition of the seed banks mainly depends on seed production and composition of the current and previous vegetation, as well as on the seed longevity of each species^{21,22}.

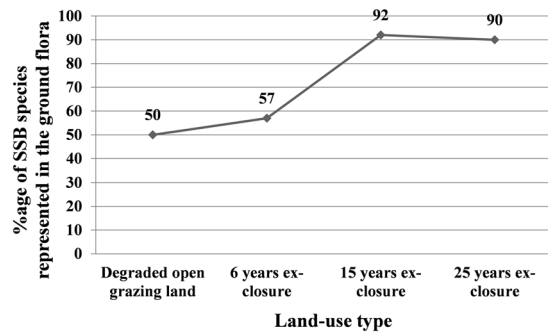


Figure 2. The proportion of soil seed bank species denoted in the above-ground flora of each land-use types.

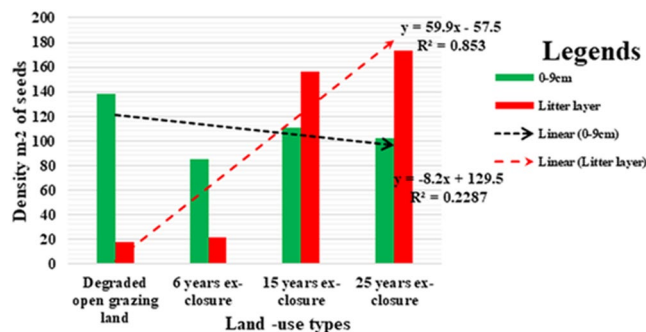


Figure 3. The density (m⁻²) of seeds in the litter layer and sum total of other layers (0–9 cm).

The variation of representation of most of the woody species of the soil seed banks in the aboveground standing woody species of ex-closures in different ages implies the presence of various longevity potential of seeds of woody species in the soil seed bank environments. Thus, the 10% of the woody species in the soil seed banks which had not denoted in the aboveground flora of twenty-five years ex-closure indicating that some seeds of woody species in the soil seed banks could stay more than twenty-five years as persistent until specific environmental requirements of woody species germinations are changed. The length of time in which seeds can remain viable in the soil can be affected by germination, dormancy, and viability of the seeds, the environmental conditions where seeds available and subsequent changes²³. Thus, this result indicated that some seeds of woody species in the soil seed banks could stay more than twenty-five years as persistent until specific environmental requirements of the species to germinations are improved.

As the age of ex-closures increases, seed densities in the mineral (0–9 cm) layers of the soils decreased (Fig. 1a–d). Such patterns could happen due to increased woody species coverage in the older ex-closures using the favourable environmental conditions created due to ex-closures resulted in the production and supply of new seeds to the litter layers from matured trees. The increasing trends of seed densities from litter to bottom layers of the soils in the DOGL was seen (Fig. 1a) and could be caused by the absence of enough matured trees in the DOGL that can supply new seeds to the litter layer and/or predation and/or damage of seeds of the available standing woody species by livestock^{24,25}.

Even as it is illustrated in Fig. 3, the total seed densities in the entire three lower (0–9 cm) soil layers showed a decreasing trend from DOGL to older ages of ex-closures. While the density of seeds in the litter layers showed an increasing trend from DOGL to older ages of ex-closures. This could happen because seeds in the mineral soil of ex-closures germinated after conducive environments created after the ex-closures establishment and new seeds production from matured trees in the older ex-closures. But, in cases of DOGL, seeds had not germinated but stored in the mineral soil with rare or no production and addition of new seeds on the litter layers. Thus, it clearly showed that persistent seeds of woody species had been preserved in the soil seed banks of degraded lands until edaphic and climatic conditions are changed and would play a vital role in the restoration process.

Conclusions

Almost all of the soil seed bank species in the older ex-closures were regenerated from the soil seed banks following the establishment of the ex-closures and represented in their respective aboveground standing woody species. However, only half of the soil seed bank species in the degraded open grazing land were denoted in their respective aboveground woody species. The rest half of the soil seed banks kept as viable until the degradation conditions improved. Only 10% of all the woody species in the soil seed banks are represented in the above-ground flora of the twenty-five years ex-closure showing that some seeds of woody species in the soil seed banks could stay more than twenty-five years as persistent until specific environmental requirements of the species to germinations are improved. Therefore, this study undoubtedly verified that soil seed banks kept up seeds of woody

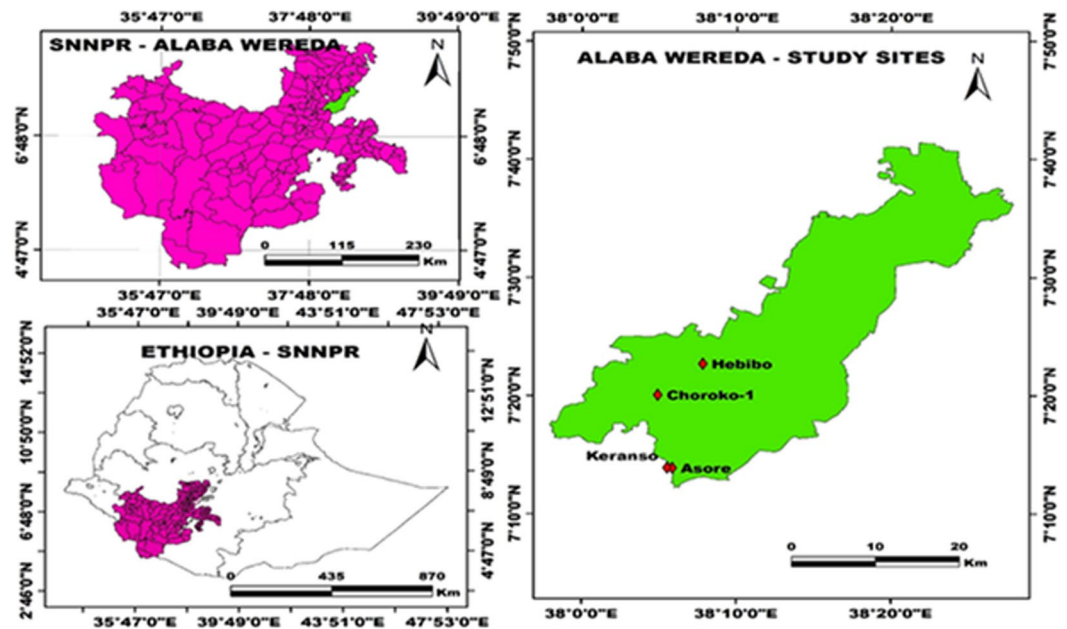


Figure 4. Location map of the study area.

species for the period of land degradations until environmental conditions improved and played the foremost role in woody species restoration in the degraded lands through ex-closure practices. Finally, while planning to establish an ex-closure in degraded land, it is also important to examine the level of degradation thereby determining the potential of soil seed banks to regenerate woody species. This could save the costs related to enrichment planting in the degraded lands.

Materials and Methods

Study area. The study area is located in Alaba district in the central Rift Valley of southern Ethiopia (Fig. 4). The area is located $7^{\circ}18'37''$ N latitude and $38^{\circ}5'49''$ E longitude within the Bilate River Catchment Area. The altitudinal range of the Woreda is 1554–2149 m.a.s. Annual rainfall varies from 857 to 1085 mm, and the annual mean temperature varies from 17° to 20° C. It is highly likely that much of the Woreda was once covered with closed dry evergreen Afromontane forests²⁶. However, deforestation and the expansion of crop production and pasture lands for a long period have reduced to the present forest cover about 7%. Crop cultivation, livestock rearing, and apiculture are the main sources of livelihood. Three ex-closures and one degraded adjacent open grazing land site in similar agro-ecological zones were selected based on their duration of the establishment. These were Choroko-1 (six years), Hebibo (fifteen years), Asore (twenty-five years) ex-closures and degraded open grazing land (Keranso) (Fig. 4).

Soil seed bank sampling. To collect the soil samples, parallel transect lines were prepared horizontally from one end of the site to the other end in 150 to 300 m width based on the size of the sites. The number of transects per site was based on altitudinal variation and the total area of the site^{2,25}. The soil samples were taken from a quadrat of 20 m \times 20 m along the transect lines. In the quadrats along the transects, two lines from one corner to the opposite corners were crossed each other and at the four corners and at the intersection point of the two lines at the center of each quadrat 15 cm \times 15 cm square was marked (Supplementary Fig. S3) and soil samples removed carefully by using a sharp knife and a spoon and put into plastic bags. The soil samples were carefully separated into four vertical layers (litter layers, 0–3 cm, 3–6 cm and 6–9 cm)²⁵. Thus, a total of 160 soil samples (4 land uses \times 4 vertically successive layers \times 10 soil samples from each site) were collected. The soil samples from similar layers in the quadrats were combined to form a composite soil sample. The litter layer was included with the soil samples as the fourth layer because according to to²³ all viable seeds and fruits present on or in the soil and associated litter/humus are considered as soil seed banks.

The soil sample collection was completed within three weeks after the starting of it to avoid any temporal bias in seed availability and composition²⁷. The samples from each of the soil layers were used to determine variations of seed distribution at each depth of the soil layers²⁸ and the samples from each site were used to study the quantity and composition of soil seed banks in the ex-closures of different age and adjacent degraded open grazing land. Soil samples from each layer were coded into plastic bags and transported to Hawassa University, Wondo Genet College of Forestry and Natural Resources for using the greenhouse of the college for incubation and facilitate the germination process of the soil seeds.

Soil seed identification. Although methods that have been used for determining the number of seeds in the soil seed banks were controversial, the most frequently used techniques for determination of quantity of seeds in the soil were (1) placing soil samples in a suitable places for germination of seeds in the soil (seedling emergence

method)²⁹ and (2) using physical separation of seeds from the soil particles based on the differences in size and density of the seeds (seed extraction method)³⁰. Many researchers prefer the seedling emergence method to seed extraction method assuming that the seedling emergence method is more reliable than seed extraction method^{31–33}. Even, the best way to determine the presence and quantity of seeds in the soil is simply observing the seedlings emerging in the sites¹¹. Both seedling emergence and sieving methods also used at the same time in different studies of soil seed banks^{15,25,34,35}. In this study, both “seed extraction” and “seedling emergence” methods were used for determining the quantity and composition of seeds of the soil seed banks (Supplementary Figs. S1, S2).

Experimental design. Soil samples were first sieved with a mesh size of 2 mm and then using a mesh size of 0.5 mm to recover seeds of various woody species^{36,37}. All the seeds recovered from the sieving process were subjected to viability tests through dissecting of the seeds in which seeds with white and firm content were considered viable^{15,25,38}. Then all viable seeds in each sample were counted²⁵. The recovered seeds were collected into paper bags and taken back to the study area for species identification by using seeds of standing vegetation as a local reference.

Soil samples remained after sieving were taken to germination trials in a greenhouse (Fig. S1) to control and detect contamination of external seed rain. The soil samples were spread in plastic trays that pierced at the bottom to facilitate proper drainage of water for germination of the seeds. Daily temperature for the greenhouse ranged from 19 to 32 °C. The seedling trays were kept continuously moist by daily watering²⁷. The soil samples were stirred once in two weeks stimulating them to germinate because mixing is known to cause more seeds to germinate³⁹. The emerging seedlings which were readily identifiable were counted, recorded and discarded²⁵. Seedlings that were difficult to identify were transplanted for further growth and identification. Seedling identification was terminated after 6 months.

Aboveground woody species sample data collection. The aboveground woody species (trees and shrubs) data collected from the three ex-closures under different ages and adjacent degraded open grazing land. A total of 120 quadrats 30 from each laid along transect lines having a quadrat size of 20 m × 20 m (400 m²). The altitude of each quadrat was recorded by using a global positioning system (GPS) devices 3 m level of accuracy. The total numbers of each woody species in each quadrat were recorded. Woody species encountered were identified by their vernacular and scientific names based on own experience supported by plant knowledge of local elders^{40,41} and the Flora of Ethiopia and Eritrea^{42–44}. For species that were difficult to identify in the field, herbarium specimens were collected, pressed, dried and transported to the National Herbarium in Addis Ababa University, for proper identification.

Data analysis. The species richness (S), diversity and density of seeds in the soil were determined by combining the data obtained by “seed extraction” and “seedling emergence” methods. The density of seeds was derived from the total number of seeds recovered from the soil samples. On the other hand, to analyze the depth distribution of seeds in each site, the number of seeds recovered in similar layers were combined and converted to provide the density of seeds m⁻² at that particular soil depth⁴⁵.

The species diversity and evenness of seeds recovered from the soil seed banks from the four study sites were calculated using the Shannon-Wiener index⁴⁶:

$$\text{Shannon diversity index, } H' = - \sum_{i=1}^s p_i \ln p_i \quad (1)$$

Where: H' = species diversity index; \ln = natural logarithm and $P_i = n/N$ is the proportion of individuals found in the i^{th} species (ranges 0 to 1); n = number of individuals of a given species; and N = total number of individuals found in that particular site.

The significance of mean species richness and diversity between the land use types were compared using one-way ANOVA. While the mean differences of seed densities concerning the land use types and vertical layers of the soil were compared using two-way ANOVA. Significance was determined at an alpha level of 0.05. All the data obtained were analysed by statistical software R version 3.4.1. The similarity of the species composition between soil seed banks and that of the standing vegetation was calculated with Jaccard's coefficient of similarity (JCS)⁴⁷.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Received: 6 June 2019; Accepted: 19 December 2019;

Published online: 22 January 2020

References

1. Dobson, A. P., Bradshaw, A. & Baker, A. á Hopes for the future: restoration ecology and conservation biology. *Science* **277**, 515–522 (1997).
2. Mengistu, T., Teketay, D., Hulthen, H. & Yemshaw, Y. The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. *Journal of Arid Environments* **60**, 259–281 (2005).
3. Tigabu, M., Mulugeta, L., Negash, M. & Teketay, D. Rehabilitation of degraded forest and woodland ecosystems in Ethiopia for the sustenance of livelihoods and ecosystem services. *IUFRO World Series* **32**, 299–313 (2014).
4. Mebrat, W. Natural regeneration practice in degraded high lands of Ethiopia through area enclosure. *International Journal of Environmental Protection and Policy* **3**, 120–123 (2015).
5. Lemenih, M. & Kassa, H. Re-greening Ethiopia: history, challenges and lessons. *Forests* **5**, 1896–1909 (2014).

6. Aerts, R., Nyssen, J. & Haile, M. On the difference between. *Journal of Arid Environments* **73**, 762–763 (2009).
7. Mekuria, W. & Aynekulu, E. Exclosure land management for restoration of the soils in degraded communal grazing lands in northern Ethiopia. *Land Degradation & Development* **24**, 528–538 (2013).
8. Miao, R. *et al.* Soil seed bank and plant community development in the passive restoration of degraded sandy grasslands. *Sustainability* **8**, 581 (2016).
9. Harper, J. L. Population biology of plants. *Population biology of plants* (1977).
10. Aponte, C., Kazakis, G., Ghosn, D. & Papanastasis, V. P. Characteristics of the soil seed bank in Mediterranean temporary ponds and its role in ecosystem dynamics. *Wetlands Ecology and Management* **18**, 243–253 (2010).
11. Roberts, H. (ACademic preSS, Cambridge, England, 1981).
12. Simpson, R. L. Seedbanks: general concepts and methodological issues. *Ecology of soil seed banks*, 3–8 (1989).
13. Van der Valk, A. Seed bank and management and restoration of natural vegetation. *Ecology of soil seed banks*, 329–346 (1989).
14. González-Alday, J., Marrs, R. H. & Martínez-Ruiz, C. Soil seed bank formation during early revegetation after hydroseeding in reclaimed coal wastes. *Ecological Engineering* **35**, 1062–1069 (2009).
15. Demel, T. Soil seed bank at an abandoned Afromontane arable site. *Feddes Repertorium* **109**, 161–174 (1998).
16. Descheemaeker, K. *et al.* Sediment deposition and pedogenesis in exclosures in the Tigray Highlands, Ethiopia. *Geoderma* **132**, 291–314 (2006).
17. Yami, M., Gebrehiwot, K., Stein, M. & Mekuria, W. Impact of Area Enclosures on Density and Diversity of Large Wild Mammals: The Case of May Ba ti, Douga Tembien District, Central Tigray, Ethiopia. *East African Journal of Sciences* **1**, 55–68 (2007).
18. Mekuria, W. & Yami, M. Changes in woody species composition following establishing exclosures on grazing lands in the lowlands of Northern Ethiopia. *African Journal of Environmental Science and Technology* **7**, 30–40 (2013).
19. Abesha, G. A. Herbaceous vegetation restoration potential and soil physical condition in a mountain grazing land of Eastern Tigray, Ethiopia. *Journal of Agriculture and Environment for International Development (JAEID)* **108**, 81–106 (2014).
20. Woldu, Z. *Environmental and Ecological Data Analysis: Basics, Concepts and Methods*. (LAP LAMBERT Academic Publishing (2012).
21. López-Mariño, A., Luis-Calabuig, E., Fillat, F. & Bermúdez, F. Floristic composition of established vegetation and the soil seed bank in pasture communities under different traditional management regimes. *Agriculture, Ecosystems & Environment* **78**, 273–282 (2000).
22. Jensen, K. Species composition of the soil seed bank and seed rain of abandoned wet meadows and their relation to aboveground vegetation. *Flora* **193**, 345–359 (1998).
23. Teketay, D. Seed and regeneration ecology in dry Afromontane forests of Ethiopia: I. Seed production-population structures. *Tropical Ecology* **46**, 29–44 (2005).
24. Nepstad, D. C., Uhl, C. & Serrao, E. A. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio (Sweden)* **20**, 248–255 (1991).
25. Teketay, D. & Granström, A. Soil seed banks in dry Afromontane forests of Ethiopia. *Journal of Vegetation Science* **6**, 777–786 (1995).
26. Friis, I., Demissew, S. & Van Breugel, P. *Atlas of the potential vegetation of Ethiopia*. (Det Kongelige Danske Videnskabernes Selskab 2010).
27. López-Toledo, L. & Martínez-Ramos, M. The soil seed bank in abandoned tropical pastures: a source of regeneration or invasion? *Revista Mexicana de Biodiversidad* **82**, 663–678 (2011).
28. Lemenih, M. & Teketay, D. Changes in soil seed bank composition and density following deforestation and subsequent cultivation of a tropical dry Afromontane forest in Ethiopia. *Tropical Ecology* **47**, 1–12 (2006).
29. Thompson, K. & Grime, J. P. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *The Journal of Ecology*, 893–921 (1979).
30. Yu, S. & Jiang, G. The research development of soil seed bank and several hot topics. *Acta Phytocological Sinica* **27**, 552–560 (2003).
31. Wang, G. & Liang, X. The Dynamics of Seed Bank on Shapotou Artificially Stabilized Dunes in Chinese Science Abstracts Series B **33**, (1995).
32. Liya, Z. Characteristics of the soil seed bank and the seedling bank in the fenced sandy meadow. *Acta Botanica Boreali-Occidentalia Sinica* **23**, 1725–1730 (2003).
33. Lemauiel, S., Rozé, F. & Clément, B. A Study of the Dynamics of the Seed Banks in a Complex Dune System, with the Aim of Restoration. *Journal of coastal research*, 991–999 (2005).
34. Argaw, M., Teketay, D. & Olsson, M. Soil seed flora, germination and regeneration pattern of woody species in an Acacia woodland of the Rift Valley in Ethiopia. *Journal of Arid Environments* **43**, 411–435 (1999).
35. Senbeta, F. & Teketay, D. Regeneration of indigenous woody species under the canopies of tree plantations in Central Ethiopia. *Tropical Ecology* **42**, 175–185 (2001).
36. Sileshi, D. & Abraha, B. Assessment of soil seed bank composition of woody species in Hgumbirda National Forest Priority Area, Northeastern Ethiopia. *Momona Ethiopian Journal of Science* **6**, 25–44 (2014).
37. Dainou, K. *et al.* Soil seed bank characteristics in Cameroonian rainforests and implications for post-logging forest recovery. *Ecological Engineering* **37**, 1499–1506 (2011).
38. Senbeta, F. & Teketay, D. Soil seed banks in plantations and adjacent natural dry Afromontane forests of central and southern Ethiopia. *Tropical Ecology* **43**, 229–242 (2002).
39. Dutoit, T. & Alard, D. Permanent seed banks in chalk grassland under various management regimes: their role in the restoration of species-rich plant communities. *Biodiversity & Conservation* **4**, 939–950 (1995).
40. Tadesse, K. *Trees of Ethiopia (a photographic guide and description)*. (Washera Publishers, 2012).
41. Teketay, D. *et al.* In *Degraded Forests in Eastern Africa* 31–75 (Routledge, 2010).
42. Hedberg, I. & Edwards, S. Flora of Ethiopia, vol. 3. *The National Herbarium, Addis Ababa and Uppsala University, Uppsala* (1989).
43. Edwards, S., Tadesse, M. & Hedberg, I. Flora of Ethiopia and Eritrea, volume 2, part 2: Canellaceae to Euphorbiaceae. *Uppsala: The National Herbarium, Addis Ababa, Ethiopia, and Department of Systematic Botany* (1995).
44. Edwards, S., Tadesse, M., Demissew, S. & Hedberg, I. Flora of Ethiopia and Eritrea, Volume 2, part 1: Magnoliaceae to Flacourtiaceae. *Addis Ababa, Ethiopia and Uppsala, Sweden: The National Herbarium, Addis Ababa University* (2000).
45. Tesfaye, G., Teketay, D., Assefa, Y. & Fetene, M. The impact of fire on the soil seed bank and regeneration of Harena forest, Southeastern Ethiopia. *Mountain Research and Development* **24**, 354–362 (2004).
46. Shannon, C. E. A mathematical theory of communication. *Bell system technical journal* **27**, 379–423 (1948).
47. Jaccard, P. Distribution de la flore alpine dans le bassin des Dranses et dans quelques régions voisines. *Bull. Soc. Vaudoise Sci. Nat.* **37**, 241–272 (1901).

Acknowledgements

The authors greatly acknowledge the Center for Environmental Science, Addis Ababa University for financial support; Hawassa University, Wondo Genet College of Forestry and Natural Resources for allowing the greenhouse to seedling germination process; Alaba special Woreda office of Agriculture and Natural Resources for guiding and good cooperation in field data collection. This research was funded by the Center for Environmental Science, Addis Ababa University.

Author contributions

S.A. carried out designing the research idea, method design, field data collection, data analysis, and interpretation, prepare draft of the manuscript, and structuring the report; M.A. participated in method design, data analysis, and interpretation, and structuring the report. Both authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41598-020-57651-1>.

Correspondence and requests for materials should be addressed to S.A.M.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2020