Persistent Soil Seed Banks for Natural Rehabilitation of Dry Tropical Forests in Northern Ethiopia

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Summary

Dry tropical forests are threatened world-wide by conversion to grazing land, secondary forest, savannah or arable land. In Ethiopia, natural dry forest cover has been decreasing at an alarming rate over the last decennia and has reached a critical level. Efforts like the rehabilitation of dry forests to curb this ecological degradation, need a stronger scientific basis than currently available. The aim of the present research was to test the hypothesis whether soil seed banks can contribute to natural forest regeneration in the dry forest of Ethiopia. Therefore, the composition of the seed bank in relation to vegetation and abiotic environment was analysed in four forest relics and four exclosures, i.e. demarcated land areas under strict conservation management, in the highlands of Tigray, northern Ethiopia. Results show strong relationships between natural vegetation, seed bank composition, soil chemical characteristics and environmental degradation, as evidenced through characteristics such as land use impact and soil depth. Most striking is the presence of only very few woody species in the seed bank of degraded areas. This suggests that seed banks only play a minimal role in natural forest recovery in the study area. If this is true, natural recovery will primarily depend on presence of seed trees in the vicinity and successful seed dispersal mechanisms. This result underlines the importance of sustainable management of the few remaining forest relics and trees outside these relics.

Résumé

Banques de semences persistantes pour la réhabilitation naturelle des forêts tropicales sèches du nord de l'Ethiopie

Les forêts sèches tropicales sont mondialement menacées à cause de leur conversion en pâturages, forêts secondaires, savanes et terres agricoles. En Ethiopie, la surface des forêts sèches naturelles a diminué d'une façon alarmante au cours de la dernière décennie et a atteint aujourd'hui un niveau critique. Les efforts comme la réhabilitation des forêts sèches en vue de freiner cette dégradation écologique nécessitent une base scientifique plus solide. L'objectif de la présente recherche était de tester l'hypothèse selon laquelle les banques de semences peuvent contribuer à la régénération naturelle de la forêt sèche en Ethiopie. Pour ce faire, la composition de la banque de semences a été analysée dans les montagnes du Tigray, au nord de l'Ethiopie, et a été relatée à la composition de la végétation et à l'environnement abiotique. Ceci a été fait dans quatre forêts reliques et quatre zones protégées, mises en défense contre le pâturage. Les résultats démontrent de fortes relations entre la végétation naturelle, la composition des banques de semences, les caractéristiques chimiques du sol et la dégradation de l'environnement. Le constat le plus frappant est la présence limitée d'espèces ligneuses parmi les semences retrouvées dans les zones les plus dégradées, qui étaient mises en défense peu avant l'échantillonnage. Ceci indique que les banques de semences ne jouent qu'un rôle limité dans la restauration des forêts naturelles dans la zone d'étude. Par conséquent, la reconstitution naturelle va fondamentalement dépendre de la présence de semenciers dans le milieu végétal et de mécanismes de dispersion de graines des essences ligneuses forestières souhaitées. Ce résultat souligne aussi l'importance de réaliser la protection et la gestion durable du nombre limité de vestiges de forêts restants.

Introduction

Ethiopia is characterized by a great bio-physical diversity, dividing the country in several agro-ecological zones, each with a specific fauna and flora. It therefore is an important centre of biodiversity and endemism (5, 24). Due to fast population growth, overgrazing and deforestation for agricultural activities, fuel wood and construction material, overall natural forest cover had decreased to a level of 2.5 percent in 1999, of which only one twelfth has a dense forest structure (28). The combination of high endemism and fast habitat degradation in Ethiopia leads to a great risk of species extinction (24).

Ecological degradation, as evidenced by a declining forest area and several erosion phenomena, is most dramatic in the northern highlands of Tigray, which are suffering from high population pressure (around 40 millions people on 80.000 km^2, with an annual population growth of 2.4% in 2003), extreme rural poverty (GDP of 90 USD in 2003), recurrent drought spells, and war events in the recent decennia (17, 23). In this region, remains of the original climax forest now only occur as sparse forest patches of just a few hectares, either surrounding churches, or in inaccessible places, like cliffs and mountain ridges (21). These small remnants of forest are called forest relics and are classified as dry Afro-montane forest ecosystems, as most forests in the highlands of Ethiopia and Eritrea. Local communities, government and NGOs are tackling the problem of soil and vegetation degradation through building stone bunds on slopes, thus creating terraces, and construction of checkdams in erosion gullies (4, 11, 25). Besides these purely technical measures, biological techniques making use of artificial or spontaneous revegetation nowadays receive more and more attention. These techniques combine both soil stabilisation and

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reforestation. One widely used option here is the creation of closed areas, also called exclosures, i.e. demarcated land areas under strict conservation management, often controlled by a local community (25). In these areas, cultivation, collection of fuel wood and grazing are forbidden, whereas harvesting of grass is strictly controlled in order to allow spontaneous forest regeneration.

In recent years, many scientific projects have been working on increasing the ecological understanding of the highlands of Tigray, e.g. the VIIR EI projects 'Strengthening soil and water conservation training and research', 'Forest rehabilitation through natural regeneration in Tigray, Ethiopia' and 'Fighting desertification in the Tigray Highlands, Ethiopia: lessons to be learnt from successes and failures of soil erosion control measures' (23). These projects should ultimately lead to the development and implementation of management guidelines in cooperation with local communities. One example of such management practice is the gradual replacement of the traditional restoration approach of planting exotics like *Eucalyptus* spp. by a natural rehabilitation strategy. The latter aims at creating closed areas where spontaneous establishment of native tree species may take place. Further improvement of management practices could be achieved if the different aspects of restoration ecology would be understood. One of these aspects, namely spontaneous regeneration with propagation material from persistent soil seed banks, is further considered in the present research.

Persistent soil seed banks, underground stocks of surviving plant seeds, further denoted as seed banks, have been shown to play a crucial role in natural forest rehabilitation in several ecosystems world-wide (2, 3, 26, 27, 29). The reappearance of individual trees may depend on their persistence in the seed bank (3). Many species in ecosystems all over the world make use of seed banks as part of their regeneration strategy. In general, soil seed banks are dominated by seeds of herbaceous species, although they can be highly variable in features such as species number and composition, seed longevity and viability, germination strategies and depth distribution of seeds in the soil (2, 3, 8, 26). The capacity of plant seeds to survive for a longer period of time in the soil, allows species to overcome the often poor establishment and low survival rates of seedlings during drier years typical of the Afro-montane ecosystem (17), and may hence contribute to the re-establishment of plant species lost from the original plant community. The seed bank thus acts as a reserve out of which new recruitment may occur if environmental conditions are favourable (7, 33). In this context, knowledge of seed bank characteristics such as species composition, species richness, spatial distribution of seeds in the soil and seed density [expressed as number of seeds per m², following Warr *et al.* (37)] therefore is critical to understand its role in forest conservation and regeneration. However, even though this has been addressed in the humid tropics (13), very limited research on this topic has been performed in dry tropical forests (6, 10, 11).

Apart from the 'underground' seed bank, attention should also go to the 'aboveground' vegetation, because of its importance in determining seed bank characteristics. As access to the seed bank can be hampered by the fact that seeds are buried in the soil, knowledge of relationships between underground seed bank characteristics and aboveground vegetation could simplify future seed bank inventories in specific situations, by creating the opportunity to draw conclusions on seed bank characteristics based on aboveground information, without the need to heavily disturb the soil itself. Last but not least, as seed bank composition and seed density probably also vary according to abiotic environmental situations, variation in the latter and its influence on seed bank characteristics need to be addressed.

Thus, the objective of the present research was (I) to gain more knowledge on the role of seed banks in stimulating spontaneous vegetation regeneration leading to natural dry tropical forest restoration, by analysing their species composition and abundance; and (II) to examine the relationship between actual seed bank and vegetation. The ultimate goal would be to implement these results in guidelines for sustainable land use management, by linking them with existing artificial plantation and natural regeneration techniques.

Materials and methods

The study area is situated in Central Tigray, in the Dogua Tembien Woreda, an administrative district lying between 1800 and 2800 meters above sea level on the rift shoulder to the West of the Danakil depression (24, 25). Average annual rainfall is about 800 mm, concentrated in the main rainy season from June till September (20). Within this district, eight sites were selected based on accessibility and variation of conditions in lithology, geomorphology, altitude, slope gradient and slope orientation (aspect), so as to generate enough variability in order to obtain a representative sample of the existing variation. Four of these sites are forest relics and four are closed areas, thus representing the major land use systems for possible forest restoration or regeneration.

In each site, four rectangular plots of 100 m² were established, from which data on abiotic environment, characteristics of aboveground vegetation and seed bank characteristics were collected. Each plot received a code format of DDD(d) XY according to the name of the location (DDD(d)) and position (XY) in an imaginary grid superimposed on the site after mapping the latter with a GPS-receiver (Trimble GeoExplorer III GIS Datalogger). Locations HARc (Haragua closed area), GAH (Gahe), KUN (Kunale) and GRA (Gratselim) are the closed areas, whereas HARm (Haragua moist forest relic), HARd (Haragua dry forest relic), WAS (Waseia) and ARB (Arbaete) represent the forest relics. An example of both types can be seen in figure 8.

Environmental variables examined include slope gradient and azimuth, geology, physical and chemical soil characteristics, and land use impact (LUI). Slope gradient and aspect were measured by means of a Suunto Clinometer and a compass, respectively. Soil depth was measured by hammering a cylindrical metal probe with a diameter of 2 cm into the soil. This was repeated ten times at random per plot, out of which mean soil depth was calculated. Macrostoniness was determined in two different ways by probing fifty times respectively at random and systematically (every meter along five 10 meter lines) in the plot. The number of times the probe made contact with stony material was counted and expressed as a percentage against the total of fifty times the probe hit the ground. No significant differences were found between both methods, and systematic measurement was arbitrarily selected for use in final analysis. Geological substrate was derived from existing geological maps, which was checked with the bedrock in the field (24). Samples for soil analysis were collected using a 2.5 cm diameter Edelman auger (Eijkelkamp), by 4 random augerings per plot. Each sample was subdivided in a top- (0-10 cm) and sublayer (10-30 cm). Analysis of these samples consisted of pH determination, colorimetric determination of phosphorus content [EU reference method (39, 40)], titrimetric determination of carbonate content, determination of texture by the Soil Service of Belgium (method by feeling (39), determination of Cation Exchange Capacity and exchangeable bases by $AgTU^+$ and atom absorption (36), and determination of total carbon and nitrogen content with the Dumas combustion method using a Solid Carbon Analyser [Vario Max C/N apparatus – Elementar Analysensysteme GmbH, Germany (38)].

Possible effect of land use on land degradation, further denoted as land use impact, was evaluated by calculation of a compound index LUI, which is a rough estimate for disturbance by people and cattle. This simple index integrates the effect of several parameters expressing disturbance. It is based on the index developed by Goris (14). The latter was adapted by adding more parameters, which were selected on the basis of broad literature research and semi-structured interviews with local farmers and key informants, the latter being officially appointed local contact persons with expert knowledge in the field of land management and degradation. Parameters included are: a measure for intensity of grazing by cattle (G) (0= no grazing; 1= limited grazing; 2= frequent grazing); a measure for the intensity of grass harvesting by people (O) (0= no grass harvesting; 1= harvesting every two or more year; 2= harvesting every year); measures for accessibility in terms of vegetation density (VD) (0= impossible to cross standing up; 1= possible but difficult; 2= easy to cross) and slope gradient (H) (0= slope more than 50%, 1= slope less than 50%); a measure for presence of *Eucalyptus* spp. plantations, being one of the most directly observable and most pronounced indications of human impact (A) (0= no plantations; 1= plantations present); and a measure for duration of conservation management (C) (0= protection started >10 years ago, 1= protection started <10 years ago, 2= no protection as long as known). Underlying rationale for VD and H is the hypothesis that disturbance will be lower when the terrain is less accessible. Information on G, O and C was obtained by semi-structured interviews with local farmers and key informants. Slope gradient for H was measured by means of an inclinometer. Information on VD and A was obtained by personal field trial and observation, respectively. The index is calculated as the sum of scores on the individual parameters:

$$LUI = G + O + VD + H + A + C \quad (1)$$

Values of LUI can range from 0 to 10. The higher the index value, the stronger the impact by people or cattle.

Although being a coarse and qualitative estimate of hypothetical nature, it is a valuable attempt to bring together some of the most important factors affecting land degradation in this area in one single index. Incorporating this in our study seemed important, as it is to be expected that land degradation has a significant influence on aboveground vegetation and seed bank characteristics, with importance and potential role of seed bank depending on specific conditions and agro-ecological zone (4, 7, 19, 34).

Species presence in the aboveground vegetation was recorded during a vegetation survey in the rainy season between August and October 2002, with the assistance of resource persons (key informants or local people recommended by the latter), who, like most people in the rural areas, have a great knowledge of plant vernacular names. Of each collected species, at least one sample, by preference a flowering specimen, was kept for identification after transplantation to a separate plant container. Based on field experience, a classification of growth forms was made, with distinction between woody species, herbs, climbers and graminoids. The same distinction was used in the seed bank analysis. Scientific names of species were obtained by linking vernacular names given by the resource persons to The Flora of Ethiopia & Eritrea (11). Crosschecking for wrong or multiple vernacular names was performed by comparing the collected sample(s) with the description and figure of the species in the flora. If identification seemed impossible or was doubtful, samples were sent for identification to the National Herbarium of Ethiopia in Addis Abeba.

Soil samples for seed bank analysis (Figure 7) were collected using a 3.2 cm diameter auger (Eijkelkamp piston sampler). Methodology followed Bakker *et al*. (2), ter Heerdt *et al*. (32) and Warr *et al*. (37). Forty-five random samples per plot were taken, each time divided in two sub-samples according to soil depth: 0-7.5 cm and 7.5-15 cm. Sample depth was determined based on general knowledge on vertical distribution of plant seeds in the seed bank (29, 30) and mean field soil depth. All sub-samples of a plot were merged into one pooled sub-sample per depth class, as a large number of small samples is preferred over a small number of large samples in order to have a more accurate representation of the seed bank as found in a specific place (34, 35). To remove the smallest soil particles, bigger stones and rough organic material, and to divide samples in a rough and a fine fraction, pooled sub-samples were sieved with water as described by ter Heerdt *et al*. (32), using three mesh sizes of respectively 5 mm, 2 mm and 0.2 mm. Fractions bigger than 5 mm and smaller than 0.2 mm were eliminated while the two remaining fractions, i.e. 5 to 2 mm and 2 to 0.2 mm, were spread out homogeneously over poly-ethylene trays filled with argex pellets and sterilized potting soil. These trays were placed on shelves constructed especially for seed bank analysis, in a laboratory in Heverlee, Belgium. Tap water was provided regularly in order to allow seed germination. An artificial day-night regime of 14 hours of daylight/10 hours of darkness was obtained by using TL-light. Temperatures fluctuated between a minimum of 13 °C and a maximum of 32 °C. Seedling emergence was checked several times a week, for a length of 17 weeks. Recorded seedlings were removed from the trays from the moment they could be distinguished as a specific species, but at least one specimen of each species in this germination experiment was transplanted and kept for future species determination. From these specimens, all flowering individuals (limited to herbs and graminoids, as no woody species or climbers flowered) were dried and compiled into a herbarium. Also, a picture database of all species in different growth stages was made. On the basis of germination on the poly-ethylene trays, data on number of seedlings and germinating species were collected and used for calculation of seed density (expressed as number of germinated seeds per m^2 (37), calculated from the known top surface of the volume sampled in the field) and seed bank species composition per plot, per location (consisting of four plots), per growth form (woody species, herbs, climbers and graminoids), and per land use type (forest relic or closed area).

Based on the findings of Skoglund (30) and our own experience, when focusing on natural regeneration, we suggest a classification of species in the seed bank in three main categories: (a) seeds of non-forest species which may hamper natural forest recovery through competition (mostly herbs or grasses); (b) seeds of forest pioneer species, both herbaceous and woody (e.g. *Euclea schimperi*, *Acacia abyssinica*, *Dodonea angustifolia*); these species are important in the intermediate steps of succession towards a forest climax because they can contribute to soil stability and development of a forest microclimate, and are hence considered as a nurse crop creating favourable germination conditions for the third category; and (c) seeds of climax tree species able to create a forest canopy and are thus essential for forest restoration (e.g. *Olea europaea* subsp. *cuspidata*, *Juniperus procera*, *Abutilon longicuspe*). Relative abundance and distribution of seeds over these three categories allows one to get an idea of the possible role of the seed bank in forest conservation and restoration.

Because of the lack of normality of data (checked through a Kolmogorov-Smirnov test (29), the presence of categorical data and the lack of homoscedasticity, non-parametric statistics were applied. Correlations were calculated using Spearman rank correlation coefficient (29) whereas Kruskal-

Wallis tests were used for analysis of spatial patterns in the data (29). Principal Components Analysis (PCA) (18) was performed on the environmental data to determine the interrelation between abiotic variables and the contribution of each of the latter to total variance in the environmental dataset. Interpretation of TWINSPAN classification was used to group plots of both types of areas in so-called vegetation or seed bank types, based on vegetation or seed bank characteristics, respectively. An ordination of plots based on vegetation or seed bank data only (indirect ordination) was performed with Correspondence Analysis (CA) (16). Canonical Correspondence Analysis (CCA) was used as a direct ordination technique, in which vegetation and seed bank data were explained by environmental data.

Results

Distribution of number of species in the aboveground vegetation over the different areas and in the seed bank over the different areas and growth forms are shown in figures 3 and 4, respectively. The ordination/classification of plots showed strong links between environmental variables, vegetation type and seed bank. Land use impact and chemical soil characteristics are the environmental variables best explaining environmental degradation, vegetation composition (Table 1 and Figure 5), seed density and seed bank composition (Tables 3 and 4, Figure 6).

A total of 145 different species germinated in the seed bank samples. Some 120 species (83%) have been identified at

Table 1
List of identified species germinated in seed bank samples

Scientific name	Family	Life form	LF Remark
Ficus vasta Forssk.	Moraceae	woody species	tree
Galinsoga parviflora Cav.	Asteraceae	herbs	
Galium simense Fres.	Rubiaceae	herbs	
Geranium favosum Hochst	Geraniaceae	herbs	
Girardinia diversifolia (Link) Friis	Urticaceae	herbs	
Glycine wightii (Wight & Arn.) Verdc.	Fabaceae	climbers	
Gnaphalium pennsylvanicum L.	Asteraceae	herbs	
Grewia ferruginea A. Rich.	Tiliaceae	woody species	shrub/tree
Helichrysum sp.	Asteraceae	herbs	
Helinus mystacinus (Ait.) E. mey. ex Steud	Rhamnaceae	climbers	
Heteropogon contortus (L.) Roem. & Schult.	Poaceae	graminoids	
Hibiscus macranthus A. Rich.	Malvaceae	herbs	shrub
Hibiscus sp. 1	Malvaceae	woody species	
Hibiscus sp. 2	Malvaceae	woody species	
Hypericum annulatus Moris	Hypericaceae	herbs	
Indigofera amorphoides Jaub. & Spach.	Fabaceae	herbs	subshrub
Juniperus procera Endl.	Cupressaceae	woody species	tree
Justicia ladanoides Lam.	Acanthaceae	herbs	
Kalanchoe sp. 1	Lamiaceae	herbs	
Kalanchoe sp. 2	Lamiaceae	herbs	
Kalanchoe sp. 3	Lamiaceae	woody species	
Kickxia elatine (L.) Dumort.	Scrophulariaceae	climbers	
Laggera sp.	Asteraceae	herbs	
Launaea taraxacifolia (Willd.) Amin ex C. Jeffry	Asteraceae	herbs	
Leucas abyssinica Benth.	Lamiaceae	herbs	
Lippia adoensis Hochst ex Walp	Verbenaceae	herbs	subshrub
Olea europaea subsp. *Cuspidata* (Wall. ex DC.) Cifferri			
Otostigia fruticosa (Forssk.) Schweinf. ex Penzig	Lamiaceae	herbs	subshrub/shrub
Oxalis anthelmintica A. Rich.	Oxalidaceae	herbs	
Oxalis corniculata L.	Oxalidaceae	herbs	
Oxygonum sinuatum (Meisn.) Dammer	Polygonaceae	herbs	
Panicum maximum Jacq.	Poaceae	graminoids	
Parietaria debilis Forssk.	Urticaceae	herbs	
Persicaria nepalensis (Meisn.) Miyabe	Polygonaceae	herbs	
Peucedanum petitianum A. Rich	Apiaceae	herbs	
Phytolacca dodecandra L'Herit	Phytolaccaceae	climbers	
Pilea rivularia Wedd.	Urticaceae	herbs	
Plantago albicans L.	Plantaginaceae	herbs	monocotyledonous
Plantago lanceolata L.	Plantaginaceae	herbs	monocotyledonous
Poa leptoclada Hochst. ex A. Rich.	Poaceae	graminoids	

Polycarpon tetraphyllum (L.) L.	Caryophyllaceae	herbs	
Pulicaria petiolaris Jaub. & Sp.	Asteraceae	herbs/climbers	
Pupalia lappacea (L.) A. Juss.	Amaranthaceae	herbs	
Ranunculus distans A. Rich.	Ranunculaceae	herbs	
Reichardia tingitana (L.) Roth.	Asteraceae	herbs	subshrub
Rhynchosia elegans A. Rich.	Fabaceae	climbers	
Rostraria cristata (L.) *Tzvelev*	Poaceae	graminoids	
Rumex nervosus Vahl	Polygonaceae	herbs	
Salvia nilotica Juss. ex Jacq.	Lamiaceae	herbs	
Satureja punctata (Benth.) Briq.	Lamiaceae	herbs	
Senecio lyratus Forssk.	Asteraceae	climbers	woody
Silene burchellii DC.	Caryophyllaceae	herbs	
Solanum indicum L.	Solanaceae	herbs	
Solanum lycopersicum L.	Solanaceae	herbs	
Solanum nigrum L.	Solanaceae	herbs	
Solanum villosum Willd.	Solanaceae	herbs	
Sonchus oleraceus L.	Asteraceae	herbs	
Tagetus minuta L.	Asteraceae	herbs	
Trifolium arvense L.	Fabaceae	herbs	
Trifolium campestre Schreb.	Fabaceae	herbs	
Trifolium rueppellianum Fres.	Fabaceae	herbs	
Urera hypselodendron (A. Rich.) Wedd.	Urticaceae	climbers	
Verbascum sinaiticum Benth.	Scrophulariaceae	herbs	
Verbena officinalis L.	Verbenaceae	herbs	
Vernonia amygdalina Del.	Asteraceae	woody species	shrub/tree
Vernonia sp.	Asteraceae	herbs	subshrub/shrub
Veronica anagalis-aquatica L.	Scrophulariaceae	herbs	
Veronica simense Fresen	Scrophulariaceae	herbs	
Vicia sativa L.	Fabaceae	climbers	
Vigna membranacea A. Rich.	Fabaceae	climbers	
Vigna schimperi Bak.	Fabaceae	climbers	
Vigna vexillata (L.) A. Rich.	Fabaceae	climbers	
Withania somnifera (L.) Dunal	Solanaceae	herbs	
Zehneria scabra (L.f.) Sond.	Cucurbitaceae	climbers	woody

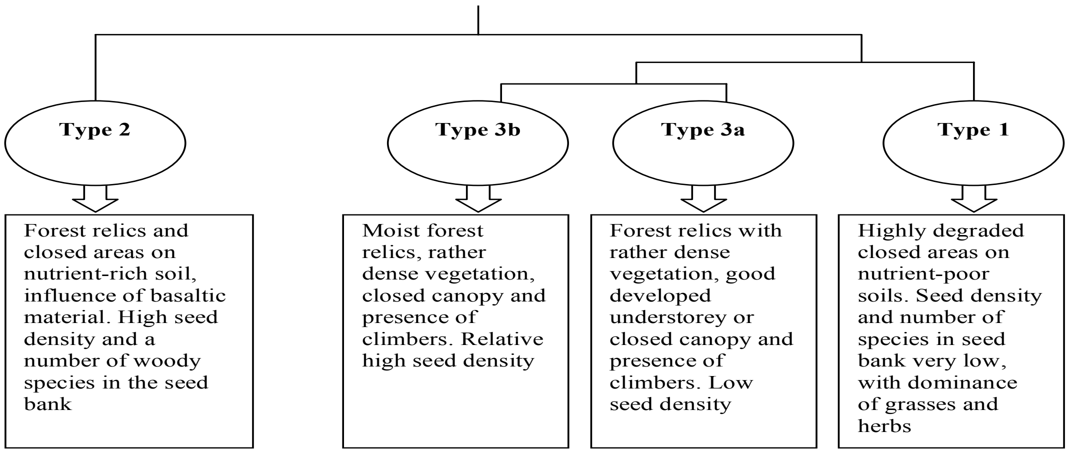


Figure 1: Dendrogram of seed bank types derived through TWINSPAN analysis.

the moment of writing. Forty-eight species had only one individual germinating. All species but one with more than 10 germinations were identified. A list of all germinated species is given in table 1.

Results from seed bank analysis (Tables 3 and 4, Figure 6) indicate that out of all environmental variables, differences in species composition and density are best explained by nutrient status and land use impact. Seed bank densities are highest in nutrient-rich soils with a relatively low pH, and in areas where land use impact is lowest, as shown by the negative correlation between seed bank density and land use impact.

Based on the results of the TWINSPAN analysis, four seed bank types could be distinguished (Figure 1). Clusters

Abbreviation	Variable name	Unity
LUI	Land Use Impact	classes 1-10
W_A_ASIE	Weight soil sample A after sieving	g
W_B_ASIE	Weight soil sample B after sieving	g

Abbreviation	Variable name	Unity
W_P_ST	Weight percentage stones	%
Bulkdens	Bulk density	g/cm^3
Claysilt	clay-silt fraction	%

Legend of physical soil variables for tables 2-4

Table 2
Spearman Rank correlation matrix of ordination scores CA vegetation with environmental variables

Vegetation			general environmental variables							physical soil variables						
	Geology	Altitude	Slope	Aspect	Stoniness	Average soil depth	LUI	W_A_ ASIE	W_B_ ASIE	W_P_ST	BULKDENS	CLAYSILT				
Ax 1	.507(**)	-.374(*)	-0.105	0.091	-0.172	-0.101	0.039	-0.062	.469(**)	-0.229	0.253	-0.211				
Ax 2	-0.203	-0.031	-0.187	0.171	-0.122	-0.27	0.007	.361(*)	0.058	0.03	0.293	-0.158				
Vegetation								Chemical soil variables								
	pH_H2O	pH_ KCL	P	Carb	totC %	orgC %	totN %	C/N	Na	Mg	K	Ca	Al	Mn	Fe	CEC
Ax 1	0.313	0.294	0.016	0.174	-0.116	-0.197	-0.243	0.317	-.452(**)	-0.321	-0.324	0.082	-0.193	-.588(**)	-0.151	-0.277
Ax 2	0.169	0.24	0.101	.423(*)	0.109	0.013	-0.09	0.045	0.095	-0.054	-0.113	0.13	-0.112	-0.311	-0.084	-0.043

** Correlation is significant at the .01 level (2-tailed). * Correlation is significant at the .05 level (2-tailed).

Table 3
Spearman Rank correlation matrix of ordination scores CA seed bank with environmental variables

Seed bank			general environmental variables							physical soil variables						
	Geology	Altitude	Slope	Aspect	Stoniness	Average soil depth	LUI	W_A_ ASIE	W_B_ ASIE	W_P_ST	BULKDENS	CLAYSILT				
Ax 1	.736(**)	-.520(**)	0.045	-0.192	-0.128	0.108	-.552(**)	0.251	.513(**)	-0.236	-0.233	-0.306				
Ax 2	.345(*)	-0.28	0.032	-0.327	0.008	-0.339	.516(**)	0.177	.456(**)	0.27	0.309	-.550(**)				
Seed bank								Chemical soil variables								
	pH_H2O	pH_ KCL	P	Carb	totC %	orgC %	totN %	C/N	Na	Mg	K	Ca	Al	Mn	Fe	CEC
Ax 1	.501(**)	.590(**)	.625(**)	0.248	0.087	0.147	0.158	0.336	-.445(**)	-0.161	0.167	.427(*)	-.681(**)	-.375(*)	-.766(**)	0.022
Ax 2	.399(*)	0.296	-.404(*)	0.27	-0.131	-0.274	-0.338	0.109	-.535(**)	-.581(**)	-.542(**)	0.009	-0.211	-.670(**)	-0.055	-.476(**)

** Correlation is significant at the .01 level (2-tailed). * Correlation is significant at the .05 level (2-tailed).

Table 4
Spearman Rank correlation matrix of seed bank data with environmental variable

Seed bank			general environmental variables							physical soil variables						
	Geology	Altitude	Slope	Aspect	Stoniness	Average soildepth	LUI	W_A_ ASIE	W_B_ ASIE	W_P_ST	BULKDENS	CLAYSILT				
nr of species	-.457(**)	0.259	0.111	0.28	-0.13	0.007	-0.436(*)	-0.199	-0.462(**)	-0.261	-.487(**)	.536(**)				
seed density	-0,24	0.106	0.205	0.31	-0.07	0.151	-0.423(*)	-0.063	-0.241	-0.287	-.507(**)	0.296				
Seed bank								Chemical soil variables								
	pH_H2O	pH_ KCL	P	Carb	totC %	orgC %	totN %	C/N	Na	Mg	K	Ca	Al	Mn	Fe	CEC
nr of species	-.424(*)	-.358(*)	.375(*)	-0.242	0.103	0.265	0.239	-0.118	.405(*)	.440(*)	.554(**)	-0.25	0.311	.680(**)	0.295	0.224
seed density	-0.345	-0.238	0.257	-0.12	-0.035	0.106	0.242	-0.168	.388(*)	.467(**)	0.32	-0.068	-0.047	.461(**)	0.006	0.309

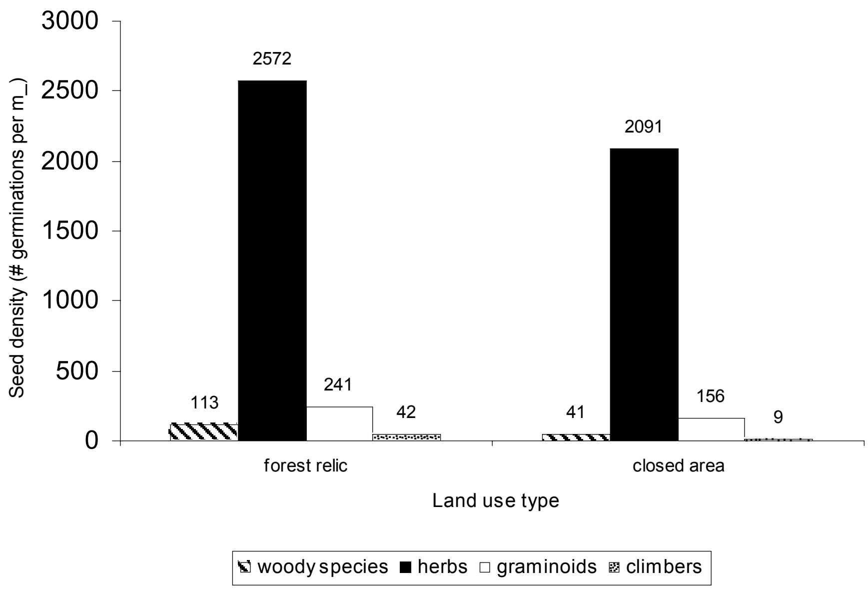


Figure 2: Distribution of seed densities over growth forms and land use types.

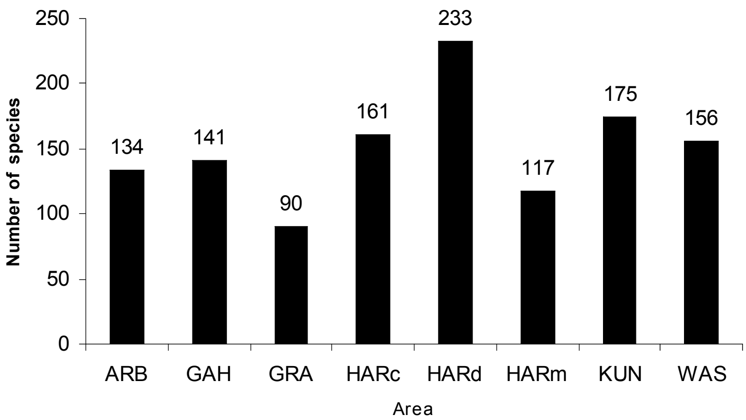


Figure 3: Distribution of number of species in vegetation over different locations, as found each time in the four 10X10 m plots.

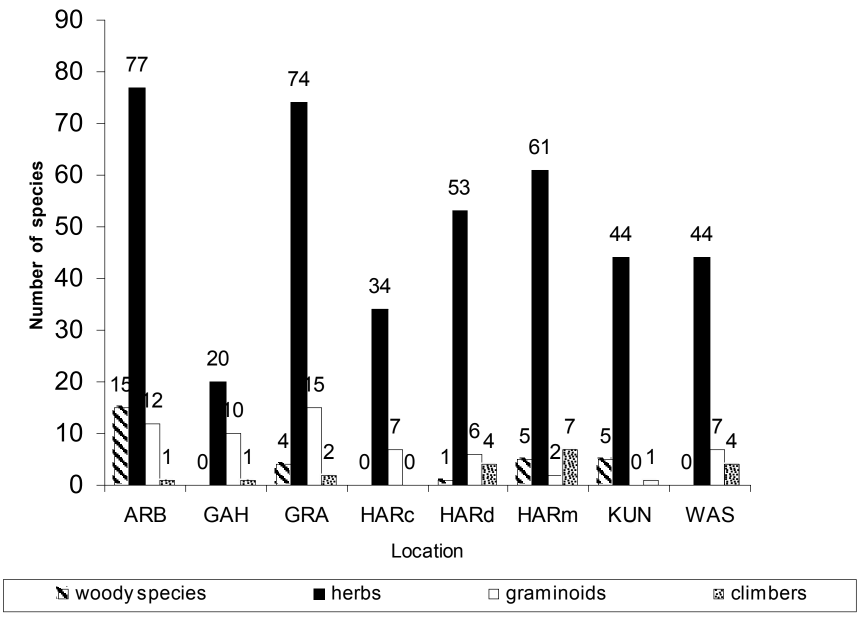
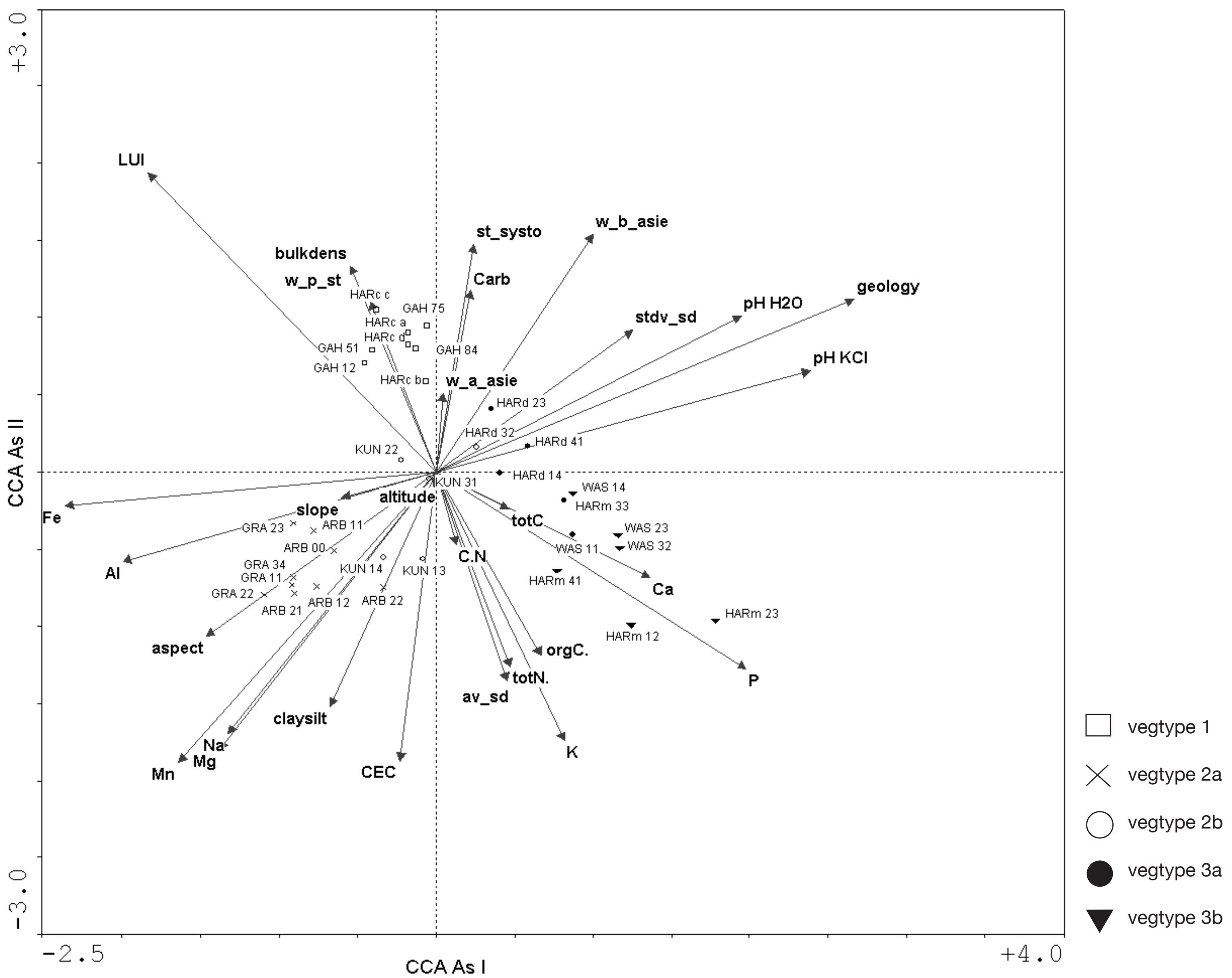
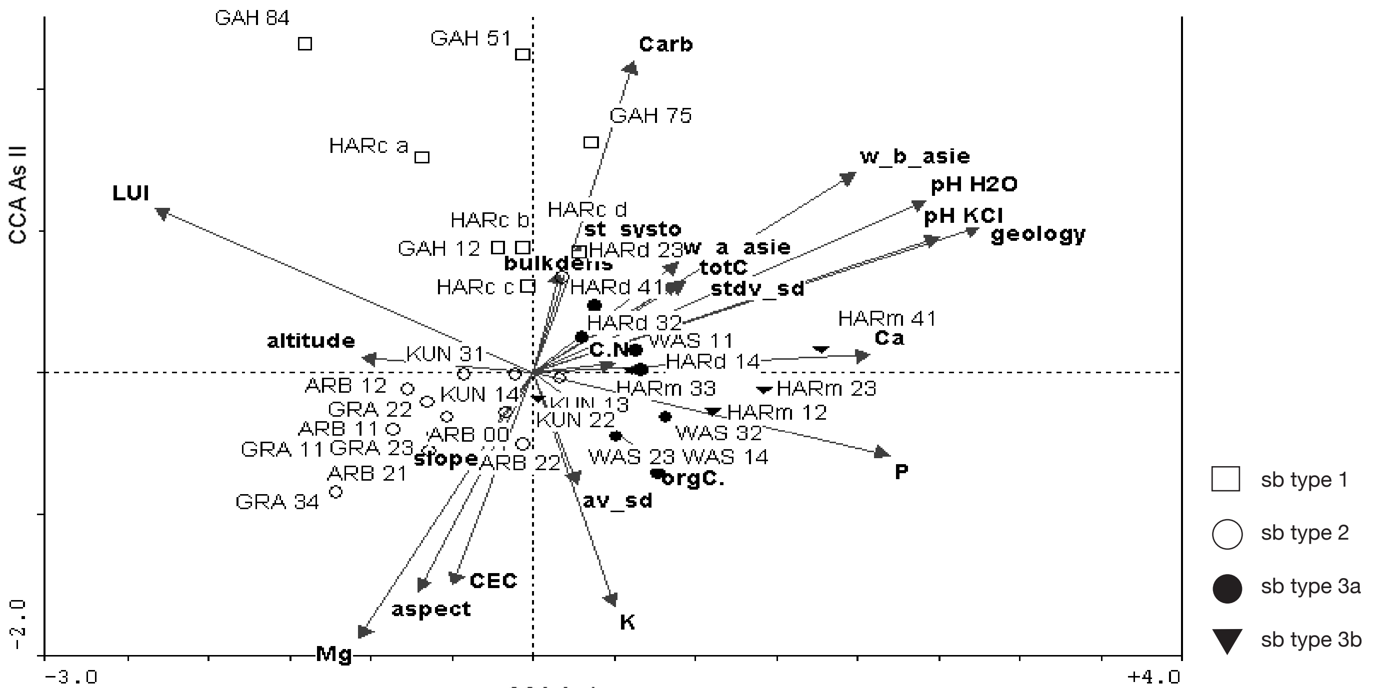


Figure 4: Distribution of number of species in seed bank over growth forms and locations.



CCA As I

Figure 5: Direct ordination based on CCA of vegetation data.



CCA As I

Figure 6: Direct ordination based on CCA of seed bank data.

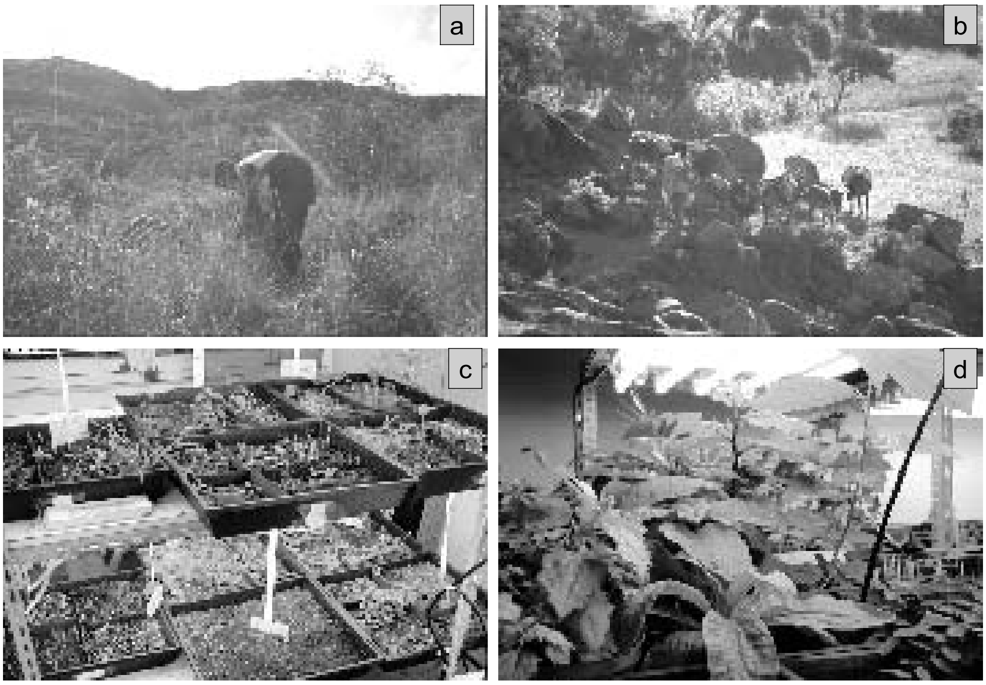


Figure 7: Overview of the different steps in seed bank analysis:
a. collection of soil samples; b. transport; c. germination of seeds and d. species identification.

Figure 8: Example of a relatively undisturbed, moist forest relic: Haragua moist forest relic (left) and a highly disturbed, dry and nutrient-poor area: Gahe closed area (right).

seem to be explained mostly by land use (with a distinction between forest relics and closed areas), geology, land use impact and soil nutrient status. A line of continuous decreasing land use impact from seed bank type 1 over 2 to 3a and finally 3b can be followed.

Key species in seed bank type 1, representing closed areas with a poor nutrient status (locations GAH and HARc), are *Sedum* sp. and *Euclea schimperi*, the latter being one of the very few woody species occurring in this poorly developed seed bank. Seed bank type 2 occurs on nutrient-rich soil (locations ARB, GRA and KUN). Although still relatively low, presence of woody species in the seed bank is higher, with species like *Olea europaea* subsp. *cuspidata* (11 germinations in ARB) and *Acacia saligna* (1, 1 and 12 germinations in ARB, GRA and KUN, respectively). Furthermore, herbaceous species like *Anagallis* sp., *Galium simense* and *Galinsoga parviflora* occur relatively abundantly in this type, with a mean seed density of respectively 60, 322 and 25 seeds per m^2. Type 3 seed banks (locations HARm, WAS and HARd) contain few woody species, except for some shrubs like *Calpurnea aurea*. Interesting, however, is the presence of different kinds of climbers, a growth form of which seeds germinated almost exclusively in this seed bank type. Here again, one of the most abundant herbaceous species is *Galinsoga parviflora*.

TWINSPAN analysis performed in the same way on the aboveground vegetation data resulted in a clustering of the different plots in remarkably similar vegetation types, explained by the same environmental variables. With decreasing land use impact, species-richness of the vegetation also decreases, whereas vegetation density (as evidenced by visual appreciation) seems to increase.

Most interesting observation in the frame of our objectives is the composition of the seed banks in terms of growth forms (Figures 2 and 4). The examined seed banks are dominated by herbs that represent 88% of all germinations in the samples. Seeds of woody species are poorly represented, with a total percentage of 3%. Moreover, they are mostly limited to forest relics where mature trees occur. Woody species thus germinated significantly more in samples taken in forest relics (4% of all germinations in forest relic samples), in contrast to those taken in closed areas (1.7% of all germinations in closed area samples). From the 17 woody species that germinated in the seed bank samples, 14 species could be identified: two *Hibiscus* spp., *Kalanchoe* sp., *Ficus sur*, *F. vasta, Grewia ferruginea, Abutilon longicuspe*, *Acacia saligna*, *Olea europaea* subsp. *cuspidata*, *Euclea schimperi*, *Cordia africana*, *Juniperus* *procera*, *Vernonia amygdalina* and *Maesa lanceolata*. An overview of seed densities for the different growth forms and land use types is given in figure 2. In summary, highly disturbed sites seem to have a poorly developed seed bank but a species-rich vegetation, whereas the almost undisturbed forest ecosystems have a well-developed seed bank and a dense vegetation, dominated by a few, especially woody, species.

Discussion

The landscape in the study area is strongly affected by a high pressure on the natural resources leading to soil degradation, erosion and a severe decline of natural vegetation (24). Degradation is most severe where land use impact as evidenced through the index LUI is strongest and where soils are naturally nutrient-poor.

Nutrient-poor and disturbed ecosystems are characterised by a species-rich aboveground vegetation, mainly consisting of herbs, in contrast with the undisturbed ecosystems that are dominated by a limited number of woody species. Following Gray and Megahan (15), the role of vegetation in erosion control can be attributed to (a) the umbrella or shield effect, as vegetation breaks the impact of raindrops before they hit the soil; (b) surface flow retardation; (c) regulation of soil moisture content and piezometric levels through transpiration and interception; and (d) root reinforcement through buttressing, anchorage and soil reinforcement. The first factor is mainly determined by permanence/absence of vegetation over the different seasons and by foliar cover, i.e. the area of ground covered by the vertical projection of the aerial portions of the plants. As evidenced in this study, vegetation in the highly degraded sites is species-rich, but its composition is greatly dominated by grasses, herbs and a few low shrubs. Although not quantitatively measured, it could be observed that foliar cover is low in these cases, as leaf area is limited, and raindrop impact is therefore bigger, leading to higher erosion risk. This effect is aggravated by a drastic decrease in foliar cover during the dry season, with most severe raindrop impact at the start of the rainy season as result. This is in contrast to undisturbed, water- and nutrient-rich forest relics, where a permanent canopy is present. Between these two extremes many intermediate situations occur.

Results from correlation analyses between seed bank data and environmental data (Table 4), direct ordination (Figure 6) and correlation analysis of ordination scores of indirect ordination (Table 3) indicate that seed density and seed bank composition are mostly explained by soil nutrient status and land use impact (LUI). The LUI, although a somewhat subjective oversimplification of the land degradation processes, seems to offer a valuable indicator approach, which merits further development. It will however need validation and further use and development before it will become a mainstream parameter. Where LUI is highest, vegetation density and foliar cover decrease, whereas soil compaction and soil particle detachment are expected to increase. This leads to a higher erosion risk. In erosion-prone areas, top soil - where most of the seed bank can be found - is washed away. As a consequence, a significant part of the seed bank is simply transported down slope. The remaining soil is shallow with high stoniness, leading to limited soil volume for seed bank development and recruitment. Therefore, one could have expected a negative correlation between seed density and stoniness, and a positive correlation between the former and soil depth. Although this trend is visible in table 4, we were not able to evidence it through a significant statistical relation.

Seed density in seed banks was higher under forest relics than under closed areas in the research area. This is confirmed by research in similar ecosystems (10). In contrast to most tropical rain forests, dry lowland forests and savannas, where both the number of seeds and the number of species are relatively small, dry Afro-montane forests store large quantities of seed in the soil (9, 19). Another contrast of dry Afro-montane forest with the former is the dominance of herbs in its seed banks (9), a characteristic also typical of seed banks in temperate zones (4). Instead of developing seed bank reserves, Afro-montane tree species usually form seedling banks on the forest floor (7).

The limited germination of woody species (Figure 2) is probably related to their bigger seed size: small and compact seeds tend to persist in the soil for a longer time than big and elongated or flattened seeds. This is mainly because large seeds are less likely to be incorporated into the soil as they have less chance of finding their way passively down cracks in the soil or being buried by soil organisms (2), and because they are more prone to predation and fungal infection (2).

Referring to the classification of species in the three categories defined before, results show that most species found in the seed bank belong to the category of non-forest species and secondly also to the category of forest pioneer species. In the research area, possibilities of natural forest restoration by species germinating from the seed bank are therefore limited, because of the overall lack of forest climax species in the seed bank. The development of an understorey vegetation consisting of herbs after disturbance, however, is to be expected, and can play an important role in the regulation of water and nutrient balances, production of organic material and maybe even limitation of erosion. In that way, some important conditions for full recovery are fulfilled. On the other hand, competition for space, nutrients and water is to be expected, thus preventing the development of species important for natural regeneration. To gain more knowledge on these processes, further research on community ecology, to understand the interactions between species present within the community, is necessary. Also, the effect of environmental conditions on seed bank characteristics should be studied more thoroughly. In that context, an interesting hypothesis to test is whether controlled grazing may contribute to forest recovery, by eliminating competitive grasses and by dispersing seeds of tree species (17). However, controlled grazing is also known to have negative effects, such as increased erosion risks. More research here is clearly needed.

Conclusion

This research demonstrates that seed banks in the study area mainly consist of herbs and grasses. Clearing of forest relics followed by intensive grazing and browsing or permanent cultivation would therefore result in a replacement of nearly all woody components by a set of herbaceous species from the soil seed bank (7). As a consequence, successful natural forest rehabilitation would primarily depend on the availability of seed trees in the vicinity and seed dispersal by birds and other vectors. This underlines the importance of sustainable managing the few remaining forest relics and relic trees (35). These islands of biodiversity in a sea of degraded landscapes are the key factor for natural forest rehabilitation (35), and the most urgent issue at this moment is their conservation (11, 17, 23). Participation by local communities is the foundation for the success of projects aiming at discouraging further environmental degradation and deforestation. The complex problems in which lack of water, wood and land have a central place, have to be dealt with in an integrated way, taking into account local knowledge and needs.

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