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Seed Dynamics and the Ecological Restoration of Hill Slopes of Kondoa Irangi, Central Tanzania

BY

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ABSTRACT

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Improper agricultural practices such as hill slope cultivation, extensive clearing of vegetation using fire over a long period, and to some extent overgrazing have converted the once fertile hill slopes of Kondoa Irangi in central Tanzania into unproductive marginal land. It is 25 years now since reclamation measures were introduced to save the hills from further degradation, but the regeneration process has been rather slow. The present study was initiated with the objective to explore alternative approaches to facilitate vegetation recovery in the hills. It consisted of a description of an Afromontane dry forest, soil seed bank, seed rain and seed longevity studies, and experiments on the influence of different soil treatments on regeneration.

There was significant seasonal variation in the seed bank ($p < 0.001$), with dry-season samples having higher densities than wet-season samples. Annual species dominated the seed bank samples in most of Kondoa Irangi Hills, but perennial species were dominant in the soil seed bank of the Afromontane dry forest. In the seed rain, both density and species richness were negatively correlated with vegetation cover. This points to the important role of anemochory and active seed rain in disturbed sites.

The intermittent and extended germination of buried seeds shown by, i.e., *Acacia tortilis*, is an adaptation to prevent synchronous germination, in unpredictable, harsh environments, whereas prompt germination after rains of e.g., *Acacia seyal*, is a strategy to avoid seed predation.

Inorganic fertilisation is not an efficient means of improving short-term productivity in poor savanna soils. Nutrient-deficiency should be corrected by moderate grazing and controlled fires.

Permanent and speedy vegetation recovery of degraded savannas such as in the Kondoa Irangi Hills, may require (1) enhanced nitrogen mineralization and seed dispersal by grazing livestock, (2) selective soil seed bank enrichment, and (3) transplanting seedlings with desired traits.

Keywords: anemochorous; conservation; Correspondence Analysis; dormancy-releasing mechanisms; hierarchical clustering; population structure; seed variance; seed viability; semi-arid; zoochorous.

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To my beloved wife Lydiah and our sons
Jacob and Brian-Valentine

Cover impression: Dispersal structures of *Tragus berteronianus* Schult (Poaceae) x 125. The seeds have the following features: complete lack of dormancy (i.e. seeds will germinate in response to showers > 10 mm within 24 hours); widely dispersed by animals (both ecto- and endo-zoochorous) and wind; and finally, the grass is cosmopolitan and short-lived annual of degraded land associated with grazing.

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

I. Lyaruu, H. V. M., Eliapenda, S. and Backéus, I. 1998. Floristic, structural and seed bank diversity of a dry Afromontane remnant forest at Mafai, central Tanzania. Manuscript.

II. Lyaruu, H. V. M. and Backéus, I. 1998. Soil seed bank and regeneration potential of the degraded hill slopes of Kondoa Irangi, central Tanzania. Submitted.

III. Lyaruu, H. V. M. 1998. Seed rain and its role in the recolonisation of degraded hill slopes in semi-arid Tanzania. *African Journal of Ecology*, in press.

IV. Lyaruu, H. V. M. 1998. Seed longevity of selected species from degraded savanna in semi-arid Tanzania. Submitted.

V. Eliapenda, S., Lyaruu, H. V. M. and van der Maarel, E. 1998. Soil amendments to facilitate regeneration of degraded hill slopes of Kondoa Irangi, central Tanzania. Submitted.

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In the co-authored paper **I**, field work was done together and data analysis was done by the first two authors. For paper **II**, field work was conducted jointly but greenhouse germination experiments, data analysis and writing up of the manuscript were done by the first author. For co-authored paper **V**, all authors are equally weighted. In this paper field work was done by the first two authors but data analysis was done solely by the corresponding author. I wrote papers **I**, **II** and **V** drafts and were improved considerably by comments from the co-authors and Håkan Rydin.

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INTRODUCTION

Tropical drylands are generally nutrient-poor ecosystems with a potentially low productivity due to insufficient and erratic rainfall, and are highly susceptible to land degradation. They are estimated to cover more than one-third of the earth's land surface (UNEP 1991). The massive land degradation common in tropical drylands is partly attributed to poor land use practises.

Two forms of land degradation common in tropical dry ecosystems are vegetation and soil degradation (Grainger 1990). Whereas soil degradation results from wind and water erosion, waterlogging, salinization, alkalinization and compaction, vegetation degradation manifests itself as reduction of vegetation cover or changes in species composition, e.g. grassland vegetation changing into bushland under a high grazing pressure or absence of fires. Both vegetation and soil degradation are common in the Kondoa Irangi Hills, where this study was conducted. Vegetation degradation is attributed to indiscriminate cutting of trees for charcoal production, and other domestic uses, whereas soil degradation results from combination of factors such as deeply weathered erodible soils, torrential rains and the topography of the study area.

Unlike desertification, which is an irreversible process mainly caused by salinization and low water table, degradation can be stopped and reversed if the degradatory forces are removed (Le Houérou 1995). The rate of vegetation recovery in degraded landscapes is dependent on the nature of the ecosystem itself and prevailing regeneration strategies in the ecosystem, as well as on the spatial and temporal scales of degradation (O'Neill *et al.* 1997). For example, regeneration from seed should be a more important strategy of replacing individuals after disturbance in tropical drylands and tropical dry forests than it will be in disturbed wet or moist forest (Kemp 1989, Skoglund 1992, Demel & Granström 1995). This is because in environments with climate seasonality, seeds remain dormant in the soil and will only germinate when proper germination conditions, particularly moisture, become available. For moist or wet environments, seeds are adapted to prompt germination as soon as they are shed and survive only as seedlings (see Garwood 1989).

Efforts to reclaim degraded drylands are constrained by the lack of nutrients in the soils, bushfires, and, most importantly, insufficient and erratic rainfall (Munyanziza & Oldeman 1996).

The present study was conducted primarily to explore other possibilities than natural regeneration to speed up the recovery process in the hills, but also included, among other things, investigation of the seed banks of different vegetation types of the Kondoa Irangi Hills, the seed rain as well as seed longevity of selected species from the area. Together with the above, various soil management practises related to improving ecosystem productivity and seedling establishment were also investigated.

Description of the study area

The Kondoa Irangi Hills (Fig. 1), abbreviated as KIH, occupy an area of ca 1300 km^2 in central Tanzania, and extend from latitude 4^0 40' to 5^0 0' S and longitude 35^0 40' to 36^0 10' E (Mbegu & Mlenge 1984). The topography of the area is dominated by steep

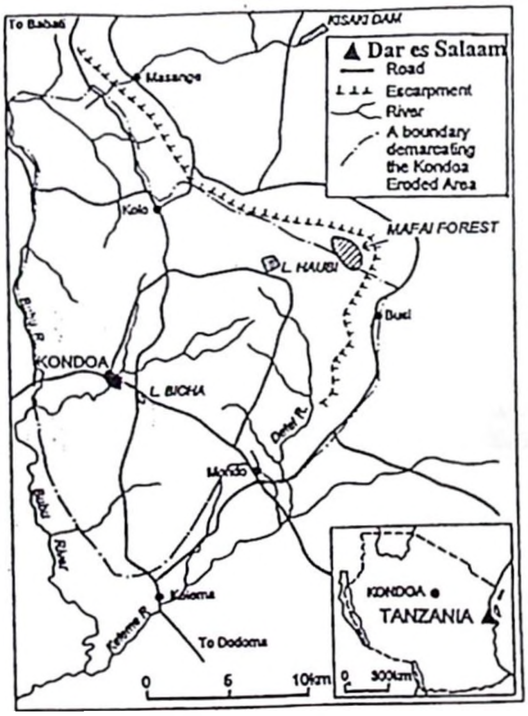

Figure 1. Map showing the Kondoa Irangi Hills and their surroundings.

sloping pediments with outcropping inselbergs and flatter cultivated valley bottoms (Payton *et al.* 1992). The hills are located at an altitude of 1000 - 2200 m above sea level and have a semi-arid to sub-humid climate with a mean annual precipitation of 600 - 1000 mm (Figs. 2 a & b), which is slightly higher in elevated parts.

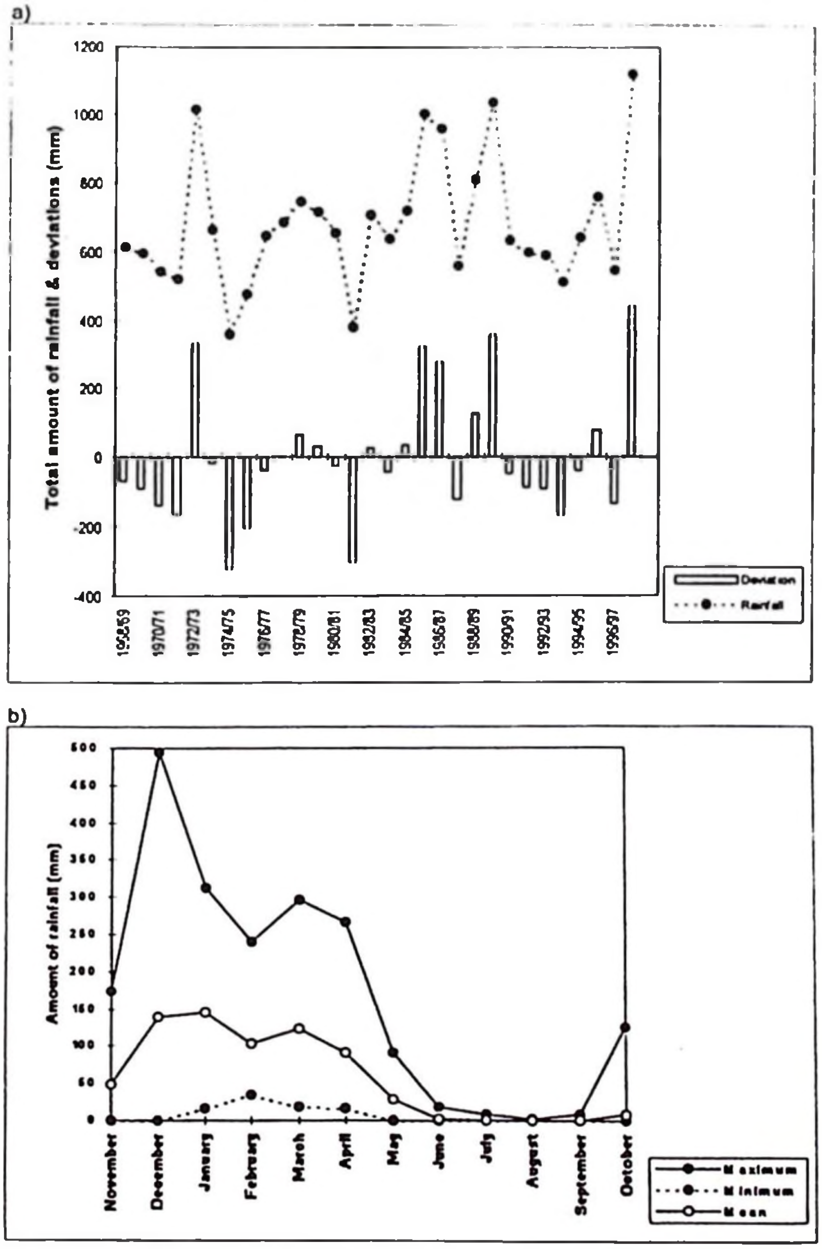

Figure 2. a) Total amount of rainfall and annual variations in the distribution at the Kondoa Town Metereological station, and b) Minimum, mean and maximum rainfall at the same station. The data are based on 30 years of observation (1968 - 1998).

There is a large variation in the yearly and monthly distribution of rainfall. Generally, the rainfall pattern is weakly bimodal; the rain period extends over seven months, from late November to May and mainly comes as short-lived, scattered but intense convectional storms (Mung'ong'o 1991, Ngana 1992).

The scope of land degradation in the Kondoa Irangi Hills

The problem of land degradation in KIH became apparent about 150 years ago after the Rangi people settled in the area. Travellers from around 1850 (cited in Mbegu & Mlenge 1984) already described vegetation in parts of central Tanzania using expressions such as " hills of denuded soils" and " dust devils" to illustrate the problem of land degradation at that time. The main factors assumed to have caused land degradation in the hills include excessive tree cutting, uncontrolled grazing, hill slope cultivation and seasonal fires. They had the overall effect of reducing the vegetation cover and reinforcing both sheet and gully erosion (Christiansson 1981). In the highest parts of KIH above Mafai village east of Haubi, we still find an Afromontane dry forest with an area of 1700 ha. This forest, which is hardly known to science is shrinking rapidly as a result of human pressure. Protective measures are urgently needed to safeguard the biodiversity of this forest.

Attempts to save the region from continued land degradation started in 1973 with the formation of the Hifadhi Ardhi Dodoma (HADO) or Soil Conservation Program in Dodoma, a governmental agency empowered with authority to reclaim degraded marginal lands in central Tanzania. Among the reclamation measures introduced by HADO were (1) complete cessation of grazing in the hills in 1979, (2) ban on hill slope cultivation and (3) introduction of ecological engineering practices such as terracing, contour banding and tree planting (see Mbegu & Mlenge 1984). At a later stage, with support and advice from SAREC, the local people were encouraged to embark on stall-feeding of few and improved breeds of cattle and goats in their households.

Objectives of the study

About 25 years ago reclamation measures were introduced in KIH; one would expect to see many changes in the vegetation of this recovering land. Backéus *et al.* (1994) noted that some parts of KIH, which had no vegetation previously, are now covered with vegetation, but other parts, particularly many gullies, are still bare. As a step towards understanding the mechanisms that may speed up natural regeneration in the hills, the present study was initiated in the framework of a multidisciplinary project known as MAn Land Interrelations in Semi-Arid TAnzania (MALISATA). For a comprehensive presentation of MALISATA, see Christiansson *et al.* (1991).

The specific objectives of the present study are:

1. To obtain floristic, structural and seed bank data necessary to promote the conservation of the rapidly degenerating remnant forest at Mafai due to human pressure [Paper I].
2. To characterise the soil seed bank and assess its usefulness in the ecological restoration of KIH [Papers I & II].
3. To study seed dispersal patterns in KIH and explore the relationship between seed rain, seed bank and standing vegetation, and finally to relate the seed rain to the recolonisation ability of these degraded hill slopes [Paper III].
4. To determine the seed longevity of some selected dominant species from KIH in order to estimate their vegetation restoration potential through the formation of viable seed banks [Paper IV].
5. To find out means of facilitating regeneration in the hills using various soil management practices [Paper V].

MATERIAL AND METHODS

Vegetation sampling of the Afromontane dry forest....[Paper I]

An initial reconnaissance survey in the dry Afromontane forest at Mafai was carried out in 1990. In 1994 a checklist of plant species was compiled. Most of the vegetation data used in this study were collected in April 1997, while additional data were collected in December 1997 and June 1998. The 1700 ha forest was sampled using five transects in various directions. A total of twenty seven 20 x 20 m plots were sampled for the trees. Trees with a diameter at breast height (DBH) of ≥ 10 cm were identified and their diameters measured. Tree height was estimated using the simple trigonometric approach commonly used by foresters.

The vegetation data were analysed for species diversity and evenness, density (stems ha^{-1}) and basal area (m^2 ha^{-1}), and the analysis of population structure was done on seventeen 15 cm DBH size classes and twelve 3 m height classes.

Soil seed bank sampling and greenhouse experiments [Papers I & II]

Soil samples for characterization of the seed bank were collected in two contrasting periods, (1) at the end of the dry season in 1994 and (2) during the wet season, immediately after the long rains in 1995. For the seed bank study of the remnant Afromontane dry forest, sampling was done once in November 1996. From each of the 27 permanent plots established earlier for long-term vegetation monitoring (see Backéus *et al.* 1994), ten soil samples, 206 cm^3 each, were collected at depths of 0 - 5 cm, 5 - 10 cm and 10 - 15 cm, for germination study in the greenhouse. From the remnant forest, 36 soil samples of 206 cm^3 were collected at various depths to include a litter layer of ca. 2 cm, 0 - 5 cm, 5 - 10 cm and 10 - 20 cm. The soil samples were spread out on sterilised sand in the greenhouse at the University of Dar Es Salaam, and the experiment was monitored for three months until no more seedlings emerged. Control trays were placed alongside the experiment to detect contamination by wind-dispersed seeds. The identity and number of emerging seedlings were recorded. Seedling counts were log-transformed before statistical treatments. The seed bank densities reported for the KIH are based on soil samples at 0 - 5 cm depth, whereas the density estimations for the montane forest were based on the average depth (see Demel & Granström 1995). Further treatments of the seed bank data included correlation analysis and a comparison of the seed bank data with the standing vegetation using similarity indices. The standing vegetation data were obtained from Backéus *et al.* (1994) and unpublished data.

Experimental design of the seed rain study................[Paper III]

The seed rain was studied in six of the 27 already existing permanent plots (see Backéus *et al.* 1994), representing the main vegetation types of KIH (with the exception of dry Afromontane forest), and was based on the seedling emergence method. The experiment was done in 1 x 1m plots from which the soil had been removed to a depth of 15 cm and replaced with sterilised soil and left to trap incoming seeds. The emerging seedlings were identified and recorded regularly before they were removed. The experiment was monitored for eight months and the data were compared with data for the seed bank and the standing vegetation obtained from the same plots.

Data analyses included analysis of variance for the log-transformed data (SAS Inst. 1990) and hierarchical clustering of species and morphological characters based on Ward linkage and squared Euclidean distances (MINITAB version 10xtra 1995 for dendrograms). Detrended Correspondence Analysis (Hill & Gauch 1980) of the seed rain, seed bank and standing vegetation data based on presence/absence of species (only axis 1 considered) was performed using the corrected version of the program CANOCO (ter Braak 1988 - 92) by Oksanen & Minchin (1997). The DCA results are presented only in this summary. Grouping of species with respect to their dispersal syndromes was done based on literature accounts (Howe & Smallwood 1982, Willson 1992, Hughes *et al.* 1994 etc.) and through personal observations.

Seed longevity of selected savanna species..................[Paper IV]

This study was based on the artificial burial of seeds of the following selected species: *Abrus precatorius*, *Acacia saligna*, *Acacia seyal*, *Acacia tortilis*, *Bidens pilosa*, *Cassia occidentalis*, *Conyza pyrrhopappa*, *Crotalaria kirkii*, *Dodonaea angustifolia*, *Faidherbia albida*, *Tephrosia villosa*, *Withania somnifera* and *Vernonia cinerascens*. The buried seeds were periodically dug up and inspected for their viabilities. Twenty viable seeds of each species were mixed with soil and buried in one envelope below-ground in a woodland vegetation. Such treatment was replicated 10 times and the envelopes containing the seeds were dug up one at a time (leaving the rest in position in the soil) after 3, 6, 9, 12 and 21 months. The seeds were sorted out and those viable were germinated in the greenhouse. The cause of death of the non-viable seeds, whether it was by *in situ* (lethal) germination, insect damage or rotting from fungal attack was established before they were discarded.

The rates of deterioration of seeds in the soil under natural conditions and their half-lifes were predicted from the relationship $S = S_0 e^{-gt}$ (Roberts & Dawkins 1967), where S = number of seeds at any time t, S_o = initial number of seeds and g = species decay constant.

Regeneration facilitation of degraded hill slopes........[Paper V]

An experiment was carried out in the field in KIH with the objective to find out how various soil management practices could be used to improve the productivity of this degraded ecosystem. Two sites each with uniform vegetation, but differing considerably in soil properties, were selected for this study. A factorial design experiment in which five treatments, i.e. fertilisation, mulching, import of a seed bank, seeding and introduction of seedlings, as well as their combinations, were replicated thrice in a systematic manner in each site. Seven dependent variables, including seedling recruitment, biomass, mortality and species turnover, among others, were tested against the treatments and their combinations. Species were identified and the individuals were collected five times during a period of 33 months. Both exotic and indigenous species with a demonstrated ability to endure in harsh environments were used in the seeding and seedling treatments. The data were subjected to Analysis of Variance using the GLM procedure in SAS (SAS Inst. 1990). Principal Components Analysis (PCA) as available in the corrected version of the program CANOCO (ter Braak 1987 - 1992), by Oksanen & Minchin (1997) was performed on species x treatment matrix with species abundance values in rows and treatments in columns.

RESULTS AND DISCUSSION

THE AFROMONTANE DRY FOREST AT MAFAI

Ecological features of the dry forest

A total of 441 trees representing 31 species and 17 families were enumerated. The largest family was Rubiaceae (9 tree species) followed by Euphorbiaceae (3 tree species). Among the tree species with the highest densities and basal areas in this forest were *Albizia glaberimma, Drypetes reticulata*, *Drypetes usambarica*, *Ochna holstii*, *Oxyanthus speciosus* and *Xymalos monospora*. Other important features of the forest included: Density 408 stems ha^{-1}; Basal Area 66.56 m^2 ha^{-1}; Shannon & Wiener diversity index 2.6406; Evenness 0.7585 and Species richness of 31 trees per 1.08 ha. Both Shannon & Wiener diversity index and species richness values obtained are much higher than those values reported from similar forests in Tanzania (see Lovett *et al.* 1997) and also from other forests in tropical Africa (Murphy & Lugo 1986, Swaine *et al.* 1987, Okali & Ola-Adams 1987).

Species and their phytogeographic links

Among the species encountered, *Trema orientalis*, *Embellia schimperi* and *Croton macrostachyus* are known to have Guineo-Congolian affinities, whereas *Albizia gummifera*, *Cussonia spicata*, *Lannea schweinfurthii*, *Maytenus acuminata*, *Schefflera myriantha*, and the orchids *Acampe pachyglossa* and *Microcoelia exilis* are phytogeographically linked to Madagascan, Cape and

Karoo-Namib floras (see Iversen 1991). *Drypetes usambarica* described in Lovett *et al.* (1997) as an Eastern Arc Mountains near endemic is disjunctly distributed to this remnant forest.

Population structures and DBH size classes

Correspondence Analysis of species and their various size classes revealed three groups (Fig. 3), corresponding to different population structures as follows: Group I had species with expanding populations as exemplified by *Albizia glaberrima*, *Drypetes reticulata*, *Drypetes usambarica*, *Ochna holstii* and *Oxyanthus speciosus*. Such population structures are associated with active and uniform regeneration and species from this group are likely to replace the present forest vegetation with continued disturbance or may disappear with the disappearance of the canopy trees as some of them, e.g. *Oxyanthus speciosus*, are below-canopy species. For an expanding population, the distribution of various size classes is such that most individuals are found in the smallest size classes while the numbers in the bigger size classes decline exponentially.

Group II with interrupted or discontinuous populations, as shown by *Ficus natalensis* and *Nuxia congesta* results from irregular recruitment through temporal gap colonisation or persistence as relicts of the former vegetation. Group III, that consists of species with declining populations, is comprised of timber trees such as *Lannea schweinfurthii*, *Podocarpus latifolius* and *Prunus africana*. Because in declining population, juvenile trees are lacking and sometimes the biggest size classes, it is rather unstable population that is most vulnerable to extinction. The decrease in population size of the timber species resulted from selective removal of big trees for timber and possibly also from seed regeneration difficulties common in indigenous species (Pócs 1988).

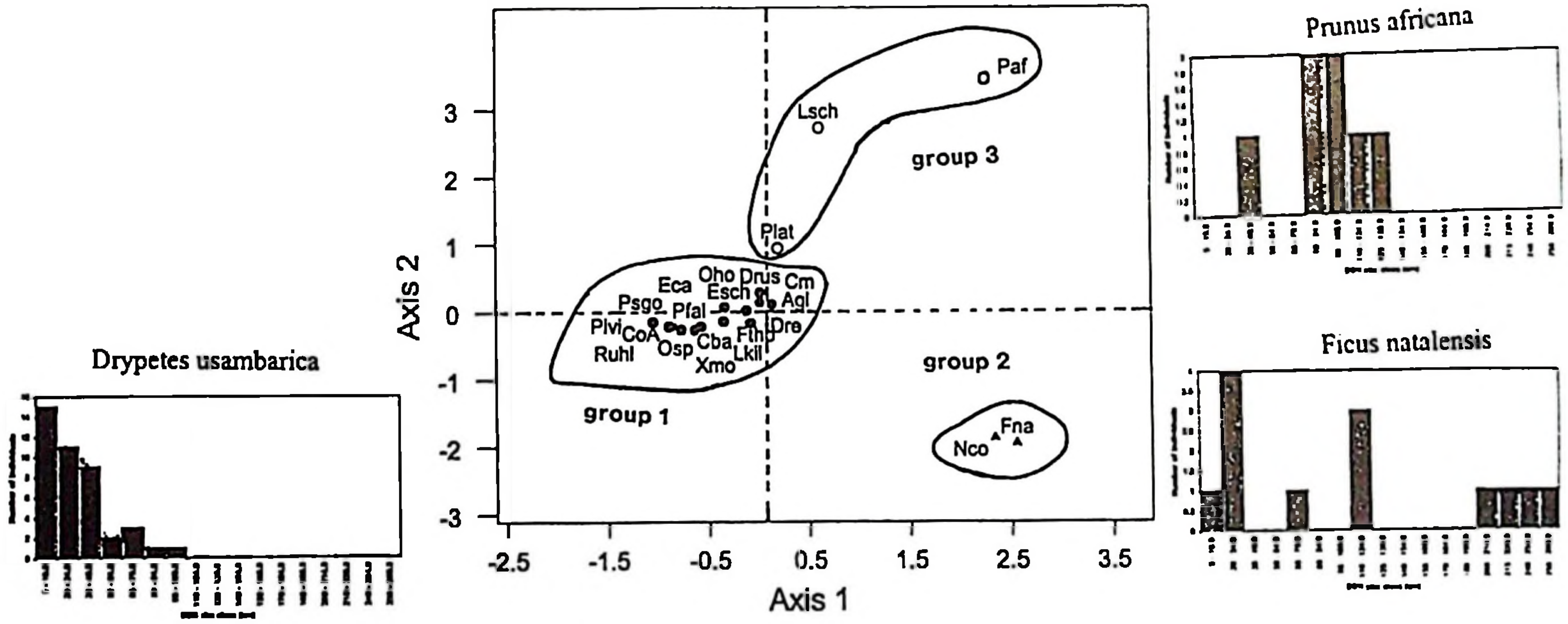

Figure 3. Correspondence Analysis (CA) of species (rows) x dbh size classes (columns) and different population structures of the tree species (only species with > 3 stems ha^{-1} included) sampled from Mafai forest. Group 1 has an expanding populations e.g. Agl = *Albizia glaberimma*; Cba = *Casearia battiscombei*; Cm = *Croton macrostachyus*; CoA = *Coffea sp. A*; Dre = *Drypetes reticulata*; Drus = *Drypetes usambarica*; Eca = *Ekebergia capensis*; Esch = *Embellia schimperi*; Fth = *Ficus thonningii*; Lkil = *Lasianthus kilimandscharicus*; Oho = *Ochna holstii*; Osp = *Oxyanthus speciosus*; Pivi = *Pittosporum viridiflorum*; Pfal = *Podocarpus falcatus*; Psgo = *Psychotria goetzei*; Ruhl = *Rhytgynia uhligii*, Xmo = *Xymalos monospora*. Group 2 with interrupted or discontinuous populations include Fna = *Ficus natalensis* & Nco = *Nuxia congesta*. Group 3 has declining populations and is composed of Lsch = *Lannea schweinfurthii*; Plat = *Podocarpus latifolius* & Paf = *Prunus africana*.

THE SEED BANK OF KIH VEGETATION

The nature of the seed bank: size, composition and richness

The seed bank of the degraded areas was very heterogeneous and showed significant seasonal variation in size, species composition and species richness. The seed bank density (sampled at 0 - 5 cm depth) ranged from 344 to 9158 seeds/m^2 in dry-season samples and from 172 to 5107 seeds/m^2 in wet-season samples. The observed seasonal variation is explained by the depletion from the seed bank of seeds with enforced dormancy through prompt germination, in response to increased moist conditions in the soil during the rainy season. Other studies have indicated that in arid environments, rainfall is the most important dormancy-releasing mechanism of buried seeds, as compared with fluctuating seasonal temperatures and light (Egley 1995). For the Afromontane dry forest, the seed bank density (sampled from 0 - 20 cm, including litter) ranged from 445 to 750 seeds/m^2 and for the litter layer the mean density was 634 seeds/m^2. The seed density decreased with depth, with most seeds localised in the superficial layers. These results are in agreement with those from other studies (see e.g. Kjellsson 1992, Demel 1996).

Comparison of the seed bank and the standing vegetation

There was poor correspondence between the species composition of the seed bank and the standing vegetation, as was also reported for other ecosystems (see e.g. Thompson & Grime 1979, Rabinowitz 1981, Belsky 1986, Garwood 1989, Alvarez-Buylla & Martinez Ramos 1990, Skoglund 1990 & 1992, Milberg & Hanson 1994, Bakker *et al.* 1996). The lack of correspondence between seed bank and standing vegetation in a disturbed ecosystem may be explained as follows:

1) the seed bank is persistent and is composed of diaspores originating from the vegetation prior to disturbance, while the current vegetation is derived secondarily.

2) the seed bank includes short-lived annuals which persist as seeds most of the time and are therefore difficult to detect during vegetation sampling.

3) the standing vegetation does not accumulate long-lived seed banks as an ecological adaptation to avoid seed predation which is very high in arid ecosystems (see account by Skagerlund 1998).

The behavioural pattern of the KIH seed bank is explained best by a combination of possibilities 2 and 3.

The seed bank and the standing vegetation were relatively more similar in the grazed grassland communities and in the dry forest. There was a significant difference in the life form spectrum in the seed bank of KIH (excluding the Afromontane forest) with annuals dominating by 60% over perennials and biennials together. In the Afromontane dry forest, perennial woody species accounted for 75 % of the seed bank, whereas mature forest tree species accounted for 20%. Climax forest species (defined here as the forest canopy species), do not form persistent seed banks but accumulate seedling banks under the forest canopy (Swaine & Whitmore 1988). The dominance of perennial species and the accumulation of a rich soil seed bank of pioneer species reported in this study is consistent with results from other dry forest studies (Guevara & Gomez-Pompa 1972, Cheke *et al.* 1979, Hall & Swaine 1980, Putz 1983, Williams-Linera 1990, Demel & Granström 1995).

CHARACTERISTICS OF THE SEED RAIN

Size, composition and clusters of the seed rain species

The seed rain densities ranged from 230 to 1667 seeds/m^2 over a period of eight months; they were negatively correlated with field layer cover and shrub/tree cover. This was expected since tall dense vegetation will have an effect of intercepting winds with active seed rain, thereby affecting the seed deposition pattern. In other words the "passive seed rain" is a characteristic typical of woodland or forest vegetation whereas the "active seed rain" is associated with an open landscape (Howe & Smallwood 1982, Stamp & Lucas 1990).

Graminoids (grasses and sedges) contributed 72% (3141 individuals) to the seed rain, shrubs < 0.1% (3 individuals), legumes 3% (138 individuals) and other herbs 25% (1097 individuals). Annual species dominated the seed rain by having 63% of the species, but no individual tree species was recorded from the seed rain. The dominance of the seed rain by annuals may be explained by their high resource allocation to seed production as well as possession of dispersal structures which facilitate mobility of seeds.

Hierarchical clustering of the seed rain data using diaspore shape and mean weight as variables produced three distinct clusters: Cluster I containing anemochorous grass seeds; Cluster II with epizoochorous herbaceous diaspores and large-sized unornamented diaspores, and Cluster III a mixture of unornamented grasses and herbs.

Relationship between seed rain (Sr), standing vegetation (Sv) and seed bank (Sb)

According to DCA interplot distances and similarities based on Sørensen's Index among any two items studied for different vegetation types, similarities increased in the order SvSb < SbSr < SvSr (Fig. 4). (SvSb stands for standing vegetation and seed bank; SbSr for seed bank and seed rain & SvSr for standing vegetation and seed rain). An increase in similarity corresponds to decreased DCA interplot distances. The observation that illustrates the importance of the passive seed rain compared with active seed rain in the regeneration process in KIH. This could also be explained by the homogeneity of the vegetation in the study area, which masks the contribution of the seed rain from adjacent vegetation.

In vegetation types where SvSb and SbSr are very dissimilar, the vegetation may form a persistent seed bank. This might also mean that there is no passive seed rain from the standing vegetation, and the converse is also true. High similarity in the relationship SvSr signifies presence of passive seed rain, whereas low values indicate active seed rain.

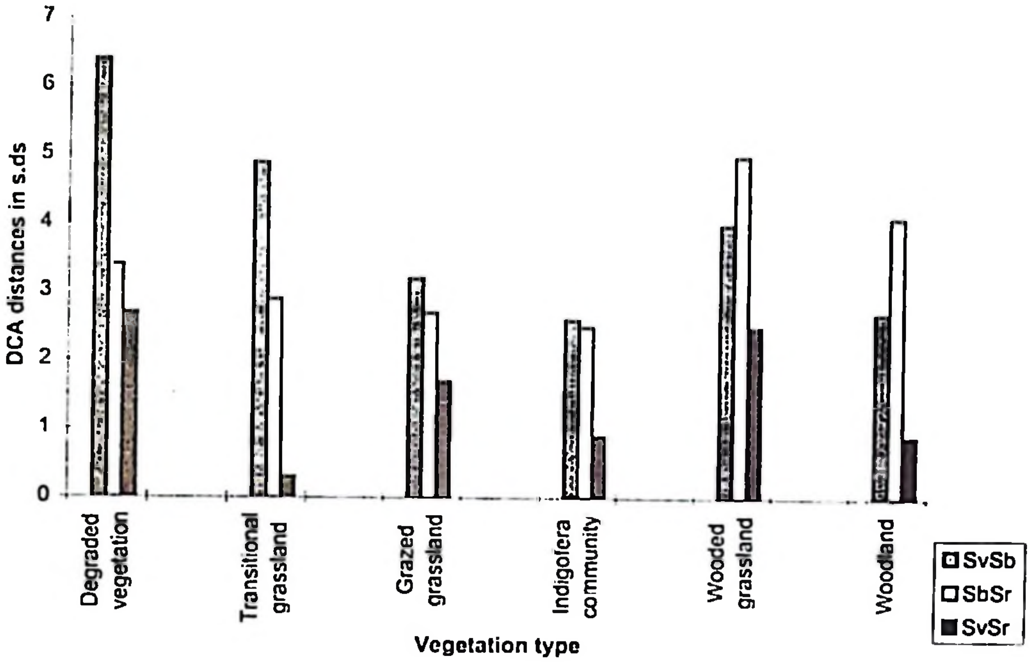

Figure 4. DCA interplot distances between standing vegetation and seed bank (SvSb), seed bank and seed rain (SbSr) and standing vegetation and seed rain (SvSr).

SEED LONGEVITY OF SOME SELECTED SPECIES

In situ or lethal germination, fungal infection and insect damage were the major sources of loss in viability among the buried seeds. Some seeds found missing in the burial envelopes might possibly have been secondarily dispersed by burrowing fauna. Fenner (1985) reported a viability loss of ca. 13% in buried seeds of *Bidens pilosa* in East Africa, whereas Schafer & Chilcote (1970) reported up to 85% loss of buried seeds in grasslands through germination. Miller (1994) reported heavy losses of *Acacia* seeds through insect damage. The *in situ* germination observed in some buried seeds is explained by the fact that such seeds possess a rather temporary enforced dormancy which is broken under moist conditions and they lack the more persistent dormancy imposed by the seed coat (Figs. 5 a & b). Hence, it follows that the occurrence of hard seed coats, common in most legumes, does not guarantee

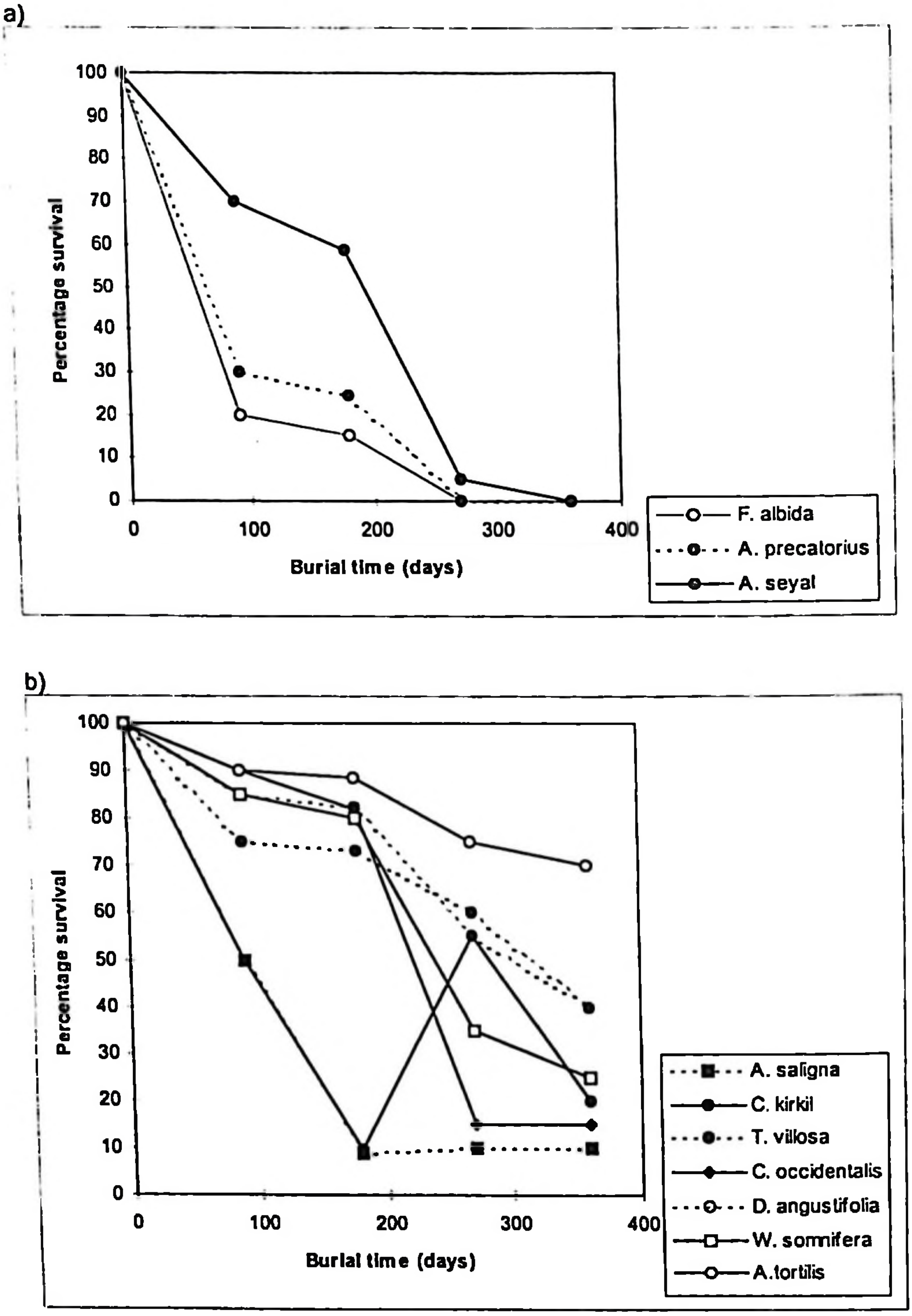

Figure 5. Survivorship curves of species studied. Species with short-term persistent seeds (a) have normally distributed curves, whereas those with long-lived seed banks (b) deviate from normality.

extended seed dormancy, but water impermeability of the seed coats is the overriding factor that determines seed dormancy. Prompt germination in response to moisture of some seeds can be viewed as an ecological adaptation to avoid seed predation in the soil known to be rampant in the study area (Skagerlund 1998). However, this hypothesis needs verification through further studies.

From the hierarchical clustering, three groups emerged, of which group I contained seeds with no dormancy, group II seeds that had enforced or temporary dormancy, and group III with dormancy imposed by the seed coat.

In the greenhouse experiment, the buried viable seeds of group III, watered continuously for six months, could attain 100% germination only after mechanical scarification. Such variations in the germination pattern are ecologically important in unstable environments such as KIH, where the ungerminated fraction of seeds serves as an insurance against local extinction in cases of catastrophic changes (O'Connor 1991).

Low values of decay constants were associated with seeds possessing dormancy imposed by the seed coat, while seeds with enforced dormancy had higher decay constants.

SOIL AMENDMENTS TO FACILITATE REGENERATION

Site comparison in the regeneration facilitation experiment

There were significant differences in seedling recruitment, species turnover, mortality, productivity and recruitment of woody species in the two experimental sites. The Gubali site had lower seedling recruitment, mortality and higher recruitment of woody species than the Chakwe site. Differences in site qualities in the degree of soil mineralization accounted for the observed variations. Another possible explanation based on seed dynamics is that fewer seeds are available at Gubali than at Chakwe. The seed rain densities are 1667 and 230 seeds/m^2 at Chakwe and Gubali, respectively, over 8 months, while the seed bank densities are 2185 and 1842 seeds/m^2 (at 0 - 5 cm depth), respectively.

There was very high positive correlation between seedling mortality and recruitment in both sites of 0.85 at Chakwe and 0.87 at Gubali (Tables 1 a & b). This result predicts water stress rather than site conditions as the overriding factor behind seedling mortality.

Table 1. Correlation between dependent variables or responses in the two sites studied (a: Chakwe; b: Gubali). Only statistically significant correlations ($p < 0.05$) are considered

a)

Factors	Pearson's Correlation Coefficient [r]	P
1. Recruitment vs Mortality	0.85	0.0001
3. Recruitment vs Turnover	0.47	0.0007
4. Turnover vs Mortality	0.38	0.0071
5. Turnover vs Biomass	0.29	0.0447
6. Turnover vs Perennial species	0.31	0.0346
7. Perennials vs Woody species	0.31	0.0298

b)

Factors	Pearson's Correlation Coefficient [r]	P
1. Recruitment vs Mortality	0.87	0.0001
2. Recruitment vs Turnover	0.39	0.0050
3. Recruitment vs Biomass	0.39	0.0057
4. Turnover vs Woody species	0.38	0.0080
5. Mortality vs Biomass	0.40	0.0051
6. Perennials vs Woody species	0.49	0.0004

Treatments and interactions with significant effects

Fertilisation and seed bank treatments were complimentary to each other in overall seedling recruitment and species turnover (Table 2). Fertilisation with inorganic compounds had an effect of reducing seedling recruitment, species turnover, mortality and biomass production. The role of inorganic fertilisers in promoting short-term productivity in arid environments is masked by water stress which is known to be the most important factor limiting germination and establishment in such environments (Walker & Noy-Meir 1982, Egley 1995). Direct addition of inorganic fertilisers to savanna soils is not recommended because it depletes the soil organic matter and thereby accentuates the problem of availability of plant nitrogen and phosphorus, as well as reducing the cation exchange capacity of the soil.

This study has revealed that mulching used in combination with other treatments enhanced seedling recruitment, species turnover and productivity. The mulching treatment applied alone had the effect of increasing mortality of non-woody species, but enhanced survivorship among woody species at the Gubali site. The practical use of mulching is to preserve soil moisture (Smith & Shackleton 1988), increase the organic composition of the soil as well as the water-use efficiency of seedlings, properties that favour selective recruitment of woody species. The two sites studied responded differently to mulching treatment as an indication that mulching is dependent on soil conditions.

Responses and their relevance to regeneration

Both the PCA ordination and the ANOVA results indicate that seedling recruitment is promoted by seed bank enrichment with an imported seed bank, seeding and by transplanting seedlings (Table 3). The effects of seeding treatment and transplantation of seedlings were more important at the Gubali site than the Chakwe site because there are better opportunities of establishment from seed in the deeper soils of Gubali than on the shallow unmineralized soils at Chakwe. As for transplanted seedlings, the transplants survived at Gubali only due to their ability to utilise moist conditions in the soil during the rainy season by growing rapidly and developing deep penetrating roots which facilitated water extraction from deeper layers, thereby minimising competition with grasses and other shallow-rooted plants.

Table 2: Overall treatment effects and site comparison of Gubali and Chakwe. Only treatments and/or interactions which are significantly different are indicated

Source of variation	df	F	P	Result/Effect
		Seedling recruitment		
FE	1	12.14	0.0008	-
SB	1	7.94	0.0061	+
SITE	1	171.59	0.0001	SITE 1 > SITE 2
MUxSB	1	4.79	0.0316	+
		Mortality		
MU	1	6.66	0.0117	-
FE	1	10.43	0.0018	-
SITE	1	111.88	0.0001	SITE 1 > SITE 2
		Total number of species		
FE	1	6.41	0.0134	-
SB	1	14.68	0.0003	+
SD	1	7.26	0.0086	+
SITE	1	88.24	0.0001	SITE 1 > SITE 2
MUxSDL	1	4.92	0.0295	-
		Biomass production		
SITE	1	47.72	0.0001	SITE 1 > SITE 2
		Number of perennial species		
FE	1	4.93	0.0293	-
MUxSD	1	4.06	0.0474	-
		Number of woody species		
SD	1	4.87	0.0303	+
SB	1	4.11	0.0460	+
SITE	1	7.99	0.0060	SITE 2 > SITE 1

Table 3. ANOVA results comparing responses of the two sites Chakwe (site 1) and Gubali (site 2) in terms of fertilisation, mulching, imported seed bank, seeding and seedlings to seedling recruitment, species turnover, woody species recruitment, biomass production and mortality. Only treatments with significant effects are included

Site	variation source	df	F	F	Effect
	Seedling recruitment				
SITE 1	FE	1	5.91	0.0209	-
	SB	1	5.14	0.0303	+
SITE 2	FE	1	3.86	0.0583	-
	Mortality				
SITE 1	FE	1	4.84	0.0352	-
SITE 2	MU	1	5.96	0.0204	+
	Total number of species				
SITE 1	FE	1	7.92	0.0083	-
	SB	1	8.00	0.0080	+
	MUxSD	1	7.38	0.0106	-
	SDxSDL	1	10.83	0.0024	+
SITE 2	SB	1	6.02	0.0198	+
	Number of woody species				
SITE 2	SD	1	11.64	0.0018	+
	Number of perennial species				
SITE 2	SDL	1	4.45	0.0428	+
	SBxSDL	1	7.67	0.0093	+
	FE	1	4.13	0.0504	-

CONCLUSIONS

This study has shown that the soil seed bank of most Kondoa Irangi Hills vegetation is dominated by diaspores of grass species, whereas that of the Afromontane dry forest has a mixture of both herbaceous pioneer species and mature forest species. Since the primary objective of rehabilitating badly eroded land is to protect the bare soil with vegetation cover so as to prevent it from further erosion, the presence of vegetation cover of any kind is useful initially. The absence of diaspores of woody species both in the seed bank (except for the Afromontane dry forest) and the seed rain should be compensated by supplementary seeding and transplanting seedlings.

Low and erratic rainfall, low nitrogen mineralization and reduced numbers of diaspores of woody species attributed to pre- and post-dispersal predation, and untimely germination are among the main constraints that limit seedling establishment in tropical drylands. In such ecosystems, seeds have developed ecological adaptations, such as prompt germination when moist, in order to avoid seed predation in the soil or extended distribution of germination to avoid synchronous seed germination, thereby providing insurance against local extinction of species. This study has shown that inorganic fertilisation of poor savanna soils is not an efficient means of improving short-term productivity, seedling recruitment or species turnover. Grazing and fires still remain the most reliable mechanisms of correcting nutrient-deficiency in tropical drylands, by taking into consideration high costs associated with fertilisation by inorganic compounds as well as their deleterious effects on the soil.

Management of degraded savannas that have been protected from grazing for a long time, such as KIH, may require careful and controlled re-introduction of livestock to enhance nitrogen mineralization and seed dispersal into the area. The reduction of grass biomass by grazing livestock, will consequently, reduce the destructive effects of fires. As a measure to enhance woody species regeneration, soil seed bank enrichment with seeds of desired qualities (e.g. keystone species with demonstrated ability to withstand water stress such as several species of *Acacia*) as well as transplanting seedlings, is necessary in KIH to promote more permanent successional changes.

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I

Floristic, structural and seed bank diversity of a dry Afromontane forest at Mafai, central Tanzania

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ABSTRACT

Flora, vegetation and seed bank were studied in a dry Afromontane forest in the Kondoa Irangi Hills, Tanzania with the objective to obtain information necessary for the promotion of conservation of this forest, which is rapidly degenerating due to human pressure. A checklist of vascular plants occurring in the forest is provided. Based on 27 plots, each of 400 m^2, the forest had the following ecological features: mean tree density 408 stems ha^{-1}; basal area 66.56 m^2 ha^{-1}; Shannon & Wiener diversity 2.6406; evenness 0.7585 and species richness 31 trees per 1.08 ha. The seed bank was dominated by woody species, including mature forest tree species, and had several species in common with the standing vegetation. The forest contains species that are phytogeographically linked to Madagascan, Western and Southern African floras and also species disjunctly distributed in this forest and the Eastern Arc Mountains of Tanzania. Correspondence Analysis of tree species based on size classes showed that the indigenous timber species had declining populations, indicating the possibility of genetic erosion, while other species showed expanding or interrupted populations. Some DBH-size classes (e.g. 145.0 - 189.9 cm) have disappeared from the forest, presumably due to their selective removal.

We recommend detailed integrated floristic and faunistic studies of the forest, targeting the ecologically sensitive indicators of habitat change such as orchids, birds, reptiles and amphibians. Finally, a proposal to conserve the forest under a community-based forest conservation scheme is put forward.

INTRODUCTION

Deforestation and fragmentation of tropical forests continue at alarming rates, resulting in serious problems including irreversible loss of genetic resources. The current rate of clearing of such forests is of global concern because this biome contains at least two-thirds of the world's species (Raven, 1988), some of them not even known to science.

According to Holdridge (1967), the earth's tropical forest is composed of dry forest (42%), moist forest (33%) and wet or rain forest (25%). In Africa, dry forests account for 70 - 80% of the forested land (Murphy & Lugo, 1986), and these are the most threatened of the major forest types in the Tropics in terms of biodiversity loss through fragmentation and deforestation. This is because tropical dry forests have fewer species than tropical moist forests, and importantly for biological and ecological reasons, they are more preferred than wetter forest zones for human settlement. Despite their importance, less attention has been given to tropical dry forest ecology compared with other tropical ecosystems.

The forest vegetation of East Africa has been studied by many researchers (see accounts by e.g. Burtt Davy, 1935; Greenway, 1973; Knapp, 1973; Lind & Morrison, 1974; Hedberg, 1951; Friis, 1992; Tamrat, 1993). The Afromontane forest, which is one of the five vegetation types of the Afromontane Region phytochorion recognised by White (1983), is subdivided into four categories i.e., Afromontane rain forest at high altitudes, Undifferentiated Afromontane forest at much lower altitudes, Single-dominant Afromontane forest, and Dry transitional montane forest (see Friis 1992). According to Friis (1992), a dry Afromontane forest which is dominated by *Podocarpus* forest mixed with *Cassipourea malosana* is part of the "Undifferentiated Afromontane forest" in the sense of White (1983).

The Mafai Forest in the Kondoa Irangi Hills, where this study was conducted, is a dry forest which seems originally to have been a *Podocarpus* forest. However, at present this description no longer holds because the forest has suffered dramatically from deforestation and selective removal of *Podocarpus* trees, which are highly prized for their quality timber.

Generally, deforestation in Tanzania has a long history, where large amounts of forest land have been cleared. This process still continues, and Mnzava (1988) estimated an annual clearance of between 300 000 to 400 000 ha of forest (bushland and miombo woodland included) in Tanzania. Recent statistics suggest 525 000 ha for the year 1990 alone (Makundi & Okiting'ati, 1995). FAO (1993) reported a deforestation rate per unit population of 109.0 ha (measured as "hectare deforestation per 1000 individuals per year") for Tanzania. This is higher than in most tropical countries. With current trends of deforestation, the remaining forests will disappear very soon. In order to counteract deforestation, regeneration measures should be taken.

There are several ways of natural regeneration in forests, but generally regeneration from the seed bank is more important in areas with pronounced seasonal variations in climate such as tropical dry forests. The occurrence of viable soil seed banks may be regarded as an insurance against local extinction of populations during unfavourable periods (Thompson, 1987; Kramer & Johnson, 1987). Tropical dry forest soils are known to contain reserves of long-lived seed banks dominated by pioneer species as well as secondary successional species (Guevara & Gomez-Pompa, 1972; Cheke *et al.*, 1979; Granström, 1982; Putz, 1983; Williams-Linera, 1990), and some of the mature forest species. This is because seasonality and climate variability in the dry tropics force seeds into dormancy cycles and seeds will only germinate in response to occurrence of proper germination conditions. It follows that the chances of vegetation regeneration from buried seeds are greater in dry forests than in wet forests, which rely mostly on seedling bank regeneration. Based on this, it is assumed that the seed bank of the dry forest at Mafai could be an important source of seeds in the process of forest regeneration.

The Mafai Forest is shrinking as a result of human encroachment in a bid to expand their farmlands. A preliminary vegetation survey indicated that the forest, with its rich biological potential, suffers from a high degree of human disturbance in terms of selective logging and firewood collection (Lyaruu *et al.*, 1997). Taking this into consideration, the current study was undertaken in order to propose more strict conservation of this forest.

Location of the study area in the Kondoa Irangi Hills

The Kondoa Irangi Hills (herein after called KIH) are located in central Tanzania at the eastern branch of the East African Rift Valley system (Fig. 1; cf. Eriksson, 1996). They occupy an area of about 1300 km^2 and extend from longitude 35^0 40’ to 36^0 10’E and latitude 4^{0}40’ to 5^0 0’ S (Mbegu & Mlenge, 1984). The hills were formed through uplifting in the late Tertiary to Recent times (Eriksson, 1996). The highest parts of KJH, above Mafai village, east of Haubi, are covered by Afromontane forest, whereas most of the KJH were originally probably dominated by miombo woodlands. The Mafai forest has an area of 1700 ha and rises steeply to an altitude of about 2200 meters from the low-lying Maasai plains located around 1200 meters above sea level. The climate of KJH is semi-arid to sub-humid with a mean annual rainfall of 600 - 800 mm (Ngana, 1992); in the forest it probably exceeds 1000 mm. The rainy season is from late November to May, and alternates with a six-month period of drought. The local distribution of the rain is governed by factors such as elevation and geographic location of different areas in relation to rain-causing winds.

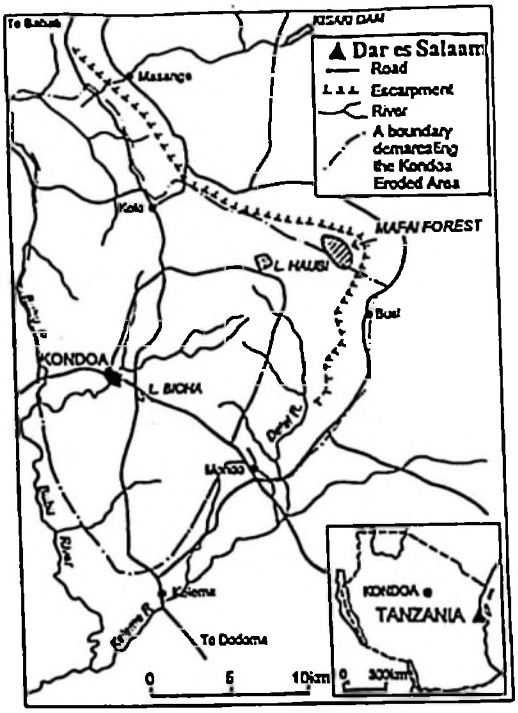

Figure 1. Map of the Kondoa Irangi Hills and their surroundings (from Eriksson, 1996).

Reasons for undertaking ecological studies of this dry forest community are the following:

1. No scientific studies have previously been carried out in this forest. According to reliable sources at the Tanzania Forestry Research Institute, the forest is not protected under any legislation except for the HADO rules (acronym for Hifadhi Ardhi Dodoma, a governmental organisation involved in soil conservation activities in central Tanzania). However, these rules are not strictly imposed. For a presentation of HADO, see Mbegu & Mlenge (1984) and Christiansson *et al.* (1993).
2. The small size and the isolation of the forest is of scientific interest. Continued forest decline may cause microclimatic changes in the future which could lead to reduction of minimum viable populations, and consequently extinction of species ecologically adapted to this forest, thus affecting species diversity (see e.g. Danielsen, 1997).
3. Selective removal of big trees may cause specific groups of plants such as epiphytes (including orchids) to lose their habitats and becoming extinct. Since all orchids are considered as endangered species by the World Conservation Monitoring Centre and the International Union for Nature Conservation, they need maximum protection in their habitats.
4. A preliminary survey indicated the presence of several plant species with high biological potential for conservation, such as the epiphytic orchids and timber trees like *Podocarpus falcatus*, *Podocarpus latifolius*, *Prunus africana*, and *Rapanea melanophloëos*.

The main objectives of this study are:

1. to assess the floristic and structural diversity of the forest;
2. to predict the seed bank regeneration potential of the forest by studying the seed bank size, composition and vertical distribution of seeds; and finally
3. to determine densities of the economically important trees, such as timber trees, as well as ecologically important species, e.g. big trees that serve as orchid habitats, and implicate this to management and conservation of this forest.

MATERIAL AND METHODS

Vegetation sampling

An initial reconnaissance survey into the forest was made in 1990. A vegetation survey aimed at producing the plant checklist was carried out in April 1994. Plant specimens were then collected with standard information for identification and deposition at the herbarium of the University of Dar Es Salaam. Specimens that could be identified on the spot were recorded in field note-books with standard information including growth form. Species that were difficult to identify in the field were identified in the Dar Es Salaam Herbarium from the collected material using Flora of Tropical East Africa (Turrill & Milne-Redhead, 1952-), Flora Zambesiaca (Exell & Wild, 1960-) and available herbarium specimens.

The floristic data used in this study were collected in April 1997, December 1997 and June 1998. Sampling was conducted in 5 transects with a total of 27 20 x 20m plots. From transect 1 (which run in West-East direction), where the logging was done much earlier than in other transects, 7 plots were sampled. Transects 2 (South West-North East direction) and 3 (South-North direction) included 4 plots each. Transect 4 can be regarded as an extension of transect 3 to the south. It had 3 plots, whereas transect 5, an easterly extension of transect one, had 9 plots. This forest part has recently been disturbed and logging was in progress at the time the survey was carried out.

All trees with diameter at breast height (DBH) of ≥ 10 cm were identified and their heights measured (DBH was measured at 1.3 m above the ground) using diameter tapes, except for those trees with large buttresses or prop roots which had their diameters measured above these protrusions. Some trees had multiple stems and in such cases each stem was measured separately. Heights were estimated using the trigonometric approach, as commonly used in forestry.

Soil sampling and greenhouse germination experiments

Soil seed bank samples were collected in November 1996, a period considered to be the peak for seed production and immediately before the rainy season. Nine sampling points from recently disturbed and much earlier disturbed parts of the forest were chosen systematically, and from each sampling point four soil samples, each of 206 cm^3, were collected at four depths, viz. litter layer, 0-5 cm, 5 - 10 cm, 10 - 15 cm and 10 - 20 cm, taking the precaution not to contaminate deeper soil layers with seeds from higher up in the profile. The soil was air-dried and then spread out in plastic trays in a thin layer, over a layer of sterilised soil that had been kept in an oven maintained at 140°C for 24 hours. The trays were then placed in random order in a greenhouse with a clear plastic roof at the University of Dar Es Salaam which had a photoperiod of 10 to 12 hours and a mean temperature of 30°C (± 5^0C) and they were watered once daily. Control trays with only sterilised soil were set alongside the experiment to detect contamination by wind dispersed seeds. Seedlings were counted, recorded and then removed as soon as they could be identified. Those that proved difficult to identify were transplanted and observed until flowering for correct identification. Grasses and herbs that did not produce flowers and could not be identified, were grouped as "unknown grass" or "unknown herb". The seed bank soil was stirred twice a month and the germination trays monitored until no more germination occurred.

Data analysis

A cumulative species-area curve for species sampled from the plots is presented in Figure 2. The vegetation data were also analysed using the Shanon & Wiener diversity from the relationship $H' = -\sum_{i=1}^{s} p_i \ln p_i$, where p_i is the proportion of the trees found in the ith species as in Magurran (1988). Further, evenness defined as $H'/\ln S$, where S is the total number of species, density (stems ha^{-1}) and basal area (m^2 ha^{-1}) for each species were measured. A paired t-test was used to test the significance of mean seed densities of the seed bank at different depths. Analysis of population structure was done by categorising the tree species into seventeen 15 cm wide DBH classes and twelve 3 m wide classes for height frequency distribution.

Correspondence Analysis was done for tree species and the DBH size classes using the corrected version of programme CANOCO (ter Braak, 1987-1992) according to Oksanen & Minchin (1997). The data matrix was a table of 29 species with densities of ≥ 3 stems ha^{-1} (in the rows) and 17 DBH classes (in the columns).

The average depth (AD) used to calculate seed bank density (see Demel & Granström, 1995) was obtained from the relationship:

$$\mathbf{AD} = \frac{(SL \times 1.0) + (ST \times 4.5) + (SM \times 9.5) + (SB \times 17)}{\textbf{Total number of viable seeds of each species}}$$

where: SL = number of seeds in the litter layer and ST, SM & SB are numbers of seeds in the soil layers 0 - 5, 5 - 10 and 10 - 20 cm, respectively. The multipliers 1.0, 4.5, 9.5 and 17 correspond to the depth from the top of the litter layer (assumed to be a uniform 2.0 cm thick) to the middle of the four respective layers. For example, for 5 - 10 cm depth, the average depth is (5 + 10)/2, and when the 2 cm litter depth is added, it gives the value of 9.5.

The ratio of distribution of seeds in the surface and subsurface layers (SSR) for each species was calculated according to a formula modified from Kjellsson (1992) as follows:

$$\mathbf{SSR} = c \ln \frac{(N_u/N_{tot})\,(3/4) + 1}{(N_L/N_{tot})\,(1/4) + 1}$$

where: N_u is the number of seeds in the litter layer, N_L is the number of seeds in each of the three subsurface soils, N_{tot} is total number of seeds in both litter and subsurface soil layers and $c = 1.7869$, a constant set to approximate the lower and upper limit for SSR to 1 and -1, respectively. Cluster analysis of the seed bank species based on Ward Linkage and squared Euclidean distances (MINITAB version 10xtra 1995 for dendrograms) was applied to species x surface to subsurface distribution ratios. The clusters were arranged in a dendrogram, which were then analysed for patterns concerning seed bank behaviour. The seed bank species were grouped into their respective dispersal modes based on literature accounts and personal observations.

RESULTS

Floristics

A total of 441 trees from 31 species representing 17 families were recorded. A checklist with 103 species (all plants included) occurring in the forest is presented in Appendix 1. The forest has a density of 408 stems ha^{-1}, basal area of 66.56 m^2 ha^{-1}, Shannon & Wiener diversity of 2.6406 and an evenness of 0.7585. All timber species, for instance *Podocarpus falcatus*, *Podocarpus latifolius*, *Prunus africana*, and *Rapanea melanophloëos*, have very low densities and are therefore categorised as being rare or very rare. The most abundant tree species in the forest are *Albizia glaberimma*, *Drypetes reticulata*, *Drypetes usambarica*, *Ochna holstii*, *Oxyanthus speciosus* and *Xymalos monospora.*

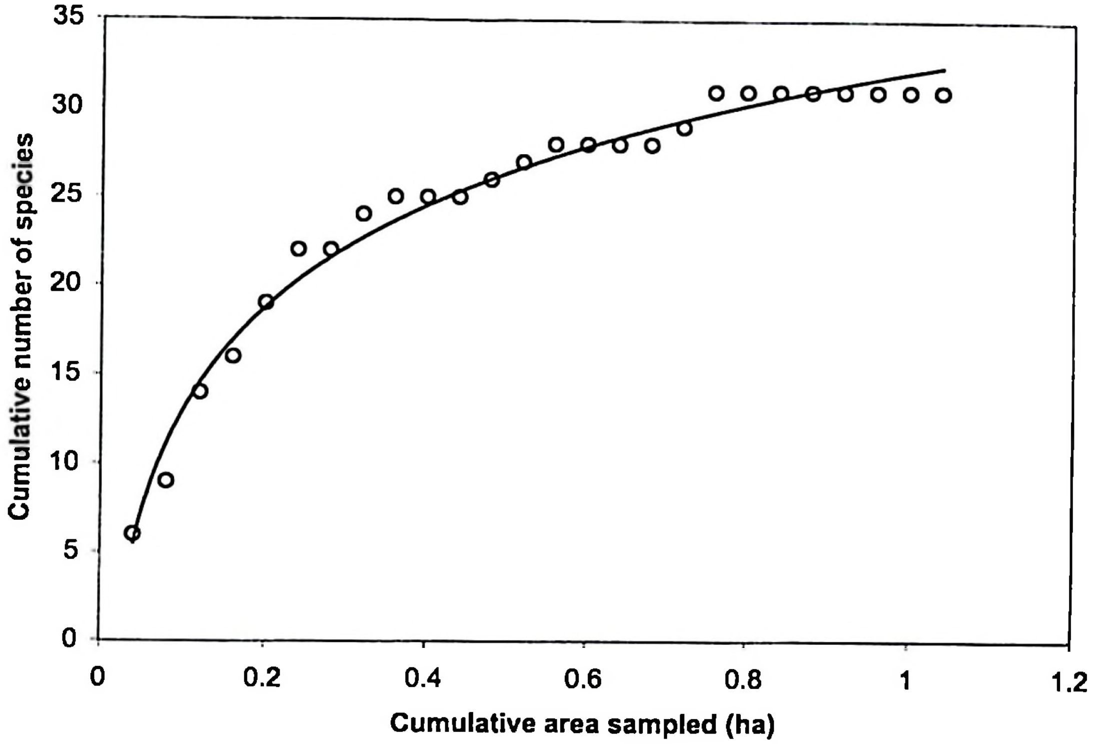

Figure 2. Cumulative species-area curve for 31 tree species sampled from an area of 1.08 ha in the Mafai dry forest.

Taxonomic and phytogeographical affinities

The largest families are Rubiaceae (9 tree species), Euphorbiaceae (3 tree species), Moraceae, Meliaceae, Podocarpaceae and Myrsinaceae (2 tree species each); the remaining families have one tree species each. Seven tree species, i.e. *Albizia glaberimma*, *Drypetes reticulata*, *Drypetes usambarica*, *Ficus thonningii*, *Ochna holstii*, *Oxyanthus speciosus* and *Xymalos monospora*, account for more than 67% of the total basal area, and ca. 72% of the tree density (Table 1).

The floristic data show that most species have distributions with a disjunction between Mafai and the Eastern Arc Mountains, notably the Usambaras with *Drypetes usambarica* known to be an "Eastern Arc

Arc near endemic" (Iversen, 1991; Lovett *et al.*, 1997). *Croton macrostachyus*, *Embellia schimperi* and *Trema orientalis* have Guineo-Congolian distributions and *Albizia gummifera*, *Maytenus acuminata*, *Schefflera myriantha* and the orchids *Acampe pachyglossa* and *Microcoelia exilis* occur in the Madagascan flora. *Cussonia spicata* and *Lannea schweinfurthii* are also common in Cape and Karoo-Namib floras (Iversen, 1991). The economic importance and phytogeographical distribution of trees found in this forest is given in Table 2.

DBH, height and forest stratification

Five species with the highest basal areas and densities contributed most to the structure of the forest (see Table 1). *Albizia glaberimma*, *Drypetes reticulata*, *Drypetes usambarica* and *Ficus thonningii* are the emergent trees while *Oxyanthus speciosus* and other members of the family Rubiaceae occupy an intermediate position in this forest due to their limited capacity to grow in height and diameter. In the DBH frequency distribution for all species together, all size classes 145.0 - 189.9 cm are lacking individuals (Fig. 3). About 60% of all individuals sampled are found in the smallest DBH size class (i.e. < 25 cm) and very few ca. 3% in the biggest size classes (> 200 cm). Above 200 cm DBH, the trees include *Ficus natalensis* and *Nuxia congesta* which are also canopy trees that are probably relicts from the former vegetation prior to disturbance.

The height class frequency distribution of the trees is shown in Fig. 4. Trees with heights < 10 m constitute ca. 27% of the total individuals sampled, whereas those with ≥ 28 m were only 12.5%. The observed pattern in Fig. 4, where most individuals are found in the smaller size classes, and where they decrease in numbers progressively towards bigger size classes, suggests presence of a stratified forest where *Albizia glaberimma*, *Drypetes reticulata*, *Drypetes usambarica*, *Ficus natalensis*, *Ficus thonningii*, *Nuxia congesta* and *Ochna holstii*, form the canopy.

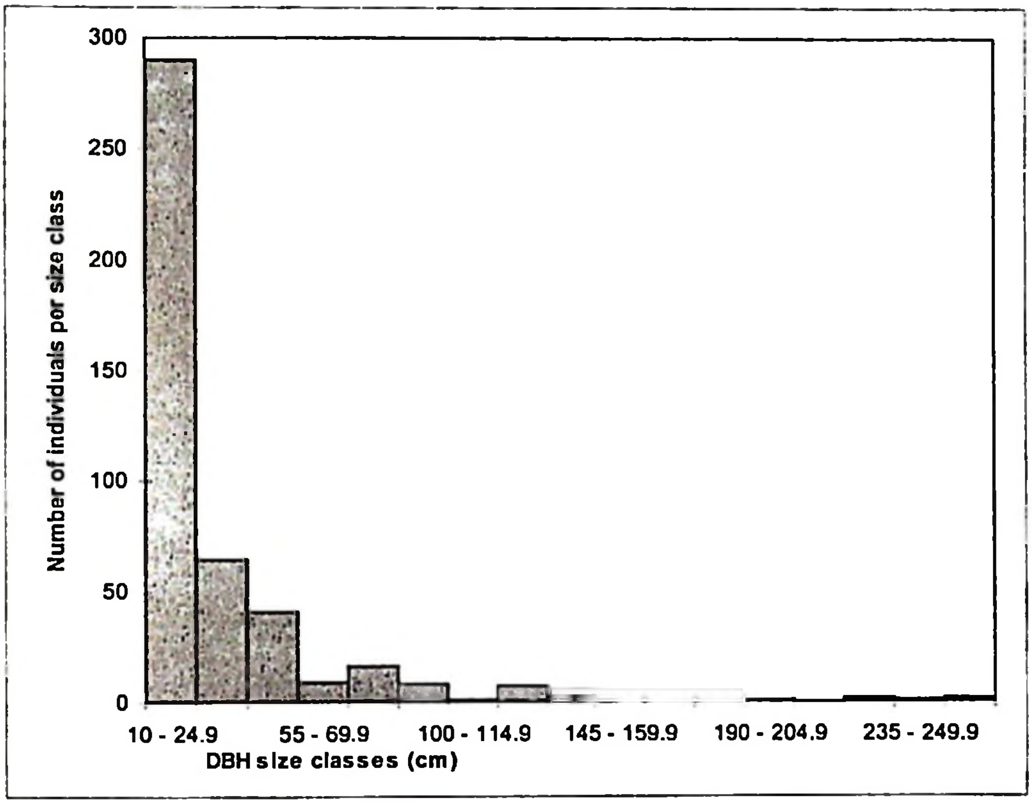

Figure 3: DBH-classes frequency distribution for 441 trees sampled from twenty seven 20 x 20 m plots in Mafai remnant forest.

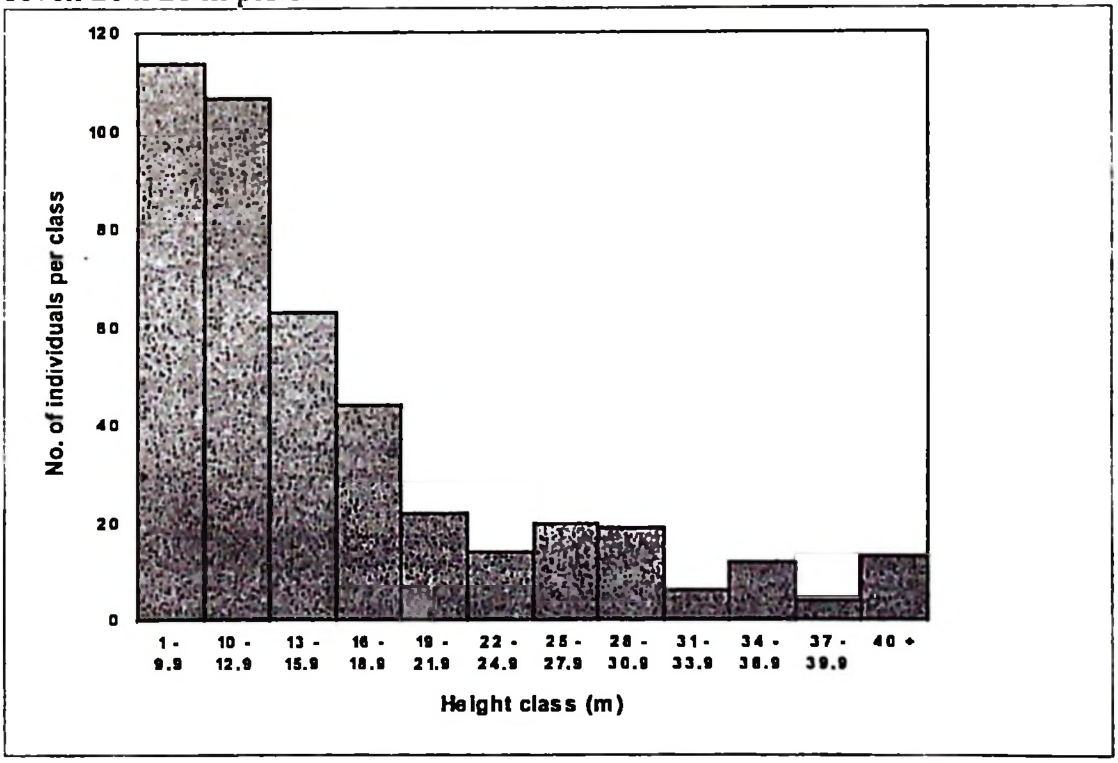

Figure 4: Height classes frequency distribution of 441 trees sampled from twenty seven 20 x 20 m plots in Mafai remnant forest.

Population structure and DBH size classes

Correspondence Analysis using DBH size classes (columns) and species (rows) (axes 1 and 2 with eigenvalues 0.447 and 0.401, respectively) produced groups with three different population structures (Fig. 5). Group 1, which corresponded to an expanding or balanced population, comprised of species dominated by the smallest DBH size classes and species with relatively high densities. These included *Albizia glaberrima*, *Drypetes reticulata*, *Drypetes usambarica*, *Ochna holstii*, *Oxyanthus speciosus* and *Xymalos monospora*. For an expanding or balanced population, the distribution of individuals of different size classes is such that most individuals are found in the lowest size classes and they decrease progressively towards the bigger size classes. The position of group 1 species is either dependent on the biology of species (e.g. all members of the family Rubiaceae, which do not attain big size classes in nature), or absence of big size classes.

The second category involves species such as *Cassipourea malosana*, *Ekebergia capensis*, *Embellia schimperi*, *Ochna holstii* and *Podocarpus falcatus* which can grow into very big trees under natural conditions. Species of group 2 in the ordination diagram have interrupted populations, which indicates irregular recruitment through patch colonisation as shown by *Cassipourea malosana* and *Nuxia congesta*. Such populations could also be accounted for by the presence of remnants from the former vegetation before disturbance as they have the biggest size classes.

Some of the timber trees in the forest, like *Lannea schweinfurthii*, *Podocarpus latifolius* and *Prunus africana,* have declining populations, and form group 3 in the ordination. A declining population is characterised by absence of juveniles and possibly the biggest size classes. Some rare tree species are present in the forest (see appendix) but were not found in the sample plots. These include *Olea capensis* ssp. *hochstetterii*, *Olea europaea* ssp. *africana*, *Psydrax parviflora* and *Schefflera myriantha*. Only *Drypetes reticulata*, *Drypetes usambarica* and *Nuxia congesta* were found to be associated with strangling figs of the species *Ficus natalensis*, and a number of *Nuxia congesta* trees were observed dead from this association.

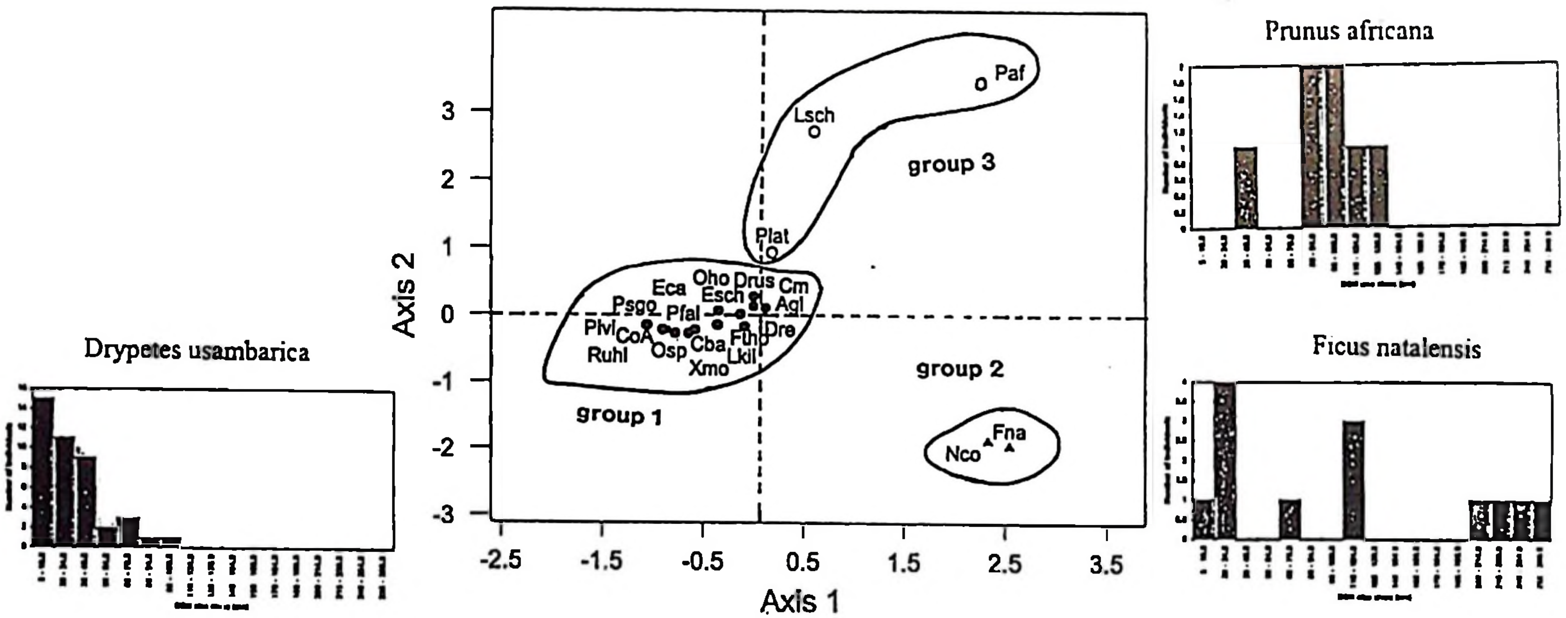

Figure 5. Correspondence Analysis (CA) of species (rows) x dbh size classes (columns) and different population structures of the tree species (only species with > 3 stems ha^{-1} included) sampled from Mafai forest. Group 1 has an expanding populations e.g. Agl = *Albizia glaberimma*; Cba = *Casearia battiscombei*; Cm = *Croton macrostachyus*; CoA = *Coffea sp. A*; Dre = *Drypetes reticulata*; Drus = *Drypetes usambarica*; Eca = *Ekebergia capensis*; Esch = *Embellia schimperi*; Fth = *Ficus thonningii*; Lkil = *Lasianthus kilimandscharicus*; Oho = *Ochna holstii*; Osp = *Oxyanthus speciosus*; Pivi = *Pittosporum viridiflorum*; Pfal = *Podocarpus falcatus*; Psgo = *Psychotria goetzei*; Ruhl = *Rhytgynia uhligii;* Xmo = *Xymalos monospora*. Group 2 with interrupted or discontinuous populations include Fna = *Ficus natalensis* & Nco = *Nuxia congesta*. Group 3 has declining populations and is composed of Lsch = *Lannea schweinfurthii;* Plat = *Podocarpus latifolius* & Paf = *Prunus africana*.

Seed bank

Elsewhere in the Kondoa Irangi Hills the seed banks are dominated by herbaceous annual species by over 60% (Lyaruu 1995), but the Mafai forest seed bank was shown to have a 75% (18 out of 24 species) dominance of woody species. Mature forest species accounted for over 20% of the seed bank. Most pioneer species were found in the deeper soil strata whereas species of mature forests were superficially distributed. There was a general decline of seed numbers with depth irrespective of the site's temporal scale of disturbance (Table 3). The seed bank species consisted of fruits and seeds of mature tree and pioneer species eaten and dispersed by birds and mammals (ecto- and endozoochorous) as well as of wind-dispersed herbs, especially species of Compositae (Table 4). In the seed bank, 14 out of 24 species (58%) were zoochorous (both birds and mammals), whereas in the standing vegetation it was 26 out of 31 species (81%).

Table 3. Mean number of seeds (n = 9) (actual number in brackets) and densities in different soil strata with the standard deviations for the whole forest, and in old and recently disturbed sites. The significant levels were tested by Tukey's Studentized (HSD) Test

STRATUM	MEAN (x ± sd)	DENSITY (seeds m^{-2})
Litter	6.3 ± 3.55	634 (at 2 cm litter depth)
0 - 5 cm	5.6 ± 2.83	1389
5 - 10 cm	3.0 ± 2.82	750
10 - 20 cm	1.78 ± 2.48	445

STRATUM	OLD (x ± sd)	RECENT (x ± sd)	P-value
Litter	6.75 ± 1.92(27)	6.25 ± 4.91(25)	> 0.05
0 - 5 cm	6.5 ± 2.59(26)	4.75 ± 3.11(19)	> 0.05
5 - 10 cm	1.75 ± 1.09(7)	5.0 ± 3.0(20)	< 0.05
10 - 20 cm	± 0(0)	3.25 ± 2.86(13)	< 0.05

The forest standing vegetation was reflected in the seed bank much more than elsewhere in the KIH vegetation (Lyaruu *et al.*, 1997) by possession of many common species, such as *Drypetes usambarica*, *Ekebergia capensis*, *Ficus natalensis*, *Ficus thonningii*, *Solanum richardii*, *Solanum dasyphyllum* and *Trema orientalis*. Not a single seed of timber trees was found in the seed bank soil samples, showing that they are absent or rare in the soil.

Table 4. Seed bank flora of the Mafai Forest (all species included), showing average depth distribution, species' density and seed dispersal mechanisms. Z_i stands for endozoochorous, Z_e for ectozoochorous (i.e. birds and mammals) and **A** for anemochorous dispersal. Species with asterisk (*) are pioneers and § indicates mature or climax species

Scientific name	Growth form	Average depth (in cm)	Density (in m^{-2})	Dispersed form/mode
Abutilon mauritianum	shrub	7.1	178	seed, Z_e A
Achyranthes aspera	herb	5.3	15	fruit, Z_e A
Ageratum conyzoides	herb	4.5	7	fruit, A
Blumea aurita	shrub	4.1	29	fruit, A
Cyperus dereillema	sedge	7.9	275	fruit, Z_i A
Dichrocephala integrifolia	herb	4.5	7	fruit, A
Drypetes usambarica§	shrub	1.0	5	seed, A
Ekebergia capensis §	tree	1.0	2	seed, Z_i
Ficus natalensis §	tree	3.4	24	fruit, Z_i
Ficus sur §	tree	5.5	85	fruit, Z_i
Ficus thonningii §	tree	10.8	30	fruit, Z_i
Inula confertiflora	herb	1.0	2	fruit, A
Kalanchoe lanceolata	shrub	9.0	25	seed, A
Oldenlandia corymbosa	herb	4.5	7	fruit, A
Oreosyce africana	climber	5.0	56	seed, A
Physalis peruviana	shrub	4.7	46	fruit, Z_i
Piper capense *	shrub	1.0	6	seed, Z_i
Psychotria goetzei *	tree	4.5	7	fruit, Z_i
Rubus rosifolius *	shrub	3.5	30	fruit, Z_i
Senecio bojeri	shrub	2.0	20	fruit, A
Solanum dasyphylum	shrub	1.0	2	fruit, Z_i
Solanum richardii	shrub	9.0	25	fruit, Z_i
Trema orientalis *	tree	6.8	95	fruit, Z_i
Vernonia brachycalyx	shrub	2.3	26	fruit, A

The distribution of seeds in the soil is an indication of seed longevity, with seeds found deeper being considered to be more long-lived than those distributed in the superficial layers. A dendrogram based on the distribution ratio of seeds on the surface and subsurface (SSR) produced two clusters at a similarity level of 42% (Fig. 6): One cluster with species assumed to possess persistent seed banks (to the left; low SSR) and the other with transient seed banks (to the right;

cluster with species assumed to possess persistent seed banks (to the left; low SSR) and the other with transient seed banks (to the right;

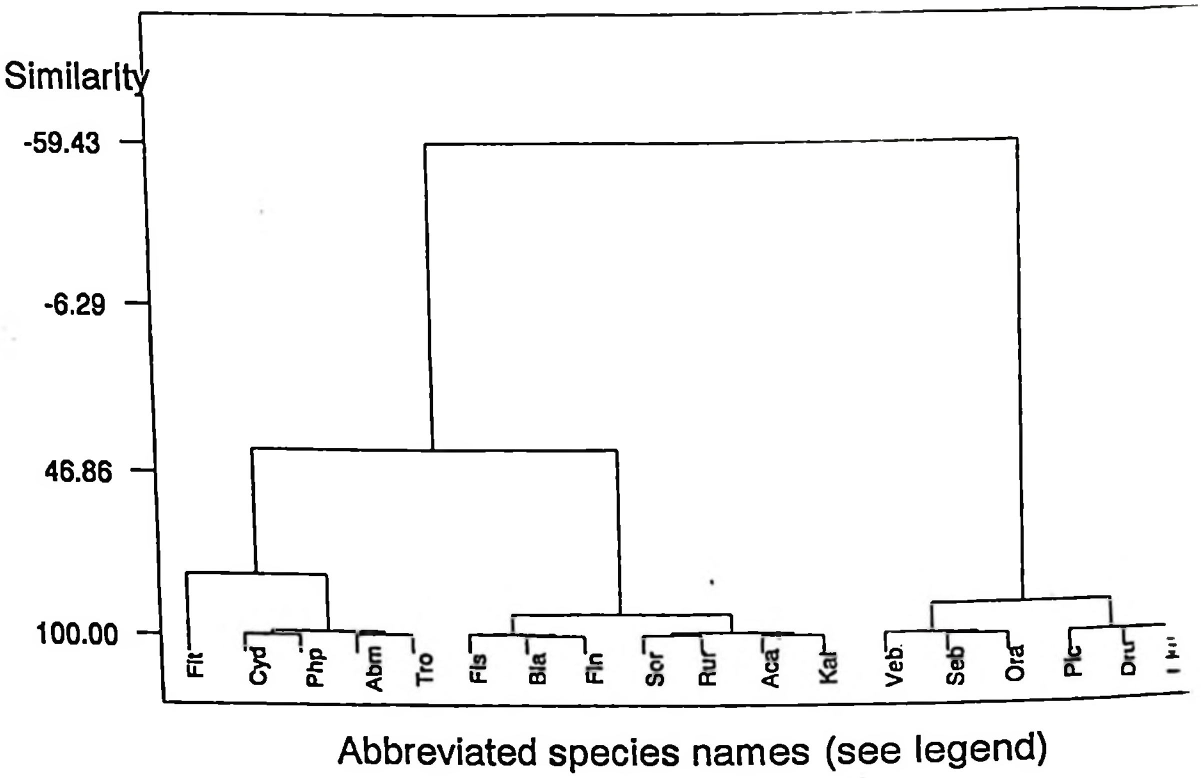

Figure 6. Dendrogram to show clusters based on seeds surface to subsurface ratios (SSR) as defined in the Material & Methods. Species are abbreviated as follows: Fit = *Ficus thonningii*, Cyd = *Cyperus dereillema*, Abm = *Abutilon mauritianum*, Tro = *Trema orientalis*, Fis = *Ficus sur*, Bla = *Blumea aurita*, Sor = *Solanum richardii*, Rur = *Rubus rosifolius*, Aca = *Achyranthes aspera*, Kal = *Kalanchoe lanceolata*, Fin = *Ficus natalensis*, Veb = *Vernonia brachycalyx*, Seb = *Senecio bojeri*, Ora = *Oreosyce africana*, Pic = *Piper capense*, Dru = *Drypetes usambarica* & Ekc = *Ekebergia capensis*.

high SSR). At a similarity level of ca. 75%, the seed bank could be divided into long-term persistent (negative SSR), short-term persistent (intermediate SSR) and transient (positive SSR close to 1) seed bank.

DISCUSSION

Tropical dry forests are less diverse and have low species richness compared with wet forests. Murphy & Lugo (1986) reported richness and basal area of 35 - 90 trees species ha^{-1} and 17 - 40 m^2 ha^{-1} in tropical dry forests, respectively. The Shannon & Wiener diversity, mean basal area and stem densities of Mafai forest are higher than those reported from the West Usambara, Mwanihana and Kihansi forests in Tanzania by Lovett *et al.* (1997). Since these forests were sampled using the variable radius plotless method (Lovett *et al.*, 1997) where only the 20 closest trees were considered, and also trees were defined to be individuals with ≥ 20 cm DBH, the results should be different. The existence of phytogeographical links to the Madagascan flora and the Guineo-Congolian flora may serve as a supporting evidence that the forests of East and West Africa were once continuous (see Iversen, 1991 and references cited therein). It means that species that were capable of surviving harsh climatic conditions during parts of the Pleistocene are now restricted to these small fragmented forests, and therefore such forests are of high conservation value.

Population structure and forest dynamics

Expanding populations of *Oxyanthus speciosus*, *Xymalos monospora* and others are an indication of active regeneration. This could imply that either these species are likely to dominate the forest vegetation entirely in the future if disturbance continues or, since they are understorey species, they may disappear with disappearance of canopy trees. Declining populations can be explained on the basis of two alternative theories: Either there has been selective removal of individuals of certain size classes over a period of time, or these species have failed to regenerate, or a possible third alternative could be a combination of both. As for the timber trees, selective logging of the big-sized trees and leaving out the few stunted and genetically impoverished individuals is the more likely explanation. To illustrate this point, among 29 individuals of *Podocarpus* recorded, the biggest individual had a DBH of 119 cm, although *Podocarpus* can attain a maximum DBH of 200 cm (Beentje, 1994). This could imply massive harvesting of *Podocarpus* species from this forest in the past. Difficulties in regenerating indigenous timber trees from seed have been documented earlier (Wilan, 1965; Pócs, 1988), and therefore the lack of juvenile timber trees could be attributed to regeneration failure.

Irregularity in species recruitment

Discontinuous population structures often indicate irregular recruitment through temporal gap colonisation in the forest or presence of relicts from former vegetation which survived previous disturbance. *Nuxia congesta* is a mature forest species which is not economically important as a timber tree, but it is an ecologically very important component of tropical forests. The biggest trees in this forest were *Nuxia congesta* and *Ficus natalensis*. These trees are likely to be remnants of the former vegetation, and probably in the absence of disturbance which removed the timber trees, the canopy will have a domination of other big trees almost equalling the size of *Nuxia congesta* now. The importance of fig trees in recolonisation of disturbed forests and in promoting species diversity in tropical rain forests, especially for the fruit-bearing trees, has been documented earlier (Terborgh, 1986). Strangling figs, e.g. *Ficus natalensis* are known to establish as hemiepiphytes on big old trees with knotholes (Laman, 1996). Being canopy species, they are shade-intolerant and therefore they have to grow faster than the host trees in order to occupy the top position of the canopy (Laman, 1996). The ecological implications of having big populations of canopy figs and reduced tree densities in a watershed area is on the water balance of the forest and streams associated with the forest, because the fast-growing figs certainly demand a lot of water (Laman, 1996).

Canopy trees and forest structure

The canopy trees are important in that, in addition to giving shape (three-dimensional structure) to the forest and maintaining the forest microclimate, they are habitats of orchids and other epiphytes. In this forest, selective harvesting of big trees is taking place up to the moment when the survey was conducted. During the survey we witnessed a number of big dead trees that had been killed by strangling figs and some of them were identified as *Nuxia congesta*. Total removal of such trees may bring about extinction of epiphytes and cause overall structural changes in plant communities in the forest. Mosses, always found in association with big trees, are important especially in dry forests in their ability to trap moisture and make it available to the forest flora for a much longer period after the rainy season (see Pócs, 1988).

As for *Albizia glaberimma*, although it has an expanding population, we consider it to be a fast-growing gap coloniser with very limited economic uses. The population of *Albizia glaberimma* may be related to the time when gaps were created in the forest (temporal) as well as to the dimensions of the gaps. Whereas the temporal scale accounts for their different sizes, spatial scale accounts for their numbers. An interesting point to note about *Albizia glaberimma* is that at the time the survey was conducted there were many seedlings beneath adult trees which were estimated to be less than three weeks old but nothing was found in the seed bank samples. Secondly, no bigger seedlings were seen below the adults except in gaps, suggesting that the species is a shade-intolerant pioneer and that its seedlings suffer high rates of mortality under the low canopy shade. Further research directed towards understanding the regeneration patterns of this species in this forest may yield very useful information.

Seed bank and regeneration potential of the forest

The seed bank density of the forest is higher than densities reported from tropical lower montane forests (161 - 406 seeds m^{-2}, Cheke *et al.*, 1979; Lawton & Putz, 1988), but within the range of those reported from tropical successional forests (e.g. 1441 - 4051 seeds m^{-2} reported in Guevara & Gomez-Pompa, 1972; Young, 1985; Garwood, 1989). High seed densities obtained from the forest provide a clear indication of disturbance and may also be linked to prolonged dry seasons experienced in dry forests, which necessitates accumulation of dormant seeds in the soil.

The property of seeds to remain dormant in the soil for a long time is important because such seeds will form future vegetation in the process of secondary succession. Species capable of forming persistent seed banks have a better chance of recolonizing disturbed sites than species with transient seed banks. Domination of the Mafai forest seed bank with woody species as well as species of mature forests is in agreement with studies from other tropical dry forests (Whitmore, 1975; Demel & Granström, 1995). The implication of this finding is that the seed bank is a reliable means of replacing individuals in this degenerating forest. But this is only possible if further deforestation or fragmentation that might influence the function of the ecosystem, such as dispersal, pollination and reducing the number of mature trees, is avoided. Absence of common timber species from the soil seed bank could mean that such seeds were not present in the soil, or that such species do not accumulate persistent seed banks, or that their seeds are heavily predated. All assumptions may be correct but their confirmation through experimentation is necessary.

CONCLUSIONS

1. Tree densities of timber trees such as *Podocarpus falcatus*, *Podocarpus latifolius*, *Prunus africana* and *Rapanea melanophloëus* are very low. In this forest, only species such as *Albizia glaberimma*, *Drypetes reticulata*, *Drypetes usambarica*, *Ochna holstii*, *Oxyanthus speciosus* and *Xymalos monospora* have balanced populations. In view of this, the timber trees in this forest have already experienced genetic erosion.
2. The soil seed bank is composed of many woody species, pioneer tree species and mature forest species and most of them are buried in the deep soil layers, but timber tree seeds are lacking. The implication is that the seed bank is a reliable means of restoring some kind of forest vegetation, but not the original vegetation, provided no further disturbance that will remove the soil takes place. As for the timber trees, more research is required so as to establish the reason for their absence in the seed bank.
3. Conservation of this forest at Mafai is proposed. This is important because most plant species found in the forest also occur in the

Eastern Arc Mountains of Tanzania, in Madagascar and in Western and Southern Africa. Such forests with wide and disjunct distributed species may be considered to be "museums" of species which have become wiped out elsewhere in the continent and therefore need protection.

4. Community-based forest conservation is suggested. This remnant forest will only be suitable for such practice when changes in the population dynamics are sufficient enough to allow conservation as well as utilisation. We recommend this knowing that community forestry and sustainable utilisation of forest products are inseparable, and that disturbed tropical dry forests could take as long as 150 years to recover fully (Murphy & Lugo, 1986). Before this action is taken, it is important to carry out integrated floristic and faunistic field studies in order to evaluate the actual biological potential of the forest.
5. We recommend inventory of all orchid species and their host trees in the forest. This is due to their global horticultural significance, and also because orchids are the life form most susceptible to extinction through forest disturbance (Turner *et al.*, 1994). And importantly, all orchids are protected species by the World Conservation Monitoring Centre (WCMC) and International Union for Nature Conservation (IUCN). Orchids may also be regarded as indicators of health conditions in tropical forests. We therefore suggest regular monitoring of orchid populations in this forest.

Table 1. Summarised information of all 31 species collected from Mafai forest arranged alphabetically in their respective families.

FAMILY	SPECIES NAME	No. of Ind.	density (stems ha^{-1})	basal area (m^2 ha^{-1})	frequency	relative density	relative frequency
ANACARDIACEAE	*Lannea schweinfurthii*	4	3.70	1.494	0.074	0.009	0.013
ARALIACEAE	*Cussonia spicata*	1	0.93	0.233	0.037	0.002	0.006
CELASTRACEAE	*Maytenus acuminata*	2	1.95	0.851	0.074	0.004	0.013
EUPHORBIACEAE	*Croton macrostachyus*	1	0.93	0.089	0.037	0.002	0.006
	Drypetes reticulata	64	59.25	7.147	0.407	0.144	0.070
	Drypetes usambarica	41	37.96	4.528	0.4801	0.092	0.083
FLACOURTIACEAE	*Casearia battiscombei*	4	3.70	0.119	0.148	0.009	0.025
LOGANIACEAE	*Nuxia congesta*	4	3.70	8.741	0.074	0.009	0.013
MELIACEAE	*Ekebergia capensis*	4	3.70	0.206	0.074	0.009	0.013
	Turraea mombassiana	2	1.85	0.064	0.037	0.004	0.006
MIMOSACEAE	*Albizia glaberrima*	39	36.11	6.496	0.590	0.088	0.102
MONIMIACEAE	*Xymalos monospora*	31	28.70	1.255	0.518	0.07	0.089
MORACEAE	*Ficus natalensis*	13	12.04	19.340	0.222	0.03	0.038
	Ficus thoningii	18	16.11	1.820	0.074	0.04	0.013
MYRSINACEAE	*Embelia schimperi*	12	11.11	1.349	0.074	0.027	0.013
	Rapanea melanophloeos	3	2.78	0.046	0.111	0.007	0.019
OCHNACEAE	*Ochna holstii*	29	28.85	1.919	0.4810	0.07	0.083
PITTOSPORORACEAE	*Pittosporum viridiflorum*	5	4.63	0.058	0.111	0.011	0.019
PODOCARPACEAE	*Podocarpus falcatus*	10	9.25	1.883	0.185	0.022	0.032
	Podocarpus latifolius	9	8.33	0.350	0.111	0.02	0.019
RHIZOPHORACEAE	*Cassipourea malosana*	8	7.41	0.886	0.296	0.018	0.0510

ROSACEAE	*Prunus africana*	7	6.48	6.224	0.222	0.015	0.038
RUBIACEAE	*Coffea sp A*	5	4.63	0.067	0.111	0.011	0.019
	Lasianthus kilimandscharicus	5	4.63	0.151	0.037	0.015	0.006
	Oxyanthus speciosus	94	87.04	1.268	0.518	0.211	0.089
	Pavetta abyssinica	3	2.78	0.090	0.037	0.007	0.006
	Psychotria goetzei	5	4.63	0.063	0.148	0.011	0.025
	Psychotria elasticantha	3	2.78	0.050	0.074	0.007	0.013
	Rhytgynia uhligii	12	11.11	0.620	0.333	0.027	0.057
	Tarrena pavettoides	1	0.93	0.009	0.037	0.002	0.006
	Tricalysia sp.	2	1.85	0.040	0.037	0.004	0.006

Table 2. Thirty-five tree species recorded from Mafai Forest in Kondoa Irangi Hills that are also found in the Usambara Mountains of Eastern Tanzania, showing their economic and phytogeographical affinities

Species	Distribution	Economic use
Albizia glaberrima (Sch. & Thon.) Ben	AM; Z-I; S-M; Z	timber; medicinal
Albizia gummifera J. F. Gmel	AFR-MAD	timber, medicinal
Casearia battiscombei R.E. Fries	AM	timber
Cassipourea malosana (Bak.) Alston	AM	construction; poles
Croton macrostachyus Hochst ex Del.	G-C; AM	medicinal; axe handles;
Cussonia spicata Thunb.	S-M; Z; AM;MAD	low quality wood, traps
Dracaena laxissima Engl.	AM; G-C	medicinal
Drypetes natalensis (Harv.) Hutch.	AM; Z-I; Z; G-C	building materials
Drypetes reticulata Pax	AM; S-M; Z-I; Z; G-C	building materials
Drypetes usambarica (Pax) Hutch.	AM	building materials
Ekebergia capensis Sparrm.	Pantropical	carpentry; joinery works
Embellia schimperi Vatke	AM; Z; G-C	edible leaves; medicinal
Ficus natalensis Hochst	Z-I; Z, AM	medicinal; fruits; fibre
Ficus sur Forssk	Pantropical	fruits; fibres
Ficus thonningii Blakelock	Pantropical	cloth; fibres;
Lannea schweinfurthii (Engl.) Engl.	S-M; Z; AM; Z-I; LV	edible fruits,; medicinal
Lasianthus kilimandscharicus K. Schum.	AM	building poles, firewood
Lasianthus pedunculatus E. A. Bruce	AM	poles, firewood
Maytenus acuminata (Thunb.) Blakelock	AFR-MAD; AM	timber; medicinal
Nuxia congesta R. Br. Fresen	Pantropical	building; useful bee tree
Ochna holstii Engl.	AFR-MAD; AM	hardwood for construction
Olea capensis L. ssp. *hochstetteri* (B.)F&G	Pantropical	first class timber; fruits
Olea europaea L. ssp. *africana* (M.) G.	Pantropical	timber; edible fruits
Oxyanthus speciosus DC.	AM	building poles; firewood
Pittosporum viridiflorum Sims	AM; S-M; Z; AFR-MAD	medicinal; hardwood;
Podocarpus falcatus (Thunb.) Mirb.	AM	first class timber; medicinal
Podocarpus latifolius (Thunb.)Mirb.	AM; Z	first class timber; medicinal
Prunus africana (Hook. f.) Kalkman	AM; AFR-MAD	first class timber; medicinal
Psychotria goetzei (K. Schum.) Pet.	AM near endemic	building poles; firewood
Psydrax parviflora(Afz.) Brids.	AM	hardwood, good timber
Rapanea melanophloeos (L.) Mez.	AM; Z-I; Z; LV	timber; medicinal; handles
Rytigynia uhligii (Schum.& Krause)Verdc.	AM	building poles; firewood
Trema orientalis (L.) Blakelock	AM; G-C	edible fruits; insecticidal
Vernonia brachycalyx O. Hoffm.	AM	medicinal
Xymalos monospora (Harv.) Warb.	AM	timber

Sources of information: Dale & Greenway (1961); Iversen (1991) and Beentje (1994).
Abbreviations: AM = Afromontane archipelago in the Eastern Arc Mountains of Tanzania; Z = Zambezian phytochorion; S-M = Somali-Maasai; G-C = Guineo-Congolian; Z-I = Zanzibar-Inhambane; LV = Lake Victoria regional mosaic; AFR-MAD = Africa-Madagascar disjuncts and Pantropical or widespread taxa.

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Appendix 1. Provisional checklist of plant species found in Mafai remnant forest in Kondoa, Tanzania as compiled by Leonard B. Mwasumbi & Haji Suleiman of the University of Dar Es Salaam Herbarium

	Scientific name & authority	Family	Habit
1.	Acalypha psilostachya Hochst	Euphorbiaceae	herb
2.	Acampe pachyglossa Reichb.f.	Orchidaceae	herb
3.	Achyranthes aspera L.	Amaranthaceae	herb
4.	Aeollanthus buchnerianus Briq.	Lamiaceae	herb
5.	Aerangis thomsonii (Rolfe) Schtr.	Orchidaceae	herb
6.	Albizia glaberimma (Schum. & Thonn.) B.	Mimosaceae	tree
7.	Albizia gummifera J.F. Gmel.	Mimosaceae	tree
8.	Aloe kulalensis L.E. Lawton & Beentje	Liliaceae	herb
9.	Aneilema pedunculosum C.B. Clarke	Commelinaceae	herb
10.	Asparagus africana	Liliaceae	climber
11.	Asparagus asparagoides (L.) Wight	Liliaceae	climber
12.	Aspilia sp.	Compositae	shrub
13.	Asplenium theciferum (H.B.K.) Mett.	Aspleniaceae	fern
14.	Canthium sp.	Rubiaceae	shrub
15.	Casearia battiscombei R.E. Fries	Flacourtiaceae	tree
16.	Cassipourea malosana (Bak.) Alston	Rhizophoraceae	tree
17.	Chlorophytum sp. aff. C. heyneri	Liliaceae	herb
18.	Cissampelos owariensis A. DC.	Menispermaceae	climber
19.	Clerodendrum pleiosciadum Gurke	Verbenaceae	shrub
20.	Coffea sp. A	Rubiaceae	shrub
21.	Croton macrostachyus Hochst. ex Del.	Euphorbiaceae	tree
22.	Cucumis sp.	Cucurbitaceae	climber
23.	Cussonia spicata Thunb.	Araliaceae	Tree
24.	Cyathula prostrata (L.) Blume	Amaranthaceae	herb
25.	Cyperus dereillema Steud.	Cyperaceae	herb
26.	Cyperus diffusus Vahl.	Cyperaceae	herb
27.	Cyphostemma kilimandscharicum (Gilg.) Wild.	Vitaceae	climber
28.	Desmodium sp.	Papillionaceae	herb
29.	Diaphanathe sp. .	Orchidaceae	herb
30.	Dissotis bussei Engl.	Melastomataceae	shrub
31.	Dracaena laxissima Engl.	Agavaceae	shrub
32.	Drymaria cordata (L.) Roem. & Schult.	Caryophyllaceae	herb
33.	Drypetes natalensis (Harv.) Hutch.	Euphorbiaceae	tree
34.	Drypetes reticulata Pax	Euphorbiaceae	tree
35.	Drypetes usambarica (Pax) Hutch.	Euphorbiaceae	tree
36.	Ekebergia capensis Sparrm.	Meliaceae	tree
37.	Embelia schimperi Vatke	Myrsinaceae	tree
38.	Festuca africana (K.Schum.) Clayton	Poaceae	grass
39.	Ficus natalensis Hochst.	Moraceae	tree
40.	Ficus sur Forssk.	Moraceae	tree
41.	Ficus thonningii Blakelock	Moraceae	tree

42. Habenaria humilior Reichb.	Orchidaceae	herb
43. Helinus mystacinus (Ait.) Steud.	Rhamnaceae	shrub
44. Hibiscus sp.	Malvaceae	shrub
45. Hippocratea goetzei Loes.	Euphorbiaceae	shrub
46. Hypoestes forskalii (Vahl.) R. Br.	Acanthaceae	herb
47. Impatiens serpens Grey-Wilson	Balsaminaceae	herb
48. Impatiens sodenii Engl.	Balsaminaceae	herb
49. Impatiens walleriana Hook f.	Balsaminaceae	herb
50. Justicia heterocarpa T.Anders	Acanthaceae	herb
51. Landolphia buchanannii (Hall.f.) Stapf	Apocynaceae	climber
52. Lannea schweinfurthii (Engl.) Engl.	Anacardiaceae	tree
53. Lasianthus kilimandscharicus K. Schum.	Rubiaceae	tree
54. Lasianthus pedunculatus E.A. Bruce	Rubiaceae	tree
55. Leptaspis cochleata Thwaites	Poaceae	grass
56. Lycopodium dacrydioides Bak.	Lycopodiaceae	herb
57. Maesa lanceolata Forssk.	Myrsinaceae	shrub
58. Maytenus acuminata (Thunb.) Blakelock	Celastraceae	tree
59. Microcoelia exilis Lind.	Orchidaceae	herb
60. Nuxia congesta R. Br. ex Fresen	Loganiaceae	tree
61. Obetia radula (Bak.) B. D. Jackson	Urticaceae	shrub
62. Ochna holstii Engl.	Ochnaceae	tree
63. Oldenlandia corymbosa	Rubiaceae	herb
64. Olea capensis ssp. hochstetterii (Bak.) F. & G.	Oleaceae	tree
65. Olea europaea L. ssp. africana (Mill.) P.S. Gr.	Oleaceae	tree
66. Oncoba spinosa Forssk.	Flacourtiaceae	shrub
67. Oxyanthus speciosus DC. ssp. stenocarpus	Rubiaceae	tree
68. Panicum maximum Jacq.	Poaceae	grass
69. Pavetta abyssinica Fresen var. abyssinica	Rubiaceae	shrub
70. Peperomia rotundifolia (L.) H.B. & K.	Piperaceae	herb
71. Physalis peruviana L.	Solanaceae	shrub
72. Phytolaca dodecandra L' Herit	Phytolacaceae	shrub
73. Piper capense L.	Piperaceae	shrub
74. Pittosporum viridiflorum Sims	Pittosporaceae	tree
75. Plecranthus alboviolaceus Gurke	Lamiaceae	herb
76. Pleopeltis excavata (Willd.) Stedge	Polypodiaceae	fern
77. Podocarpus falcatus (Thunb.) Mirb.	Podocarpaceae	tree
78. Podocarpus latifolius (Thunb.) Mirb.	Podocarpaceae	tree
79. Polystachya isochiloides Schum.	Orchidaceae	herb
80. Polystachya transvaalensis Schtr.	Orchidaceae	herb
81. Prunus africana (Hook. f.) Kalkman	Rosaceae	tree
82. Psychotria elaclistantha (K.Schum.) Petit	Rubiaceae	shrub
83. Psychotria goetzei (K. Schum.) Pet.	Rubiaceae	tree
84. Psydrax parvifolia (Afz.) Brids.	Rubiaceae	tree
85. Pteridium aquilinum (L.) Kuhn.	Dennstaedtiaceae	fern
86. Rapanea melanophloeos (L.) Mez.	Myrsinaceae	tree
87. Reissantia parviflora (N.E.Br.) N. Halle	Celastraceae	shrub
88. Rothmania fischeri (K.Schum.) Bullock	Rubiaceae	shrub

89. Rubus rosifolius Sm.	Rosaceae	shrub
90. Rytigynia uhligii (K. Schum.) Roby.	Rubiaceae	tree
91. Schefflera myriantha (Bak.) Drake	Araliaceae	climber
92. Setaria homonyma (Steud.) Chiov.	Poaceae	grass
93. Solanecio manii (Hook.f.) Jeffrey	Compositae	shrub
94. Solanum nigrum L.	Solanaceae	herb
95. Solanum richardii Dunal	Solanaceae	shrub
96. Solanum schumanianum Dammer	Solanaceae	shrub
97. Tarenna pavettoides (Harv.) Sim.	Rubiaceae	shrub
98. Tiliacora funifera (Miers) Oliv.	Menispermaceae	climber
99. Trema orientalis (L.) Bl.	Ulmaceae	tree
100. Turraea sp.	Meliaceae	tree
101. Urera hypsedodendron (A.Rich.) Wedd	Urticaceae	herb
102. Urtica massaica Mildbr.	Urticaceae	herb
103. Xymalos monospora (Harv.) Warb.	Monimiaceae	tree

II

Soil seed bank and regeneration potential of degraded hill slopes of the Kondoa Irangi, central Tanzania

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Abstract

A soil seed bank study of the severely degraded Kondoa Irangi Hills, Tanzania, was conducted with the objective of characterising the seed bank, in terms of seed density and composition, and establishing the relationship between the seed bank and the standing vegetation. The total seed bank density (at 0 - 5 cm depth) ranged from 344 to 9158 seeds/m^2, and from 172 to 5107 seeds/m^2 for the years 1994 and 1995, representing a dry and a wet-season, respectively. The seed bank was very heterogeneous, both spatially and temporally, and showed significant variation in size and composition in both years. The correlation between species number in the seed bank and the above-ground vegetation was not significant for any major plant group except for the graminoids in 1995 ($p < 0.05$). This observation, and the overall low values for the similarity index (0.0 - 0.44) between the seed bank and the above-ground vegetation in all plots, the dominance of the seed bank by annuals in both seasons, and the occurrence of early successional species in most samples, is a manifestation of the prolonged vegetation disturbance in the area. Seed numbers in the seed bank decreased with depth, with only three species found in all depth strata. Re-vegetating the degraded hill slopes with woody vegetation, relying only on the seed bank may prove difficult because such seeds are lacking in the soil at present.

Keywords: annuals, degradation, perennials, seedling emergence, Sørensen's similarity index, standing vegetation, succession

Abbreviations: KIH stands for Kondoa Irangi Hills

Nomenclature: Turrill & Milne-Redhead (1952-) and Exell & Wild (1960-)

Introduction

This study deals with the severely degraded Kondoa Irangi Hills, central Tanzania. Land degradation in the KIH started ca. 150 years ago when the Rangi people settled in the area. The main factors known to have caused land degradation here are partly still obscure but include overexploitation of forests and woodlands for woody products, farming on fragile hill slopes, heavy grazing and periodic fires (Christiansson 1981; Mung'ong'o 1991). This area was protected by law from grazing, charcoal burning and fuelwood collection in 1979, and the livestock were moved into the plains of the lower Irangi (Mbegu & Mlenge 1984).

Apart from a pilot study by Bergsten (1993), the seed bank properties of KIH have not yet received much attention.

Generally the term 'seed bank' refers to an aggregation of diaspores in the soil and on the surface. These diaspores are potentially capable of germinating and replacing adult plants which die due to disease, senescence, disturbance or consumption by animals (e.g. Roberts 1981; Leck *et al.* 1989). The potential of the dormant seed bank in the "regeneration succession" (sensu van der Maarel 1988) of degraded vegetation following a major disturbance is well documented-see e.g. Darwin (1859), Baker (1989), and Lavorel *et al.* (1991). The term is used both for a particular species and for all species together in a given portion of soil. In the latter case I will speak of "total seed bank". In cases where no long-lived seed bank exists, vegetative propagation and the seed rain become crucial in the restoration process (McGee & Feller 1993). In rain forests where moisture does not limit seedling establishment, the role of the seed bank in regeneration following disturbance is therefore less significant (Garwood 1989 and references cited therein) as compared to the seed rain (Saulei & Swaine 1988; Enright & Cameron 1988; Skoglund 1992; Martínez-Ramos & Soto-Castro 1993).

Unlike in wetter forest communities, seed bank regeneration is the most important strategy in areas with seasonal climates, such as deserts and arid land (Kemp 1989). The seed bank dynamics of savanna ecosystems have not received adequate attention (Skoglund 1992) as most studies have been focused on temperate ecosystems, notably on weeds, due to their agricultural significance (Hills & Morris 1992; Garcia 1995).

Successional studies have shown that, depending on the magnitude of disturbance, the degradation process can be irreversible or the recovery process slow or fast when the degradatory factors are removed. It will also depend on the seed bank composition, the current seed rain and most importantly whether such degradation was accompanied by deterioration of soil and soil-water conditions and the microclimate (Roberts 1981). Apart from magnitude, disturbance also encompasses spatial and temporal dimensions (see Glenn-Lewin & van der Maarel 1992). The spatial dimension of disturbance is the extent of disturbance which includes the total area affected and volume and its location in relation to environmental gradients, while temporal dimensions include frequency and predictability.

This study had the following objectives:

1. to determine the size and composition of the total seed bank of KIH, and its implication to the ecological restoration of the area; and
2. to establish the relationship between total seed bank and the above-ground vegetation.

Material and methods

Location of the study area

The KIH occupy an area of ca. 1300 km^2 in the Dodoma region of central Tanzania and extend from longitude 35° 40' to 36° 10'E and latitude 4 ° 40' to 5° 0'S (Mbegu & Mlenge 1984). The topography of the area is dominated by steeply sloping pediments with outcropping inselbergs and flatter, cultivated valley bottoms (Payton *et al.* 1992). The slopes are intersected by seasonal rivers that cut into strongly weathered erodible sandy soils (Payton *et al.* 1992). The elevation of the area is 1000 - 2200 m and the overall climate is semi-arid to sub-humid with an annual rainfall of 600 - 800 mm (Ngana 1992). Generally, in elevated parts of Kondoa, the rainfall exceeds 1000 mm per annum. The rainy season in Kondoa extends over seven months, from late November to May, and the rain distribution pattern is related to elevation and geographic location (Ngana 1992).

In this study, "forest" is differentiated from "woodland" by having higher density of trees with intermingling crowns and a closed canopy.

Vegetation sampling

The floristic data (summarised in Table 1) used in this study to describe the relationship between the total seed bank and the standing vegetation, were obtained from 27 permanent plots established in 1991 (Backéus *et al.* 1994). The plot sizes are 20 m x 20 m, and were chosen so as to represent the main floristic vegetation types of KIH. Seven of the plots are located outside the protected area, and are meant for comparative studies. Backéus *et al.* (1994) described eight vegetation types in 65 plots initially sampled to include various types of woodlands, grasslands and secondary forests. The 27 protected plots, represent only six vegetation types and three of them were considered as aberrant stands. In this study, one of the three plots described as aberrant relevés by Backéus *et al.* (1994) is kept as highly degraded site and is coded A. The grazed grasslands (coded I with 7 plots) correspond to vegetation type 8 in Backéus *et al.* (1994) and grasslands on disturbed soils (coded II with 4 plots correspond to vegetation type 7). Most grasslands are in early stages of succession and are dominated by annual species. Grasslands with scattered trees are indicated as wooded grasslands. They are coded III, and include two plots (previously described as aberrant relevés in Backéus *et al.* 1994). Woodlands (coded IV with 10 plots) correspond to vegetation types 3, 4 & 5 in Backéus *et al.* (1994); they are represented by *Acacia tortilis* woodland, *Brachystegia microphylla* woodland and *Brachystegia spiciformis* woodland. Both secondary forests (coded V with 3 plots which correspond to vegetation type 1) and woodlands are in later stages of succession and have apparently recovered from the degradatory forces with a dominance of perennial species.

Soil sampling and greenhouse germination experiments

Soil samples were collected in two periods which were considered to be critical- October to November 1994, the end of the dry-season, a period considered to be the peak for seed production, which falls before the onset of germination; and April to May 1995 (wet-season), immediately after the long rains and before new seeds are produced. From each of the 27 permanent plots, ten soil samples, 206 cm^3 each, were collected using a standard soil auger at predetermined regular intervals, and stored in plastic bags. For the general characterisation

Table 1. Floristic composition of the above-ground vegetation in the Kondoa Irangi Hill slopes based on 27 plot described in Backéus *et al.* (1994). Only species occurring in ≥ 50% of the plots in at least one vegetation type are considered. Vegetation types are explained in the text. For cover-abundance values; 0 = absent, 1 = rare; 2 = frequent & 3 = dominant and GF = growth form; G = grass; H = herb; T = tree; S = shrub & SS = subshrub

		Vegetation type					
	GF	A	I	II	III	IV	V
n = number of plots		1	7	4	2	10	3
Acacia senegal	T	1	0	0	2	1	0
Acacia tortilis	T	0	1	1	1	3	0
Achyranthes aspera	H	0	0	0	0	2	1
Acanthospermum hispidum	H	1	1	0	0	0	0
Aristida congesta	G	2	2	1	1	1	0
Blepharis affinis	H	3	1	1	0	0	0
Brachystegia microphylla	T	0	0	0	0	3	1
Brachystegia spiciformis	T	0	0	1	0	2	1
Cassia abbreviata	T	1	1	1	1	1	1
Catunaregam spinosa	S	0	0	1	0	2	0
Chloris virgata	G	1	1	0	2	0	0
Clerodendrum myricoides	T	0	0	1	0	1	2
Combretum molle	T	0	1	1	0	2	1
Commelina sp.	H	1	0	1	1	2	1
Conyza pyrrhopappa	SS	0	0	1	0	2	1
Crabbea velutina	H	0	1	1	0	1	2
Dactyloctenium aegypticum	G	2	1	0	2	1	0
Digitaria milanjiana	G	0	0	0	0	1	0
Dodonaea angustifolia	S	0	0	1	0	2	1
Duosperma crenatum	H	2	1	0	0	0	0
Eragrostis cylindriflora	G	0	2	1	3	1	0
Eragrostis patens	G	0	1	0	0	0	0
Eragrostis viscosa	G	2	0	0	0	0	0
Euphorbia candelabrum	T	0	0	0	0	1	3
Harpachne schimperi	G	2	3	1	3	1	0
Heteropogon contortus	G	0	1	2	2	2	0
Hibiscus calyphyllus	H	0	0	1	1	1	1
Hyparrhenia filipendula	G	0	0	1	0	3	1
Indigofera rhynchocarpa	S	0	0	1	0	1	2
Lippia javanica	SS	0	0	1	0	1	2
Panicum maximum	G	0	0	0	2	3	1
Pennisetum polystachyon	G	0	1	0	0	0	0
Pogonarthria squarrosa	G	0	0	2	0	2	0
Ruellia tuberosa	H	0	1	0	2	1	1
Rhus natalensis	S	0	0	0	1	1	2
Rhynchelytrum repens	G	0	2	2	2	3	1
Setaria homonyma	G	0	0	0	0	0	2
Solanum incanum	SS	0	1	0	1	1	1
Sporobolus festivus	G	1	0	3	1	0	0
Stylosanthes fruticosa	H	1	1	2	1	1	0
Tephrosia pumila	H	0	2	1	0	1	0
Tridax procumbens	H	0	1	0	0	0	0
Triumfetta rhomboidea	H	0	1	1	0	2	1
Vangueria infausta	S	0	0	1	0	1	2
Vernonia glabra	H	0	2	1	0	1	0
Waltheria indica	H	1	1	1	1	1	0

of the seed bank, the soil was collected at 0 - 5 cm depth. For a depth distribution study, samples were collected at 0 - 5 cm, 5 - 10 cm and 10 - 15 cm from 13 selected plots chosen to represent the main vegetation types of the area. Precaution was taken not to contaminate the deeper soil layers with seeds from the upper layers.

All seedling counts were carried out in a greenhouse with a transparent plastic roof at the University of Dar Es Salaam, which had a natural photoperiod of 10 to 12 hours and a mean temperature of 34°C (±5). The soil was air-dried and then spread out over a layer of sterilised soil (put in an oven at 140 ^{0}C for 24 hours) in a thin layer in plastic trays. The trays were then placed in random order in the greenhouse and watered once a day. Control trays with only sterilised soil were set alongside the experiment to detect contamination by wind dispersed seeds. Seedlings were removed as soon as they could be identified, counted and recorded, whereas those which proved difficult to identify were transplanted and observed until flowering for correct identification. Grasses and herbs which did not produce flowers and could not be identified, were grouped as "unknown grass" and "unknown herb" respectively. The seed bank soil in the trays was stirred twice a month to bring ungerminated seeds from below to the surface. The germination trays were monitored for three months and the experiment was stopped when it was observed that germination had declined to zero. Voucher specimens are kept in the herbarium of the University of Dar Es Salaam and duplicates will be deposited in the herbarium of Uppsala University.

Since no attempt was made to determine the number of ungerminated seeds, the use of the term 'seed bank' in this paper refers strictly to the number of germinated seeds.

Data analysis

Before any statistical analyses were performed, the seedling counts were log- transformed using the relation $y^1 = \ln(y + 1)$. To compare the overall differences in the distribution of major plant groups in the seed bank based on their life histories, the data were analysed by one-way non-parametric ANOVA (Kruskal-Wallis test using a Chi-square approximation and an F-test) according to Zar (1984). The SAS statistical package (SAS Institute Inc. 1985) was used.

The similarity between the seed bank and the above-ground vegetation for each plot based on presence/absence data was calculated using Sørensen's Index defined as:

$$Si_{jk} = 2a / (2a + b + c)$$

where a is the number of species common to plots j and k, and b and c are the numbers of species only found in j and k, respectively (Sørensen 1948). The frequency distribution of the most dominant species in different vegetation types in both seasons was calculated and so was the overall dominance of species in both seasons.

The correlation between the number of species in the seed bank and the above-ground vegetation for all 27 plots was calculated using Spearman's Rank Correlation Coefficient (Spearman 1904; see Zar 1984), separately for graminoids, herbs and phanerophytes. In order to further check the relation between seed bank and above-ground vegetation, Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) based on presence/absence of species were performed on the vegetation and seed bank data using the program package CANOCO (ter Braak 1987; 1987-1992). The divisive cluster analysis program TWINSPAN (Hill 1979) was applied to the species composition of the seed bank.

Results

Composition of the seed bank

A total of 2188 seedlings representing 111 species emerged from the dry-season seed bank soil samples (0 - 5 cm), together with a number of unidentified grasses and herbs. No seedlings were recorded from the control trays. The wet-season samples gave 1418 seedlings representing 79 species (Fig.1, 2 & Table 2a, b). The species were grouped into graminoids (grasses and sedges), phanerophytes (trees and shrubs) and herbs. Most herbs and grasses emerged during the first three weeks. Sedges and hard-seeded legumes were the latest to emerge, attaining peak germination after two months. Three fern

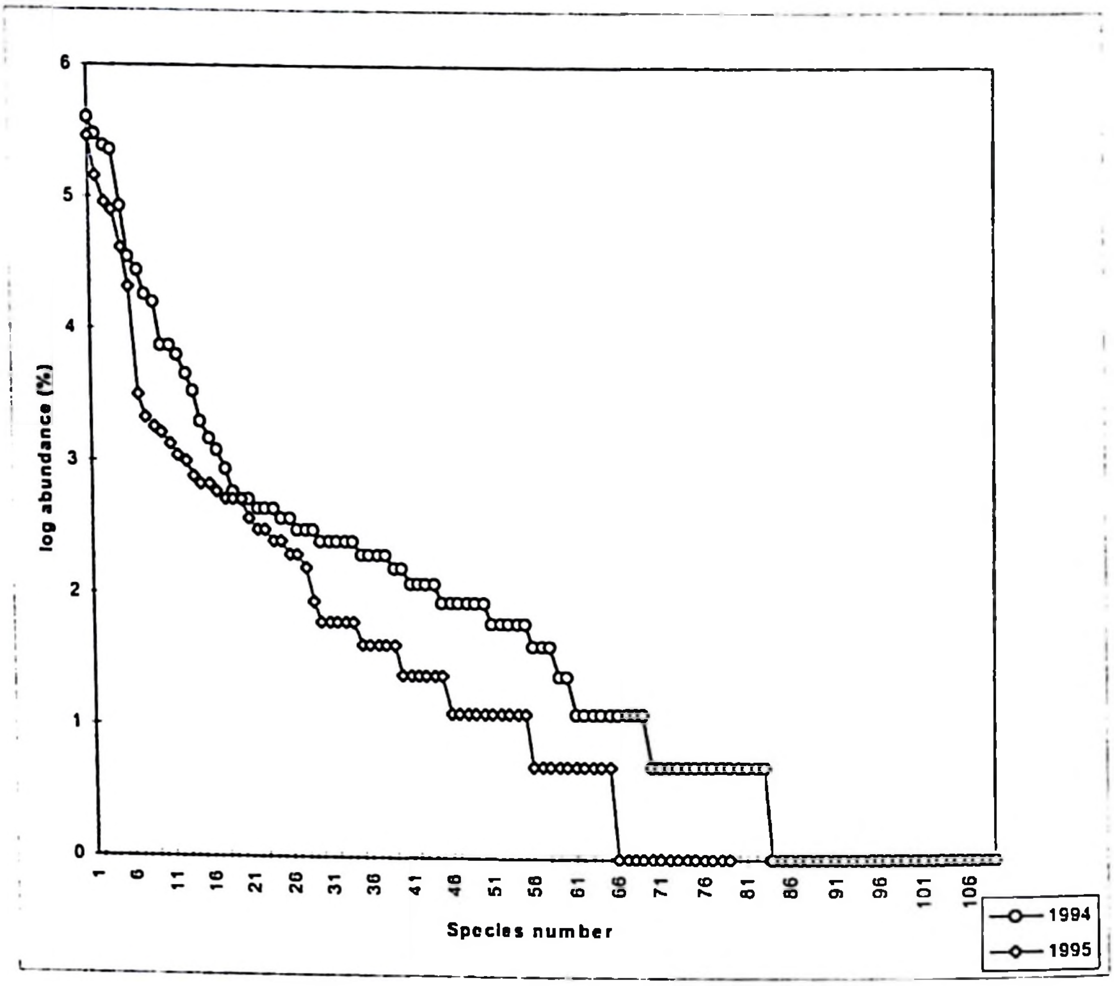

Figure 1. Rank abundance curves for all seed bank species in all plots for the two sampling periods. Flattening of the curve indicate species with the same rank.

species were recorded but not included since the analysis was limited to phanerogams. In both seasons, the 25 most common species in the seed bank were all herbs and grasses, with no single representation of woody species (Table 3a, b). The distribution of certain species in both seasons indicated that some species were entirely dominating the grassland seed banks (e.g. *Chloris virgata* and *Dactylocytenium geminatum*) and some were associated with woody vegetation such as *Ageratum conyzoides* (Fig. 2).

The species richness of the seed bank was significantly different in the two seasons, and the dry-season samples had the highest species richness compared to wet-season samples; Kruskal-Wallis

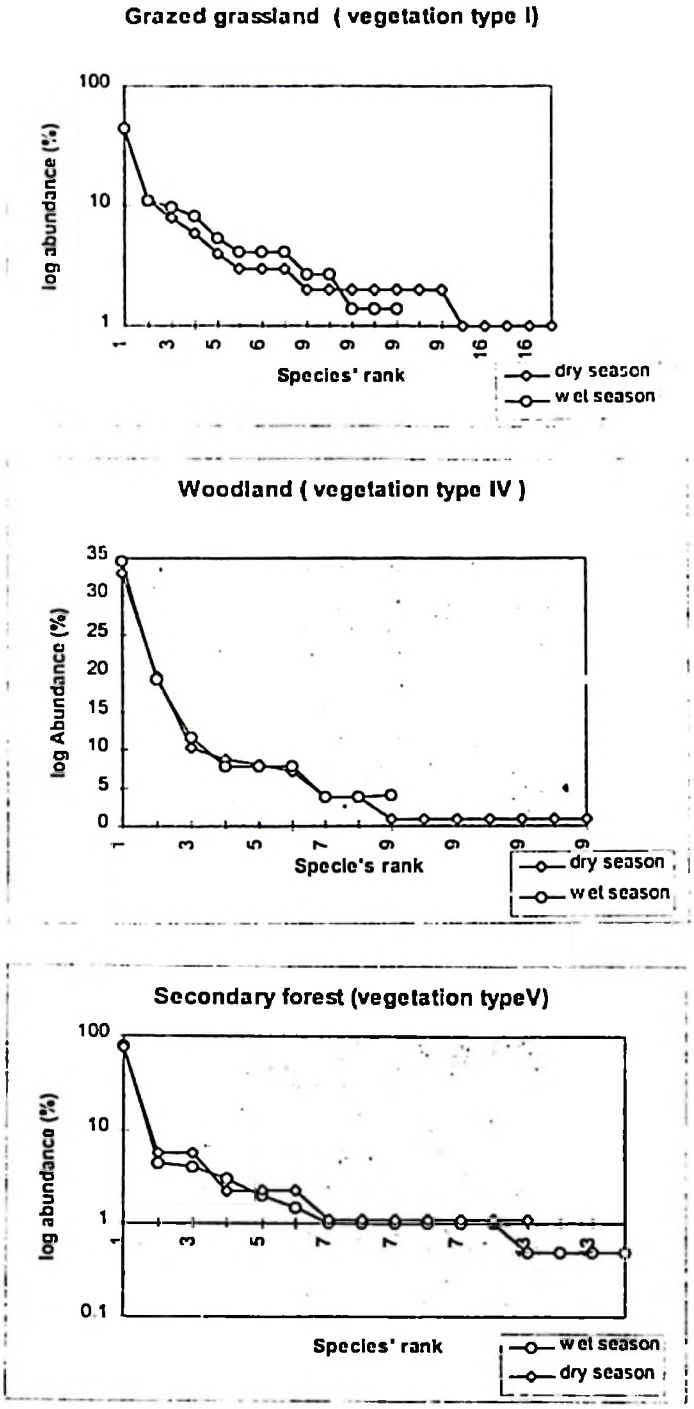

Figure 2. Rank abundance curves for three selected plots representing woodland, secondary forest and grazed grassland for the two sampling periods. Flattening of the curve indicate species with the same rank.

Test ($\chi^2 = 69.83$, df = 3, $p < 0.001$). The woodland plots had a higher species richness in the dry-season than in the wet-season (Fig. 2), an observation which was opposite to secondary forest and grazed grassland.

The seed bank size ranged between 344 and 9158 seeds/m^2 in the dry-season samples, and this declined in the wet-season samples with a range between 172 and 5107 seeds/m^2 (Table 2a, b). The seasonal variation in the seed bank size was highly significant (Kruskal-Wallis Test $\chi^2 = 638.95$, df = 25, $p = 0.001$). The annuals were more than the perennials (Kruskal-Wallis Test $\chi^2 = 16.73$, df = 1, $p < 0.001$; $\chi^2 = 11.53$, df = 1, $p < 0.001$), by having ratios of 71 to 40 and 54 to 25 for dry and wet-season samples, respectively.

The data for some groupings of species were not normally distributed even after transformation (Table 4), which suggested aggregation of seeds under natural conditions.

Table 4. Analysis of variance test for normality (Shapiro & Wilk 1965) for the major plant groups in the KIH seed bank. NS indicates not normally distributed and * indicates normally distributed

Category	W: Normal value		Probability		Significance	
	1994	1995	1994	1995	1994	1995
Life history						
Annual	0.947	0.935	0.207	0.1005	*	*
Perennial	0.936	0.904	0.112	0.0168	*	NS
Plant group						
Graminoids	0.954	0.934	0.311	0.1084	*	*
Herbs	0.940	0.964	0.138	0.4887	*	*
Phanerophytes	0.562	0.552	0.0001	0.0001	NS	NS

Species such as *Oldenlandia corymbosa*, *Dactyloctenium geminatum*, *Ageratum conyzoides*, *Chloris virgata* and the sedges showed localised seed abundance in that they were found in big numbers in some samples and missing in others thereby influencing greatly the seed bank density.

Some taxa which had no previous record in the standing vegetation were recorded from the seed bank samples in 0 - 5 cm soil layer only. These included *Nesaea erecta*, *Hybanthus enneaspermus*, *Iphigenia oliveria*, *Wahlenbergia arcta*, *Stellaria media*, *Spergula arvensis* and *Wahlenbergia erecta*.

Relation between seed bank and standing vegetation

The data used to study the relationship between seed bank and standing vegetation are provided in Table 5. Values for the Sørensen's Similarity Index (SI), between the vegetation in each plot and the seed bank were very low, ranging from 0 to 0.44 (Table 2a, b). There was a significant difference in the SI values among the dry-season vegetation types (ANOVA F = 8.34, df= 10, p = 0.016). These were higher in the grazed grassland samples suggesting existence of passive seed rain in this vegetation type. However, the difference was not significant among the wet- season samples.

Table 5. The number of species of the main growth forms found in the seed bank and the standing vegetation of the Kondoa Irangi Hills permanent plots. The data were used to study correlation and similarity. SV = number of species in the standing vegetation, and SB = number of species in the seed bank for the dry-season samples. The wet-season seed bank species numbers are shown in brackets. Vegetation types explained in Material & Methods

Plot no.	Veg.type	Graminoids		Herbs		Shrubs	
		SV	SB	SV	SB	SV	SB
21	I	9	3(9)	13	6(8)	5	0(0)
22	I	5	8(4)	14	11(1)	9	0(0)
23	I	8	6(6)	13	9(3)	8	2(0)
24	I	8	5(10)	7	8(9)	5	0(1)
25	I	9	10(6)	11	5(3)	3	0(0)
26	I	9	9(7)	10	6(5)	2	0(1)
27	I	8	5(7)	9	4(3)	4	0(0)
3	II	7	5 (5)	11	3(7)	8	0(0)
11	II	10	3 (3)	8	13(4)	6	2(0)
19	II	6	5(2)	9	0(2)	4	1(0)
20	II	0	4(1)	9	3(2)	4	1(2)
15	III	12	5(3)	22	4(1)	14	0(0)
18	III	10	5(6)	9	8(5)	2	0(1)
1	IV	7	4(4)	26	3(5)	18	0(0)
2	IV	10	7(6)	18	6(2)	8	1(1)
4	IV	10	4(3)	14	3(3)	20	1(1)
5	IV	7	9(3)	8	7(2)	9	0(0)
6	IV	9	6(2)	4	0(0)	6	0(0)
7	I	4	4(4)	13	8(6)	21	2(3)
12	IV	6	8(3)	13	5(5)	11	0(1)
13	IV	8	2(3)	7	4(4)	4	0(1)
14	IV	5	4(1)	8	4(4)	7	0(1)
8	V	3	4(5)	11	7(12)	17	2(0)
9	V	4	1(2)	8	7(3)	17	0(0)
10	V	4	6(5)	15	7(1)	11	2(1)
16	A	7	12(11)	8	8(5)	6	0(0)

The abundance of seeds decreased with depth, with only few species appearing in all depth classes (Table 6).

Table 6. Depth distribution of the seed bank species in seed numbers from 13 plots sampled at three depths - 0 - 5 cm, 5 - 10 cm and 10 - 15 cm. The three categories stand as: A = Long-term persistence, B = Short-term persistence and C = Short-lived or transient

species	nos. in each class depth (cm)			seed bank category
	0-5	5-10	10-15	
Oldenlandia corymbosa	23	11	7	A
Ageratum conyzoides	4	1	1	A
Cyperus rotundus	4	1	1	A
Acalypha indica	0	0	3	A
Tephrosia pumila	0	0	1	A
Dactyloctenium aegyptium	0	3	0	B
Kyllinga alata	0	1	0	B
Nesaea erecta	0	1	0	B
Achyranthes aspera	0	1	0	B
Heteropogon contortus	0	1	0	B
Spermacoce chaetocephala	1	0	0	C
Sphaeranthus suavelons	1	0	0	C
Euphorbia hirta	4	0	0	C
Panicum trichocladum	2	0	0	C
Ocimum suave	2	0	0	C
Bulbostylis burchellii	1	0	0	C

Table 7. Spearman's Rank Correlation analysis of the relation between species number in the seed bank and above-ground vegetation for graminoids, herbs and phanerophytes

	Spearman's Rank Correlation (r_s)	
	1994	1995
r_gSV	0.277	0.359*
r_hSV	-0.009	-0.128
r_pSV	0.340	0.133

There was no significant correlation between the species numbers of the major plant groups in the seed bank, i.e. graminoids, herbs and phanerophytes, and the above-ground vegetation (Table 7), except for the graminoids in the wet-season ($rs = 0.359$, $p < 0.05$).

Ordination of the vegetation and the seed bank data together was not informative except for revealing two distinct clusters- one side with the seed bank data and on the other side the vegetation data. The TWINSPAN classification did not produce interpretable clusters; therefore, the results were omitted.

Discussion

Relevance of methods

Estimations of seed bank size depend on the method used, the number and size of samples, the distribution pattern of various species in the vegetation and the sampling season (see Major & Pyott 1966; Kropác 1966; Roberts 1981; Bigwood & Inouye 1988; Thompson *et al.* 1997). Species with seed clumping which are annuals, such as *Cyperus rotundus*, *Nesaea erecta*, *Acalypha indica*, *Chloris virgata*, *Oldenlandia corymbosa*, *Ageratum conyzoides* and *Dactyloctenium aegyptium*, contributed many seeds in the seed bank estimates. The above species were abundant in both dry and wet-season samples indicating their prolific seed production and probably possession of some kind of dormancy which control their germinability. Species which were found to be important in one season sample only and missing in the other such as *Kohautia coccinea*, *Bulbostylis burchellii*, *Cyperus flavescens* and *Rhynchelytrum repens* could be associated to sampling artefact as seeds are distributed randomly in the soil. Taking one forest site and one species as an example, *Ageratum conyzoides* contributed 155 individuals of the site's total seed bank of 208 individuals from 17 species, accounting for a relative abundance of 75% in the dry-season and 72% of the seed bank in the wet-season. Generally the distribution of individuals within species in the 10 samples in each site was very patchy ranging from 1 to 45 in the dry-season and 0 to 30 in the wet-season. Seed clumping may be associated with seed shadow patterns, short distance dispersal and lack of effective dispersal agents or could be attributed to hoarding by animals especially in tropical forests where zoochory is an important dispersal mechanism. Rusch (1992), Rusch & Fernández-Palacios (1995) and Thompson *et al.* (1994) have found similar small-scale clumping in the seed banks of *Cerastium semidecandrum* in Sweden and *Garonopus*, *Cerastium* and *Trifolium* in England.

The seedling emergence method used in this study evaluated the proportion of seeds that were readily germinal (Brown 1992) but ignored the fraction which did not germinate due various types of dormancy. However, since most of the seeds had germinated after three weeks, we may assume that the method gives a representative picture of the seed bank size. Other methods known to estimate the seed bank size more accurately are less important to study secondary succession as they do not distinguish between viable and non-viable seeds.

General trends in the results

The KIH seed bank showed significant seasonal variation in seed density, with a maximum in the dry-season. The two sampling periods corresponded to when there was maximum seed input into the soil from most plant species (dry-season) and when the seed bank could be expected to be depleted of non-dormant seeds through germination (wet-season).

For the KIH, lack of moisture is likely to be the most important factor limiting seed germination. The optimum germination requirements for most seeds in terms of moisture level are met during the rainy season. It may be assumed that whereas the dry-season seed bank samples comprised mainly last season's seed input, the wet-season samples consisted mostly of dormant seeds which failed to respond to increased moisture levels as well as seeds from very short lived plants. Other results supporting this conclusion have been reported by Jain (1976) in California grasslands and Russi *et al.* (1992) for Mediterranean grasslands.

The annuals were more abundant than the perennials in both seasons. This is because annuals have high resource allocation to seed production compared to perennial species.

Comparison of seed bank and standing vegetation

Generally there was a poor correspondence between seed bank and above-ground vegetation in most vegetation types. This has been reported in many studies (Kropâc 1966; Thompson & Grime 1979; Hall & Swaine 1980; Rabinowitz 1981; Vlahos & Bell 1986; Belsky 1986; Schneider & Harald 1987; Skoglund 1990; Milberg & Hansson 1994; Bakker *et al.* 1996). The poor correspondence of the seed bank and the above-ground vegetation can be explained as follows:

1 The present vegetation is secondarily, derived either as a result of continued disturbance or progressive succession, and the seed bank could be part of the former vegetation.

2 The seed bank is only partly derived from the above-ground vegetation and predominantly, the standing vegetation results from actively imported seed rain. The later is likely to be the most appropriate explanation since the study has already shown that the seed bank is depleted of diaspores during the rainy season, suggesting that it is not persistent.

However, there was a good correspondence between the number of species in the seed bank and the above-ground vegetation among the graminoids in the wet-season. The significant correlation in the wet-season samples ($rs = 0.359$, $p < 0.05$) is supported by results from other grassland studies (see e.g. Milton 1939; Hayashi & Numata 1971; 1975; Houle & Phillips 1988; Ungar & Woodell 1993). This is attributed to the dominance of annual grasses in these grassland communities that are known to have high resource allocation to seed production (Fenner 1985) and to their short life span.

Relation between total seed bank and grazing history

Long-term intensive grazing, which occurred in the study area previously, has been reported to increase the total seed bank size (Major & Pyott 1966; Russi *et al.* 1992), particularly seeds of annual species (Harper 1977; Allen *et al.* 1995). The heavily grazed plots outside the protected area (vegetation type I) had considerably higher seed bank densities and annual species dominated here. Relatively higher values of the Similarity Index between the seed bank and above-ground vegetation in the grazed plots (Table 2a, b) which were significantly higher than those for woodland and secondary forest indicate that the seed bank is short lived and is derived from the site vegetation to a higher degree in the former.

Seed distribution in relation to depth and persistence

Species most frequently recorded from the lower soil strata were all annual species and important agricultural weeds. Such species are known to possess long-lived seed banks (Cook 1980; Kivilaan & Bandurski 1981; Roberts 1981; Simpson 1990). According to Kjellsson (1992) and Demel & Granström (1995), the average depth of seeds in the soil is a useful indicator of their longevity and ability to form persistent seed bank. Based on this observation, I considered species recorded in all depth strata as most probably being long-term persistent and those in the middle and upper strata as largely short-term persistent. However, some seeds could have reached their final depths through secondary dispersal by several means including burrowing animals and worms (McRill & Sagar 1973; Thompson *et al.* 1994). The early successional woody species may have a considerable viability. Seeds of *Rubus* have been estimated to have a life span of more than 60 years in the soil (Marks 1974).

Seed clumping shown by species such as *Oldenlandia corymbosa*, *Stellaria media*, *Nesaea erecta*, *Acalypha indica*, *Chloris virgata* and *Cyperus* spp. may be a result of either their small stature and the position they occupy in the vegetation or lack of dispersal appendages (true for the herbs) among the taxa. Alternatively, this may be linked to ephemeralness of the species.

The occurrence of taxa (listed on page 9) with no previous record in the standing vegetation from the uppermost soil layer (0 - 5 cm), indicates that they exist only as seeds when germination conditions are unfavourable. These species, some of which are Eurasian weeds, are ephemeral, and complete their life cycles in a very short time taking advantage of moisture availability during the rainy season.

Implications for the revegetation of the Kondoa Irangi Hills

The vegetation classification of Africa by White (1983), indicated that the KIH were densely covered with *Brachystegia* (miombo) previously. Frequency analysis of the seed bank data indicated that the 25 most dominant species in both seasons were herbs and grasses, and no single woody species representative was found. The dominance of the total seed bank by annual species and failure to detect significant numbers of diaspores of woody species in the seed bank pose a challenge to the restoration of the woody vegetation in the KIH, especially in areas where trees are lacking at present.

The absence of diaspores of woody species in the soil could be attributed to one of several fates seeds are likely to encounter in their environments. Pre-dispersal seed predation, fungal decay, deep burial by ants and termites (Miller 1994) and post-dispersal seed predation by rodents (Janzen 1971) and birds are major sources of seed losses in arid environments. Apart from hard-seeded legumes, many tropical tree seeds lose their viability within a short time after they are shed

(Olesen 1995), and importantly, they have intermittent seed production (Demel 1996).

Although livestock were evicted from the hills in 1979, there are still some herds which feed on seeds and pods of most *Acacia* spp., which form part of their diet during the dry-season. Miller (1994) demonstrated that browsers and grazers were able to consume up to 92% of *Acacia tortilis* and 76% of *Acacia nilotica* annual seed crops in the same habitats in Southern Africa. Although this is not yet established, post-dispersal seed predation by rodents and ants could be a major source of seed loss in the study area. Further research should focus on studying annual seed production of dominant species in the study area and their fate in their environment.

It is important to note that seeds of different species differ greatly in dormancy and germination requirements and therefore greenhouse conditions are not always suitable for the germination of all species. Periodic fires and grazing which are the main dormancy-releasing mechanisms in many hard-seeded tropical seeds (see Hodgkinson *et al.* 1990; Russi *et al.* 1992; Demel 1996) are lacking under greenhouse conditions, making the comparison of germination under controlled greenhouse conditions and natural germination rather difficult. As an example, germination of seeds of a pioneer shrub *Dodonaea angustifolia* is greatly enhanced by fire (Demel 1996; Munkert 1997), whereas for many legumes germination is greatly enhanced by their passage through guts of grazing animals (Mwalyosi 1990; Russi *et al.* 1992; pers. observation for *Acacia tortilis* seeds in the study area where cow dung are found with numerous seedlings). All these processes increase seed permeability by reducing the thickness of the seed testa.

In this study, the soil samples were spread in thin layers over sterilised soil and therefore it was possible to locate the big seeds of woody species visually, whether they were viable or not, but such seeds were not found in the soil samples. This being the case, in the absence of appropriate manipulation such as introduction of seeding and transplanting of seedlings into the area, attempts to re-vegetate the degraded KIH with woody vegetation while relying on the seed bank and the seed rain is bound to fail since there are no diaspores of woody species in the soil.

Tables 2a & b. Summary of the seed bank data of the 27 plots of the KIH arranged according to vegetation types (a for dry-season and b for wet-season samples). Sørensen's similarity index (SI) is calculated for the total seed bank (sampled at a depth of 0 - 5 cm) and the above-ground vegetation in each plot. * indicates not sampled and § indicates plots sampled for depth distribution study. For vegetation types see Material & Methods. Number in brackets correspond to typology of Backéus *et al.* (1994)

Plot no.	Vegetation type	Number of individuals	Number of species (S)	Density (seeds/m^2)	Similarity (SI)
2a: dry-season					
21§	I(8)	183	9	4493	0.36
22	I(8)	108	20	2652	0.33
23§	I(8)	35	17	860	0.22
24	I(8)	73	13	1793	0.25
25§	I(8)	103	15	2529	0.42
26§	I(8)	68	15	1670	0.42
27§	I(8)	31	9	762	0.33
3	II(7)	31	8	761	0.18
11	II(7)	64	18	1572	0.10
19§	II(7)	20	6	492	0.23
20	II(7)	125	8	3069	0.19
15§	III(A)	79	9	1940	0.11
18§	III(A)	59	13	1449	0.331
1§	IV(5)	102	7	2505	0.10
2§	IV(3)	127	15	3118	0.36
4	IV(5)	89	8	2185	0.16
5	IV(5)	151	15	3708	0.16
6	IV(5)	39	6	958	0.08
7	IV(5)	43	14	1056	0.17
12§	IV(4)	75	14	1842	0.23
13	IV(4)	22	6	541	0.15
14	IV(4)	28	8	688	0.14
17 *	IV(5)				
8§	V(1)	86	13	2112	0.13
9	V(1)	14	8	344	0.16
10	V(1)	60	15	1474	0.17
16§	A(A)	373	20	9158	0.34
Total		2188	111		

Plot no.	Vegetation type	Number of individuals	Number of species (S)	Density (seeds/m^2)	Similarity (SI)
2b: wet-season					
21§	I(8)	86	17	2112	0.38
22	I(8)	21	5	516	0.18
23§	I(8)	42	9	1031	0.16
24	I(8)	100	20	2455	0.41
25§	I(8)	42	9	1031	0.24
26§	I(8)	60	13	1473	0.44
27§	I(8)	157	10	3855	0.26
3	II(7)	81	13	1989	0.19
11	II(7)	21	7	516	0.06
19§	II(7)	11	4	270	0.08
20	II(7)	45	5	1105	0.19
15§	III(A)	24	4	590	0.08
18§	III(A)	41	12	1007	0.18
1§	IV(5)	45	9	1105	0.10
2§	IV(3)	26	9	639	0.27
4	IV(5)	26	7	639	0.12
5	IV(5)	12	5	295	0.13
6	IV(5)	2	2	492	0
7	IV(5)	50	13	1228	0.19
12§	IV(4)	47	9	1154	0.15
13	IV(4)	40	8	982	0.15
14	IV(4)	9	6	221	0.23
17	IV(5)	56	7	1375	0.14
8§	V(1)	208	17	5107	0.13
9	V(1)	7	5	172	0.11
10	V(1)	37	7	909	0.05
16§	A(A)	122	15	2996	0.33
Total		1418	79		

Tables 3a & b. Frequency of the most abundant seed bank species arranged according to their abundance rank (see Fig. 1) in the different vegetation types found in KIH. The species rank in the other sample is given in brackets, and where there is no number indicate that the species is missing in the other sample. Under vegatation type, the figure indicates the total number of plots where the species occur. GF/LH = growth form/life history; H =herb; G = graminoids; a = annual; p = perennial

Species names	GF/LF		No. of indiv.	Vegetation types				
				I	II	III	IV	V
3a: Dry-season samples								
1. *Harpachne schimperi*	Gp	(5)	269	1	1	1	3	1
2. *Kohautia coccinea*	Ha	-	254	6	3	2	6	1
3. *Dactyloctenium geminatum*	Gp	(8)	217	4	0	0	0	0
4. *Oldenlandia corymbosa*	Ha	(1)	211	3	2	2	7	2
5. *Bulbostylis burchellii*	Ga	-	93	1	2	0	7	0
6. *Cyperus flavescens*	Ga	-	76	0	0	2	1	0
7. *Cyperus rotundus*	Ga	(14)	74	2	1	1	5	2
8. *Ageratum conyzoides*	Ha	(2)	72	0	1	0	1	2
9. *Tragus berteronianus*	Ga	(19)	48	4	0	0	1	0
10. *Chloris virgata*	Ga	(3)	46	2	0	1	1	0
11. *Stylosanthes fruticosa*	Hp	(69)	39	1	0	0	1	0
12. *Heteropogon contortus*	Ga	(35)	38	1	1	0	1	1
13. *Urochloa mossambicensis*	Ga	(10)	35	5	1	0	0	0
14. *Polygala erioptera*	Ha	-	26	0	0	2	1	0
15. *Stellaria media*	Ha	-	24	0	0	1	0	0
16. *Digitaria abyssinica*	Gp	(26)	22	2	1	0	1	0
17. *Wahlenbergia arcta*	Ha	(33)	19	2	1	0	0	1
18. *Oldenlandia nematocaulis*	Ha	-	16	0	0	2	0	0
19. *Panicum trichocladum*	Ga	(38)	15	2	0	0	2	1
20. *Kyllinga alata*	Ga	(6)	15	0	0	1	1	1
21. *Digitaria perrottetii*	Ga	(11)	14	0	0	0	4	0
22. *Erythrocephalum* sp.	Ha	(23)	14	0	0	0	1	0
23. *Cynodon nlemfuensis*	Gp	(75)	14	3	0	2	0	0
24. *Ocimum suave*	Ha	(44)	13	4	0	0	2	0
25. *Fuirena leptostachya*	Ga	(15)	13	0	0	1	1	0

3b: Wet-season samples

Species names			No. of	Vegetation types				
	GF/LH		indiv.	I	II	III	IV	V
1. *Oldenlandia corymbosa*	Ha	(4)	246	3	3	2	9	3
2. *Ageratum conyzoides*	Ha	(8)	182	0	0	0	1	2
3. *Chloris virgata*	Ga	(10)	141	5	1	1	0	0
4. *Rhynchelytrum repens*	Gp	-	106	6	2	0	0	0
5. *Harpachne schimperi*	Gp	(1)	79	4	0	0	1	0
6. *Kyllinga alata*	Ga	(20)	34	3	1	2	5	2
7. *Hyparrhenia filipendula*	Gp	(31)	30	0	0	0	4	0
8. *Dactyloctenium geminatum*	Gp	(3)	27	3	0	0	1	0
9. *Hirpicium diffusum*	Ha	(37)	25	2	0	1	0	0
10. *Urochloa mossambicensis*	Gp	(13)	24	2	0	0	0	0
11. *Digitaria perrottetii*	Ga	(21)	22	0	0	0	2	0
12. *Panicum maximum*	Gp	(48)	21	0	0	0	1	1
13. *Triumfetta deknditiana*	Ha	(76)	19	1	0	0	1	1
14. *Cyperus rotundus*	Ga	(7)	18	1	0	0	5	1
15. *Fuirena leptostachya*	Ga	(25)	17	0	0	1	0	0
16. *Portulaca oleracea*	Ha	-	16	0	1	1	0	0
17. *Zornia glochidiata*	Ha	(49)	16	6	0	1	0	0
18. *Cyperus cuspidatus*	Ga	-	16	4	0	1	2	0
19. *Tragus berteronianus*	Ga	(9)	13	4	0	1	0	0
20. *Eragrostis aethiopica*	Ga	-	12	0	0	1	0	0
21. *Spergula arvensis*	Ha	(38)	12	0	1	0	1	0
22. *Kalanchoe densiflora*	Ha	(65)	11	0	0	0	2	1
23. *Erythrocephalum* sp.	Ha	(22)	11	0	0	0	2	0
24. *Aristida adoënsis*	Gp	-	10	6	0	1	0	0
25. *Triumfetta rhomboidea*	Ha	(45)	9	0	0	0	2	0

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III

Seed rain and its role in the recolonisation of degraded hill slopes in semi-arid central Tanzania

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ABSTRACT

A seed rain study in semi-arid central Tanzania was conducted with the objective of providing guidelines on how to rehabilitate the degraded vegetation on the hill slopes of the Kondoa Irangi. The seed rain included predominantly wind-dispersed diaspores which accounted for 78% of the species (45 out of 57) and 97% of the diaspores. The density ranged from 230 to 1667 seeds m^{-2} over an eight-month period. Both species richness and seed density were negatively correlated with vegetation cover. The increasing seed densities with decreasing vegetation cover signifies the importance of anemochory in areas undergoing regeneration succession. Cluster analysis of the seed rain data based on squared Euclidean distances produced a dendrogram with three distinct clusters, representing anemochorous seeds, epi-zoochorous seeds and a mixture of both but dominated by seeds with no obvious dispersal appendages. Management including controlled re-introduction of livestock to the hills to increase nitrogen mineralisation, species diversity and to reduce grass biomass, and hence the severity of fires, may be an appropriate solution to speed up the vegetation recovery process.

Keywords: active seed rain, passive seed rain

Running title: Seed rain and recolonisation in Tanzania

Nomenclature: Turrill & Milne-Redhead (1952-) and Exell & Wild (1960-)

INTRODUCTION

Seed rain has been defined as the influx of new seeds into a given area originating from the nearby vegetation (Howe & Smallwood, 1982; Parker, Simpson & Leck, 1989). As the name suggests, "seed rain" in a strict sense will only apply to wind-dispersed seeds (see Holzapfel, Schmidt & Shmida, 1993), although other modes of dispersal (such as bird and animal dispersal) have also been referred to as seed rain (Loiselle, Ribbens & Vargas, 1996). In this study, I consider "seed rain" to be the total input of new seeds into the study area from the nearby vegetation and the site vegetation during the period of observation, regardless their dispersal modes. For plants which reproduce sexually, seed production, seed dispersal and seedling establishment are crucial stages in their life cycles. Apart from successful establishment, new seeds that are dispersed into a given area could be incorporated into the seed bank (Sem & Enright, 1996), suffer post-dispersal predation or may be subjected to secondary dispersal or horizontal transport (McRill & Sagar, 1973). Seed dispersal is advantageous to plants because it brings seeds into suitable uncolonised microsites such as forest gaps (e.g. Augspurger, 1984) or disturbed habitats (Baker, 1974). Dispersal also minimises inbreeding depression, parent neighbourhood and sibling competition (Willson, 1992 & 1993), as well as seed predation (Janzen, 1970).

The main objective of the ecological studies of which the present paper is a part is to provide guidelines on how to revegetate the hill slopes in a degraded semi-arid area in Tanzania, and later to allow the utilisation of the same land by man and domestic animals in a sustainable manner. Factors which cause land degradation influence seed dynamics of any vegetation in different ways. Rainfall influences seed production and viability in semi-arid environments (O'Connor & Pickett, 1992). Long-term heavy grazing is known to eliminate palatable species through direct consumption of the inflorescence, thereby reducing the size of the seed rain and consequently the seed bank (Brown, 1985). Moderate grazing increases species diversity and species richness (McNaughton, 1977; ten Harkel & van der Meulen, 1996), as well as nitrogen mineralisation and nutrient uptake following defoliation (McNaughton & Chapin, 1985). Grazing also contributes to the seed rain, both actively and passively. The above factors could bring about local extinction of obligate seed producing grasses which are sensitive to grazing and burning such as *Themeda triandra* Forssk. and *Heteropogon contortus* (L.) Roem. & Schult. (O'Connor, 1991).

Location of the study area

The study was performed in the semi-arid Kondoa Irangi Hills (hereafter called KIH) in central Tanzania, which have a long history of land degradation (Christiansson, Kikula & Östberg, 1991). The hills extend from latitude 4^0 40' to 5^0 0' S and longitude 35^0 40' to 36^0 10' E (Mbegu & Mlenge, 1984). The terrain is dominated by steep sloping pediments which, on valley bottoms, form extensive flatlands currently under agriculture (Payton *et al.*, 1992). The altitude of KIH is between 1000 and 2200 m above sea level, and the mean annual precipitation is 600 - 800 mm (Ngana, 1992), most of the rain coming during six months, from late November to April. However, elevated parts of KIH receive more than 1000 mm of rainfall. The KIH were de-stocked in 1979 in an attempt to save the land from further land degradation.

The present study aims to:

1. describe the seed rain and identify main ecological indicator groups among the grasses of KIH vegetation;
2. predict the dispersal spectra of the seeds based on parameters such as mean weight, presence or absence of dispersal appendages, their form when present, and variance (a ratio based on seed length, width and depth; explained under data analysis);
3. determine the relationship between seed rain, seed bank and above-ground vegetation of the study area, and to associate these relationships with vegetation restoration, while testing the hypothesis that dispersal distance is a function of seed weight; and
4. predict the nature of the diaspores in the seed rain in terms of transience and persistence in the soil.

The present study is part of the ecological component of a multidisciplinary research programme known as "Man-Land Interrelations in Semi-Arid Tanzania" (see Christiansson *et al.*, 1991).

MATERIAL AND METHODS

Seed rain sampling

Since the conventional seed trap technique could not be used due to problems of maintaining the seed traps in position in the field, the indirect method of utilising "seedling-emergence" was chosen. Experiments commenced in August 1995 and were continued until May 1996 (i.e. throughout one full rainy season). Six already existing permanent plots, representing the main vegetation types of KIH (with the exception of secondary forest vegetation) were selected and used for this study (see Backéus, Rulangaranga & Skoglund, 1994 for vegetation classification). In these plots, 1 x 1 m subplots were marked and all soil was removed to a depth of 15 cm. The resulting 0.15 m^3 pit was filled with sterilised sand (kept in an oven maintained at 140 ^{0}C for 24 hours) and left to trap any incoming seeds. In this way, diaspores from the local seed bank were assumed to be eliminated. To minimise " edge effects" or direct additions of seeds from the main plot into the subplots, a 15 cm wide strip of the surrounding vegetation was cleared in all directions. Seedlings emerging from the trapped seeds could only be quantified for about eight months as this experiment was dependent on the rainy season. As soon as the seedlings could be identified they were counted, and removed. Voucher specimens were collected and are deposited in the herbaria of the Universities of Dar es Salaam and Uppsala.

Vegetation survey and floristic sampling

The main floristic vegetation types identified in KIH (Backéus, Rulangaranga & Skoglund, 1994) include secondary forest, disturbed forest and woodland. The woodland is further subdivided into wooded grassland and woodland proper, depending on the ratio between the woody component and the grasses. These are relatively stable communities mainly dominated by perennial species which have apparently recovered from the degradatory forces in contrast to the unprotected grazed grassland. Other vegetation types include degraded vegetation, grazed and ungrazed grasslands at different stages of succession and grassland in a transition to woodland. Degraded vegetation is defined as sites with little vegetation cover where the top

soil and in some cases the lower horizons have been washed away by erosion. Most of the grassland communities are in the early stages of succession and are dominated by annual species. A deviating vegetation type- previously considered aberrant by Backéus, Rulangaranga & Skoglund, (1994)- is the "*Indigofera* community" which is peculiar by having single-species dominance of *Indigofera kirkii* Oliv. The floristic composition of 27 20m x 20m permanent plots established in 1991 (see Backéus, Rulangaranga & Skoglund, 1994) is updated regularly, and the data up to April 1995 were used in the seed rain study (Table 1).
The total tree and shrub cover and field layer cover were estimated as percentages of the total plot area. The cover values were used together with the seed rain data to study the correlation between the seed rain size and cover.

Seed bank sampling and glasshouse experiments

Ten soil samples, 206 cm^3 each (sampled at a depth of 0 - 5 cm), were collected systematically from the permanent plots which had been selected for the seed rain study between October and November 1995. Germination of the seed bank soil samples were performed in a glasshouse at the University of Dar es Salaam. The soil was air-dried and spread in plastic germination trays, over a layer of sterilised soil, placed in a glasshouse and watered daily. Emerging seedlings were identified, counted, and removed as soon as they could be identified, and were assigned to their respective functional groups as graminoids (i.e. grasses and sedges), herbs and shrubs. The seed bank soil in the trays was stirred twice a month to bring ungerminated seeds from below to the surface. The experiment was monitored for three months when no more seedlings germinated. Detailed results are presented in a separate seed bank paper.

Data analysis

After identification, the diaspores were allocated to one of the three main functional groups: graminoids (sedges + grasses), herbs, and shrubs. The herbs (defined here as all broad-leaved dicots and monocots excluding graminoids and woody species) were further split into legumes and others. Based on literature accounts (see Howe & Smallwood, 1982; Willson, 1992; Hughes *et al.*, 1994) and personal

Table 1. Number of species (from the 27 permanent plots) of the main functional groups found in the seed bank and the standing vegetation of the Kondoa Irangi Hills. The data which were collected in 1995 were used together with the seed rain data from the respective seed rain plots (marked with *) for correlation and similarity studies. SV stands for the number of species in the standing vegetation and SB stands for the number of species in the seed bank. The plots are arranged according to their vegetation types

Plot no.	Vegetation type	Graminoids		Herbs		Shrubs	
		SV	SB	SV	SB	SV	SB
5	Degraded vegetation	7	9	8	7	9	0
6	Degraded vegetation	9	6	4	0	6	0
13	Degraded vegetation	8	2	7	4	4	0
14	Degraded vegetation	5	4	8	4	7	0
16	Degraded vegetation*	7	12	8	8	6	0
21	Grazed grassland	9	3	13	6	5	0
22	Grazed grassland	5	8	14	11	9	0
23	Grazed grassland	8	6	13	9	8	2
24	Grazed grassland*	8	5	7	8	5	0
25	Grazed grassland	9	10	11	5	3	0
26	Grazed grassland	9	9	10	6	2	0
27	Grazed grassland	8	5	9	4	4	0
3	Wooded grassland	7	5	11	3	8	0
4	Wooded grassland	10	4	14	3	20	1
10	Wooded grassland	4	6	15	7	11	2
15	Wooded grassland	12	5	22	4	14	0
18	Wooded grassland*	10	5	9	8	2	0
12	Transitional grassl.*	6	8	13	5	11	0
1	Woodland	7	4	26	3	18	0
2	Woodland*	10	7	18	6	8	1
7	Woodland	4	4	13	8	21	2
8	Secondary forest	3	4	11	7	17	2
9	Secondary forest	4	1	8	7	17	0
11	Secondary forest	10	3	8	13	6	2
19	*Indigofera* community*	6	5	9	0	4	1
20	Aberrant relevé	0	4	9	3	4	1

observations, the diaspores were assigned to the following dispersal modes : (1) wind-dispersed, (2) animal-dispersed (ectozoochorous) and (3) apparently unassisted (applies to diaspores with no dispersal appendages). Diaspores from plants which constitute livestock food were assumed to be endozoochorous. Categorisation of the seed rain diaspores of grasses into their respective ecological indicator groups was based on literature accounts by Fröman & Persson, (1974), Tainton, Bransby & Booysen, (1976) and personal observations.

Cluster analysis of the seed rain species based on Ward's linkage method with squared Euclidean distances (MINITAB version 10xtra 1995 for dendrograms), was applied to a species x morphological characters matrix. The variables included mean diaspore weights, variances and presence or absence of appendages. Variance is defined as a quotient that expresses how diaspore shape deviates from a sphere (see Thompson, Band & Hodgson, 1993). The clusters formed were then analysed for patterns concerning modes of dispersal. Complete data were available for 24 seed rain species.

Statistical analyses of the seed rain, standing vegetation and the seed bank data were carried out for lognormal transformed data using one way ANOVA and SAS statistical package (SAS Inst., 1985); in order to determine the correspondence between the different functional groups in each of them. Similarities between seed bank, standing vegetation and the seed rain were calculated using Sørensen's (1948) Index.

The fourth objective of this study was achieved by determining the mean weights of diaspores and calculating their variances. Diaspores were weighed singly or in a batch of 100 to 500- and their mean weights calculated.

Variance was calculated on the basis of measurements in three dimensions of ten diaspores for each species. It is assumed that seeds with low variance ratios (i.e. small and compact seeds) will likely form persistent seed banks due to the ease of infiltrating into the soil.

The procedure adopted to calculate variance (see Thompson, Band & Hodgson,(1993) for explanation) was as follows:

1. For ten diaspores of each species, mean length [l], width [w] and depth/breadth [d] were obtained;
2. The values obtained in this way were each divided by the biggest value among them (which in most cases was the length). The

quotients were summed up and divided by three to give the mean [**X**];

$$X = ((l/l + w/l + d/l)/3$$

The deviations of **l/l**, **w/l** and **d/l** from the mean X were calculated, squared and summed up to give a value **X1** which was divided by three to obtain the variance.

RESULTS

Characteristics of the seed rain

A total of 54 species from 20 families, representing mainly graminoids, herbs and one shrub, were recorded in the seed rain, with no tree species represented. Graminoids contributed 72% (3141 individuals) to the seed rain, shrubs much less than 1% (3 individuals), legumes 3% (138 individuals) and other herbs 25% (1097 individuals). The individuals encountered in the seed rain had weights ranging over four orders of magnitude, from 1×10^{-5} g (*Cyperus rotundus* L.) to 4.24×10^{-2} g (*Dodonaea angustifolia* L.f.), with all grass and most other diaspores found in the range of 10^{-3} - 10^{-4} g. Annual species dominated the seed rain with 63% of the species.

The grass species found in the seed bank and the seed rain of KIH were categorised into two main ecological indicator groups and an intermediate category. The first group includes species that are indicators of disturbance and poor soils, which are widespread throughout KIH: *Aristida adoënsis* Hochst., *Aristida barbicollis* Trin. & Rupr., *Eragrostis viscosa* (Retz.) Trin., *Perotis patens* Oliv., *Sporobolus helvolus* (Trin.) Th. Dur. & Sch., *Sporobolus panicoides* A. Rich. and *Tragus berteronianus* Schult (see Tainton, Bransby & Booysen, 1976). The second group includes species which cannot withstand intensive defoliation and are also fire-sensitive (O'Connor, 1991). These are perennial, late-successional species. The species in this category are *Brachiaria brizantha* (A. Rich.) Stapf., *Setaria sphacelata* (Schumach.) Moss. and *Panicum maximum* Jacq. The intermediate category has a mixture of both annual and perennial species and are found in sites at different successional levels and is dominated by *Rhynchelytrum repens* (Willd.) C.E. Hubbard.

Cluster analysis of the seed rain data

In the dendrogram based on Euclidean distances from the seed rain data using variance and the mean diaspore weight (Fig. 1) as variables, three distinct clusters can be recognised at a similarity level of ca. 15%.

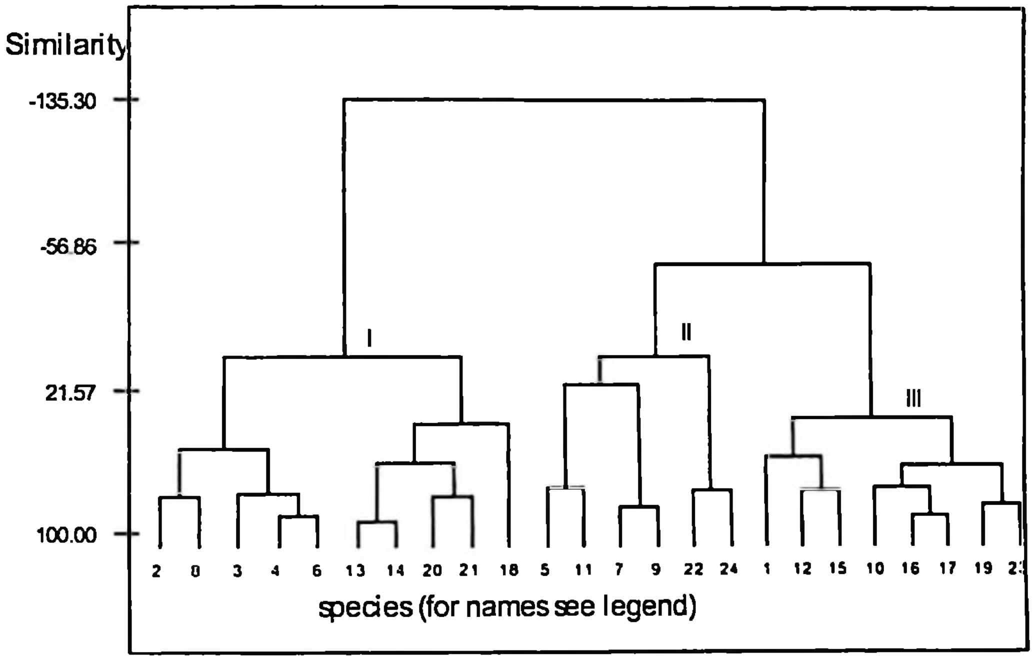

Figure 1. Dendrogram of the seed rain data based on squared Euclidean distances and Ward linkage method, using seed variance, seed mean weight and presence or absence of appendages as variables. The species names are: 1 = *Dactyloctenium geminatum*, 2 = *Chloris virgata*, 3 = *Tragus berteronianus*, 4 = *Digitaria abyssinica*, 5 = *Oxygonum sinuatum*, 6 = *Alloteropsis cimicina*, 7 = *Urochloa mossambicensis*, 8 = *Harpachne schimperi*, 9 = *Spermacoce senensis*, 10 = *Perotis patens*, 11 = *Acanthospermum hispidum*, 12 = *Sporobolus helvolus*, 13 = *Digitaria milanjiana*, 14 = *Cynodon nlemfuensis*, 15 = *Waltheria indica*, 16 = *Sesamum angustifolium*, 17 = *Cyperus rotundus*, 18 = *Aristida barbicollis*, 19 = *Setaria homonyma*, 20 = *Ocimum suave*, 21 = *Rhynchelytrum repens*, 22 = *Sida acuta*, 23 = *Triumfetta rhomboidea* and 24 = *Dodonaea angustifolia*.

Cluster I includes grass species which have wind dispersal appendages. Cluster II is composed of herbaceous species which are epizoochorous, as well as unornamented large-sized diaspores. Cluster III is a mixture of grasses and herbs with no obvious dispersal structures. A plot of diaspore variance against mean weight (Fig. 2), shows three clusters which are slightly different from the Euclidean distance-based clusters.

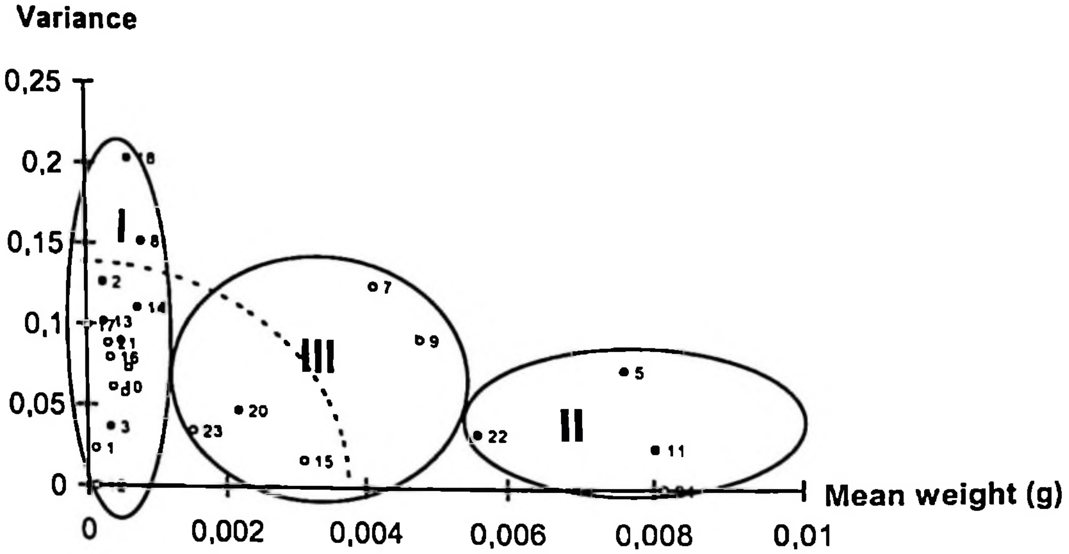

Figure 2: Plot of mean diaspore weight and variance to show clusters according to their modes of dispersal. The dotted line arbitrarily separates diaspores assumed to have long-lived seed bank to the bottom left from short-lived and intermediate categories. Filled circles indicate presence of appendages and empty circles absence. * differentiates diaspores with appendages adapted for animal dispersal on the exterior from others. The species names are: 1 = _Dactyloctenium geminatum_, 2 = _Chloris virgata_, 3 = _Tragus berteronianus_*, 4 = _Digitaria abyssinica_, 5 = _Oxygonum sinuatum_*, 6 = _Alloteropsis cimicina_, 7 = _Urochloa mossambicensis_, 8 = _Harpachne schimperi_*, 9 = _Spermacoce senensis_, 10 = _Perotis patens_, 11 = _Acanthospermum hispidum_*, 12 = _Sporobolus helvolus_, 13 = _Digitaria milanjiana_, 14 = _Cynodon nlemfuensis_, 15 = _Waltheria indica_, 16 = _Sesamum angustifolium_, 17 = _Cyperus rotundus_, 18 = _Aristida barbicollis_*, 19 = _Setaria homonyma_, 20 = _Ocimum suave_*, 21 = _Rhynchelytrum repens_, 22 = _Sida acuta_*, 23 = _Triumfetta rhomboidea_ and 24 = _Dodonaea angustifolia_.

Delimitation of these clusters did not take into account the presence or absence of appendages. The clustering is more advantageous in that the nature of seeds in the soil is predicted. Cluster I is a mixture dominated by small aerodynamic diaspores and very small unassisted diaspores. Cluster II contains individuals that are large in size and are epizoochorous, except for _Dodonaea angustifolia_ seeds. Cluster III is dominated by unassisted diaspores, except for the fruits of *Ocimum suave* Willd. The diaspores found below the dotted line on the left hand side of the figure represent species that are likely to form persistent seed banks because of their small size and compactness. The two properties are assumed to improve the infiltration rate of such seeds into the soil (Thompson, Band & Hodgson, 1993).

Seed rain density versus standing vegetation and seed bank

Seed rain density ranged from 230 to 1667 seeds m^{-2} over a period of eight months. High seed rain densities were negatively correlated to field layer cover and total tree and shrub cover (Table 2).

Table 2: Correlation analysis of transformed data followed by one way ANOVA to determine the relationship between total field layer cover/ tree and shrub cover, species richness and the seed rain density

Category	r-value	F	p-value
Seed rain density vs field layer	-0.887	36.76	0.0003
Seed rain density vs tree cover	-0.643	14.90	0.0040
Species richness vs field layer	-0.800	36.76	0.0003
Species richness vs tree cover	-0.371	0.63	0.4490

Correlation analysis of the main functional groups in the standing vegetation, seed bank and seed rain was significant only among the graminoids (Table 3).

Table 3. Correlation analysis of the number of common species (log-normal transformed data) of the main plant functional groups excluding shrubs (in terms of species presence) in the standing vegetation (Sv), seed bank (Sb) and seed rain (Sr). * indicates significance at p = 0.05

Category	Graminoids r-value	Herbs r-value	"all groups" r-value
SvSb	0.48	-0.14	0.24
SbSr	0.75*	0.31	0.61
SvSr	0.15	-0.40	-0.30

Seed rain densities, species richness and similarities between any of the two pairs (Tables 4a -c) were highest in grazed grassland and degraded vegetation, followed by wooded grassland and the lowest values were recorded from woodlands.

Tables 4a - c. Similarity Index (SI) values for the seed rain, seed bank and above ground vegetation as expressed by the Sorensen's (1948) Index. The data are untransformed

4a

plot no.	Number of species vegetation	seed rain	common species	SI	Vegetation type
16	14	13	12	0.47	Degraded vegetation
18	31	5	8	0.30	Wooded grassland
19	18	4	9	0.45	Indigofera community
24	23	15	14	0.42	Grazed grassland
12	40	8	8	0.25	Transitional grassland
2	39	5	8	0.27	Woodland

4b

plot no.	seed rain	seed bank	common species	SI	Vegetation type
16	19	8	6	0.30	Degraded vegetation
18	11	8	2	0.17	Wooded grassland
19	11	1	2	0.25	Indigofera community
24	19	10	10	0.40	Grazed grassland
12	6	7	2	0.23	Transitional grassland
2	11	6	2	0.19	Woodland

4c

plot no.	vegetation	seed bank	common species	SI	Vegetation type
16	21	9	5	0.25	Degraded vegetation
18	33	4	6	0.24	Wooded grassland
19	25	1	2	0.13	Indigofera community
24	28	11	9	0.31	Grazed grassland
12	6	7	2	0.23	Transitional grassland
2	11	6	2	0.19	Woodland

DISCUSSION AND CONCLUSIONS

Limitations of the interpretation of the results

Unlike the conventional method of studying the seed rain that employs seed traps, the germinated non-dormant seeds in this study represented only a fraction of the total seed rain. Seed traps would have recorded seed counts and would likely have excluded post-dispersal predation. Studying the seed rain by the seedling emergence method is a very practical approach in regeneration studies where the main interest is the viable seed population. The observation period was short, but included at least one full rainy season. Generally, seed rain experiments take much longer time (Burrows, 1994), and reported seed densities are much higher (Skoglund, 1990). The small sample size used in the correlation studies may have led to the lack of significance of the results.

Wind dispersal and its associated factors

The observed dominance of grasses in the seed rain can be explained as follows: Grass seeds are small and some have morphological adaptations for wind dispersal. Secondly, grasses have prolific seed production (Stöcklin & Bäumler, 1996). It has been observed that seeds weighing less than 5×10^{-5} g are effectively dispersed by wind even if they lack dispersal appendages (Hughes *et al.*, 1994). Most grass and herbaceous seeds weigh between 1×10^{-4} and 1×10^{-1} g and therefore, in this range, all dispersal modes are possible. Seeds which lack dispersal devices can achieve long-distance dispersal either by being accidentally consumed with food material (Collins & Uno, 1985), or by constituting the food material itself. The negative correlation between seed rain size within sites and tree and shrub cover can be explained by the fact that cover has an effect of reducing wind velocity, thereby minimising the chances of wind dispersed diaspores from reaching these sites. Therefore, one may expect "passive seed rain" predominantly in woodlands and "active seed rain" in grasslands. Active seed rain implies influx of new seeds to the site from outside whereas passive seed rain refers to seeds which originate from on-the-site vegetation.

Relationship between seed rain, seed bank and the above-ground vegetation

The different similarity levels of the seed rain, seed bank and the standing vegetation indicate the importance of seed bank, passive seed rain and active seed rain to regeneration in the KIH. The observation that 60% of the recorded seed rain species were not present in the standing vegetation, clearly shows the importance of active seed rain for regeneration in the study area. The contribution of the active seed rain as calculated from the number of species was different at each site depending on the successional level. The more open sites, i.e. the grasslands and degraded habitats, had ca. 50% active seed rain species, whereas the sites with high cover values and perennial vegetation such as woodland and wooded grasslands had much lower active seed rain, between 0 and 38%. Only one species (*Acalypha indica* L.) was found both in the seed rain and the seed bank but was absent in the standing vegetation. This species is known to form a persistent seed bank (Simpson, 1990).

The standing vegetation and the seed bank are least similar in woodland and transitional grassland vegetation, but are most similar in grazed grassland and severely degraded sites. The standing vegetation and the seed rain are very similar except in woodland, wooded grassland and transitional grassland vegetation types. Two scenarios emerge where the standing vegetation and the seed bank are least similar as in woodland and transitional grassland vegetation (Table 4 c). The implication could be that the site has active seed rain which does not become incorporated to form part of the seed bank. The second alternative is that the seed bank is a reflection of former vegetation which once grew on the area. The strong deviation of the seed bank from the seed rain in woodland and wooded grassland sites is accounted for by persistence of diaspores in the soil for more than one year.

Selection for a long-lived seed bank among species is favoured by small seed size and compactness, characters which facilitate movement of seeds into the soil (see Thompson, Band & Hodgson, 1993). High similarity between the seed bank and the seed rain as in grazed grassland sites, where they are both very similar to the standing vegetation, indicates passive seed rain and domination of species with transient seed bank. The above finding of passive seed rain in grasslands contradicts that reported by Howe & Smallwood (1982) and could be explained by the vast homogeneity of the KIH vegetation in such a way that there is no clear cut limit between passive and active seed rain. It is logical to assume that in the KIH, species with persistent seed banks occur in late successional vegetation such as woodlands and wooded grasslands whereas transience is much more common in recently disturbed vegetation.

The status of legumes in the seed rain

Most legumes can fix atmospheric nitrogen in a form that can be utilised by other plants. This is important in ecosystems where degradation has rendered the soils nutrient-deficient. The legume component of the seed rain was composed of herbaceous annual species such as *Indigofera cuneata* Bak., *Indigofera volkensii* Taub., *Tephrosia pumila* (Lam.) Pers. and *Zornia glochidiata* DC. which are unpalatable, (except *Z. glochidiata*) non-nitrogen fixers (Pandey & Singh, 1992) and one perennial species *Crotalaria cylindrostachys* Bak. The low contribution of legumes of 9% of the total seed rain species (5 out of 54) in the KIH is not surprising as even lower values (less than 1%) have been reported in nutrient-poor savannah grasslands (see Pandey & Singh, 1992 and references therein).

To summarise the above discussion, I argue that in view of their size, nature and composition, the seed rain and the seed bank of the KIH will play an important role in changing this recovering degraded land into an agro-pastoral community, provided certain conditions such as increased mineralisation are met. My argument is that the presence of diaspores (which are plenty in both the seed rain and the seed bank) in an area undergoing secondary succession is a primary condition that has to be met, prior to any other condition.

Secondly, the most important pasture grasses for semi-arid areas in terms of biomass production and high-quality forage, such as *Brachiaria brizantha* (A. Rich.) Stapf., *Cynodon nlemfuensis* Vanderyst and *Themeda triandra* Forssk. are zoochorous (O'Connor, 1991), and they grow well on nutrient-rich soils. Since such diaspores were hardly recorded in this study, controlled re-introduction of livestock in KIH may be an appropriate solution as it would increase their numbers and overall species diversity through seed dispersal, as well as enhancing nitrogen mineralisation into the soil (McNaughton & Chapin, 1985). This will be possible only after determining the new carrying capacity of the recovering land and compromising with the local people on how to manage the new land.

Finally, for the KIH ecosystem, active seed rain and transient seed bank are characteristics of open habitats such as grasslands and disturbed sites, whereas passive seed rain and seed bank persistence is common in late successional vegetation such as woodland.

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IV

Seed longevity of selected species from degraded savanna in semi-arid Tanzania

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Abstract

Artificially buried seeds were followed by periodic exhumation and germination during 21 months in Kondoa Irangi Hills, central Tanzania. Viable seeds from thirteen selected species were buried in polythene envelopes at a depth of 15 cm below a woodland vegetation. Lethal germination, fungal decay and insect infestation were singled out as the most important contributors to loss of viability among seeds. Hierarchical clustering based on a seed's mean viability, seed shape and presence or absence of dispersal appendages, produced three distinct groups: (1) non-dormant seeds (2) seeds with enforced dormancy and (3) seeds with seed coat imposed dormancy. The low decay constants of some species is an indication of their abilities to form persistent seed banks. The intermittent and extended germination of seeds of the same species from the same batch shown by some species is an ecological adaptation to prevent synchronous germination in unpredictable harsh environments, whereas prompt germination of some *Acacia* seeds is a strategy to avoid seed predation in the soil. Seed dormancy, which predicts seed longevity, is strongly dependent on seed moisture content and partly on other environmental factors, notably low temperatures, light and increased carbon dioxide levels.

Keywords: *Acacia tortilis*, degraded vegetation, enforced dormancy, induced dormancy, innate dormancy, mortality, rehabilitation

Nomenclature: Flora of Tropical East Africa (Turrill & Milne-Redhead 1952-) and Flora Zambesiaca (Exell & Wild 1960-)

Introduction

Knowledge of longevity of buried seeds is important for predicting responses of ecosystems to management and catastrophic changes (Roberts 1981) and may play an important role in the conservation and restoration of plant communities (Bakker 1989). In order for seeds to remain viable in the soil, seeds must possess mechanisms that keep them alive and at the same time prevent them from germinating. As a result, seed dormancy, quiescence and also ability of dormant seeds to detect and respond to appropriate germination cues are inherent properties of viable seed banks. The form of dormancy possessed by seed, whether innate, enforced, induced or hard-seededness, will determine if species can form a transient or a persistent seed bank (Thompson and Grime 1979, Baskin and Baskin 1989, Thompson et al. 1997). In terms of population dynamics, short-term persistent seed banks, that may be linked with enforced dormancy of the seed bank species, in most cases are useful to maintain equilibrium in plant populations in years with low seed production (Bakker 1989), whereas long-term persistence, which is linked to all types of dormancy especially hard-seededness, is important for rehabilitation of degraded plant communities (Bakker 1989).

Research has indicated that seeds under storage conditions differ considerably from seeds in natural habitats in that dry stored seeds lose viability much faster (Cook 1980). This is because, in air-dry stored seeds, the moisture content is reduced to a certain level that will prevent germination during storage, and because of this treatment the normal functioning of their enzyme systems is impaired. They also differ in their patterns of mortality, in that in buried seeds mortality is directly related to the breakdown of dormancy mechanisms which prevent fully imbibed seeds from germinating, whereas in stored seeds the loss of viability is assumed to be normally distributed (Cook 1980).

There are other factors apart from seed dormancy and quiescence known to influence seed longevity in the soil. Artificial seed burial experiments have revealed that seed longevity increases with increasing depth of burial (Kivilaan and Bandurski 1981, Tsuyuzaki

1991). This is because light and fluctuating temperatures are the main dormancy releasing factors in the soil. Soil properties are known to influence seed longevity as well. For example, seeds in water-logged or acidic soils maintain dormancy for much longer periods and are therefore long-lived (Champness and Morris 1948). Cultivation or any form of disturbance that turns the soil, e.g. uprooting of big trees, reduces seed longevity (Robert and Feast 1973) by improving soil aeration and exposing seeds to light. High temperatures are reported to reduce seed dormancy (Schafer and Chilcote 1970).

Information on seed longevity in the soil can be obtained conventionally by sampling the soil seed bank at different soil depths and preventing influx of new seeds into the area by covering the sampled area, followed by controlled germination and re-sampling for a period of time (Roberts 1963), or through artificial seed burial and periodic exhumation of seeds (Egley and Chandler 1978, Demel and Granström 1997). If seeds are not secondarily dispersed to deeper soil layers by worms, ants, termites etc., detection of seeds from the seed bank of a species which is not represented in the standing vegetation is an indication of it having seeds with extended longevity (see e.g. Ødum 1974).

There is no information regarding longevity of seeds in semi-arid Tanzania, and therefore it is the aim of this study to determine the longevity of seeds of selected species in such environment. This is because seed survival strategy is an important characteristic of plant adaptation to extreme environments, where many factors are known to limit recruitment and seedling establishment.

This study was conducted in the Kondoa Irangi Hills in Dodoma region of central Tanzania (hereafter called KIH). Among the selected seed species used in the present study were seeds of *Acacia seyal* Del., *Acacia tortilis* (Forsk.) Hayne s.l., *Faidherbia albida* (Del.) A. Chev.(syn: *Acacia albida*) and *Acacia saligna* (Lab.) Wendl. *Acacia* species can be regarded as keystone species in African savannas. The choice of other leguminous species *Abrus precatorius* L., *Cassia occidentalis* L., *Crotalaria kirkii* Bak. and *Tephrosia villosa* (L.) Pers, was based on their potential for nitrogen mineralization, which is important for rehabilitating degraded vegetation, and partly on their dominance in the study area. Seeds from the early successional pioneer shrub, *Dodonaea angustifolia* L. f., which readily colonises various parts of this degraded vegetation, were also studied. The study also included *Bidens pilosa* L., *Conyza pyrhopappa* L. and *Vernonia cinerascens* Sch.-Bip. to represent the family Asteraceae. *Withania somnifera* (L.) Dunal of the family Solanaceae was included to diversify the number of families studied.

Material and Methods

Brief description of the study area and species

KIH can be regarded as a focal point of restoration activities dealing with reclamation of degraded and marginal lands in Tanzania (Mbegu & Mlenge 1984, Christiansson et al. 1993). For detailed presentation of KIH see further Backéus et al. (1994) and Lyaruu (1995). The overall climate of the area is semi-arid to more or less sub-humid in the high elevation parts. It has a weakly bimodal annual precipitation of 600 - 800 mm (Ngana 1992) but it is much more in the elevated parts of Kondoa Irangi. The rainy season extends from late November to May and it comes in the form of short-lived intense storms. The soils are texturally coarse loamy sands to sandy loams (Mbegu & Mlenge 1984), but in flatter areas black cotton soils (vertisols) are common.

Seeds used in this study were collected randomly throughout KIH but were buried below ground in one site in a woodland vegetation, which probably receives the highest amount of rainfall in KIH. The soils of this woodland vegetation can be described as free-draining sandy loams. Attributes of species used in the present study are presented in Table 1.

Seed collection, viability test and experimental set-up

Thirteen species included in this study were selected from four families representing mainly dominant trees and shrubs in the study area, i.e.: Leguminosae (8), Asteraceae (3), Sapindaceae (1) and Solanaceae (1). Naturally dried seeds were collected between September and October 1994 in Kondoa and were stored at room temperature before they were used in March 1995. Before storage,

Table 1. List of species studied with information on their families, habit, seed surface ornamentation and status whether indigenous, exotic or naturalized. For seed ornamentation, 0 = smooth seeds without appendages and 1 = presence of achenial pappus

Species	Family	Habit	Appendages	Status
1. *Abrus precatorius*	Papilionoideae	Woody Climber	0	naturalized
2. *Acacia saligna*	Mimosoideae	Tree 3 - 6 m	0	exotic
3. *Acacia seyal*	Mimosoideae	Tree 3 - 12 m	0	indigenous
4. *Acacia tortilis*	Mimosoideae	Tree 4 - 21 m	0	indigenous
5. *Bidens pilosa*	Asteraceae	Erect herb	1	indigenous
6. *Cassia occidentalis*	Caesalpinioideae	Erect herb	0	naturalized
7. Conyza pyrhopappa	Asteraceae	Shrub	1	indigenous
8. *Crotalaria kirkii*	Papilionoideae	Erect herb	0	indigenous
9. *Dodonaea angustifolia*	Sapindaceae	Treelet	0	indigenous
10. Faidherbia albida	Mimosoideae	Tree 6 - 30 m	0	indigenous
11. *Tephrosia villosa*	Papilionoideae	Straggling herb	0	indigenous
12. *Vernonia cinerascens*	Asteraceae	Shrub	1	indigenous
13. *Withania somnifera*	Solanaceae	Shrub	0	indigenous

defective seeds with insect damage were sorted out and removed. Seeds were considered to be viable if they appeared healthy, intact and could resist deformation when pressed between the fingers. Before the experiment was set, an indication of viability for each species with large seeds was obtained by cutting through the endosperm of twenty seeds followed by the 2, 3, 5-triphenyl-tetrazolium chloride (TTC) staining procedure. For small seeds, viability was assessed by direct germination of twenty seeds placed between blotting paper in petri dishes in the laboratory. Emergence of radicle from these seeds was an indication of viability. For all seeds that were buried, the viability was assumed to be 100% initially.

Twenty seeds from thirteen species (= 260 seeds) mixed with small amounts of soil to simulate field conditions were placed in 5 x 10 cm polythene envelopes. The envelopes were not sealed to allow free circulation of air. Ten such envelopes were buried at a depth of 15 cm below ground in woodland vegetation, assuming that amenable conditions may not trigger germination from this depth. While keeping the remaining envelopes in position, one envelope was exhumed at a time after 3, 6, 9, 12 and 21 months and the contents inspected. It was intended to monitor the experiment for a period of four years, but since all seeds had died by the time of the fifth excavation, the experiment was abandoned. The seeds were sorted out to separate the dead from living seeds, and if possible to establish the cause of their death. The viable seeds were then sown in sterilised soil in the greenhouse, and were watered at least twice daily. For each species, the time when germination started for each species, the number of germinated seeds, and the time required for complete germination were recorded. Collection of such information was laborious and therefore complete data on the time of germination is available only for the second batch of exhumed seeds. Seedlings were plucked out as soon as they could be identified in order to minimise competition in the pots. Seeds that did not germinate after six months of watering were mechanically scarified and germinated.

Data analysis

Due to skewness in distribution, the data were log-transformed before statistical treatment.

ANOVA using the GLM procedure in SAS (SAS Inst. 1990) followed by Duncan's Multiple Range test to compare significance levels among means were performed on the groups obtained from hierarchical clustering. Mean viabilities for each pair among the species studied were compared using a paired t-Test. In this study, viabilities presented are the mean values of viable seeds of each species recovered during the five periods of exhumation.

Hierarchical clustering of groups was performed using the programme MINITAB version 10xtra (1995) for dendrograms and Euclidean distances (complete linkage) method. The variables included in the cluster analysis were species' mean viability, variance, and presence or absence of dispersal appendages. Variance as defined here is a quotient that expresses how diaspores deviate from being spherical (see Thompson et al. 1993). It is assumed that small seeds with low variances (i.e. compacted seeds without appendages for dispersal) are much more long-lived in the soil compared with elongated seeds. This is related to the ease with which small seeds infiltrate into the soil and, by being small, they are not easily spotted and predated compared with large seeds. The procedure adopted to calculate variance (see Thompson et al. 1993) was as follows:

1. Calculation of mean length (L), width (W) and depth/breadth (D) of ten diaspores per species under the binocular stereomicroscope.

2. Dividing each of the three values by the biggest value (which was generally length). The three quotients were summed up and divided by three to give a mean value X_1, i.e. $X_1 = (L/L + W/L + D/L)/3$
3. The deviations of **L/L, W/L** and **D/L** from the mean value X_1 were calculated, squared and summed up to give a value X_2 which was finally divided by three to obtain the variance.

The rate of deterioration of seeds in the soil was calculated from the relationship $S = S_0 e^{-gt}$ (Roberts and Dawkins 1967), where S is the number of viable seeds in the soil at time **t**, S_0 is the number of seeds at the start of the experiment and g is a decay constant which is species specific. This relationship thus assumes that seed viability in the soil declines exponentially with time (see e.g. Cook 1980).

Results

Causes of viability losses among species

Three major sources of viability loss of the buried seeds were identified: lethal or *in situ* germination, fungal infection with subsequent rotting and insect infestation. It may be assumed that seeds found missing in some envelopes had been predated or secondarily dispersed. Lethal germination was common in the seeds of *Acacia saligna*, *Acacia seyal*, *Cassia occidentalis*, and *Faidherbia albida*, while rotting as a result of fungal attack was common in *Abrus precatorius*, *Bidens pilosa*, *Conyza pyrhopappa*, *Tephrosia villosa*, *Vernonia cinerascens* and *Withania somnifera*. Seeds of *Acacia tortilis*, *Crotalaria kirkii* and *Dodonaea angustifolia* succumbed to insect damage.

Seed viability and cluster delimitation

Pairwise comparisons of mean viabilities of all species and t-Test values are presented in Table 2. The mean viability is explained by seed variance ($R^2 = 0.67$) by a linear relationship $y = 0.839 - 3.107x$. The more or less spherical seeds had higher viability than the more elongated seeds (see Fig. 1).

Table 2. Paired t-Test to compare mean (± s.e) viabilities of species studied except the species with very short-lived seeds. The mean viability is expressed as the mean number of seeds that remained viable during the five periods of exhumation. The symbols are: ns = not significant, * $p < 0.1$, ** $p < 0.05$ and *** $p < 0.01$. Falb = *Faidherbia albida*; Apre = *Abrus precatorius*; Asal = *Acacia saligna*; Ckir = *Crotalaria kirkii*; Asey = *Acacia seyal*; Cocc = *Cassia occidentalis*; Tvil = *Tephrosia villosa*; Dang = *Dodonaea angustifolia*; Wsom = *Withania somnifera* & Ator = *Acacia tortilis*

Species										Mean viability
Falb										4.8 ± 3.9
Apre	2.09^{*}									7.6 ± 3.3
Asal	1.62^{ns}	0.60^{ns}								6.7 ± 3.7
Ckir	3.12^{**}	1.08^{ns}	1.65^{ns}							9.0 ± 3.4
Asey	1.64^{ns}	0.44^{ns}	0.14^{ns}	1.5^{ns}						7.0 ± 4.2
Cocc	2.81^{**}	0.88^{ns}	1.42^{ns}	0.14^{ns}	1.24^{ns}					8.8 ± 4.2
Tvil	4.61^{***}	2.63^{**}	3.16^{**}	1.54ns	2.91^{**}	1.60^{ns}				11.0 ± 3.4
Dang	4.72^{***}	2.37^{**}	3.30^{**}	1.30^{ns}	3.03^{**}	1.72^{ns}	0.15^{ns}			11.2 ± 3.5
Wsom	3.62^{***}	1.65^{ns}	1.46^{ns}	0.60^{ns}	1.99^{*}	0.71^{ns}	0.90^{ns}	1.04^{ns}		9.8 ± 3.8
Ator	4.90^{***}	2.99^{**}	3.50^{***}	1.93^{*}	3.25^{**}	1.98^{*}	0.45^{ns}	0.30^{ns}	0.95^{ns}	11.6 ± 3.8
	Falb	Apre	Asal	Ckir	Asey	Cocc	Tvil	Dang	Wsom	

Hierarchical clustering delimited three significantly different groups (Fig. 2). One-way ANOVA results followed by Duncan's Multiple Range Test indicated that mean viability was significantly different between the groups $F_{[2\ 10]} = 33.62$, $p < 0.001$) and increased in the order Group III > Group II > Group I (Fig. 3). Variance, which is an indication of seed shape, was different between the groups ($F_{[2\ 10]} = 16.47$, $p < 0.001$); but only group I was significantly different from the other two groups.

GROUP I- This is composed of three members of the family Asteraceae which are ornamented with dispersal appendages. These species did not survive in the soil and showed 100% loss of viability after three months burial and are likely to possess a transient seed bank in the sense of Thompson and Grime (1979).

GROUP II- This category consists of five leguminous species with intermediate viabilities between groups I and III. Although all are hard-seeded species, they are likely to possess enforced dormancy imposed by water shortage and therefore have short-term persistent seed banks, which become exhausted by germination in response to rainfall.

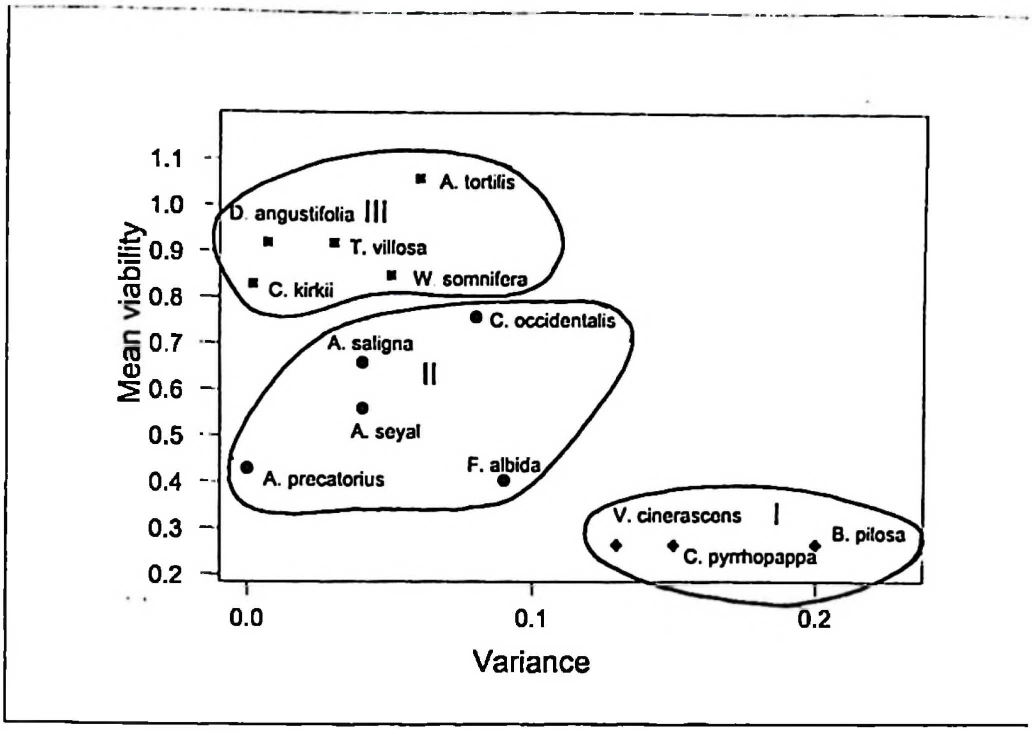

Figure 1. Variation in mean variance and mean viability (log-transformed data) of the species studied. The clusters correspond to the groups in Figure 2.

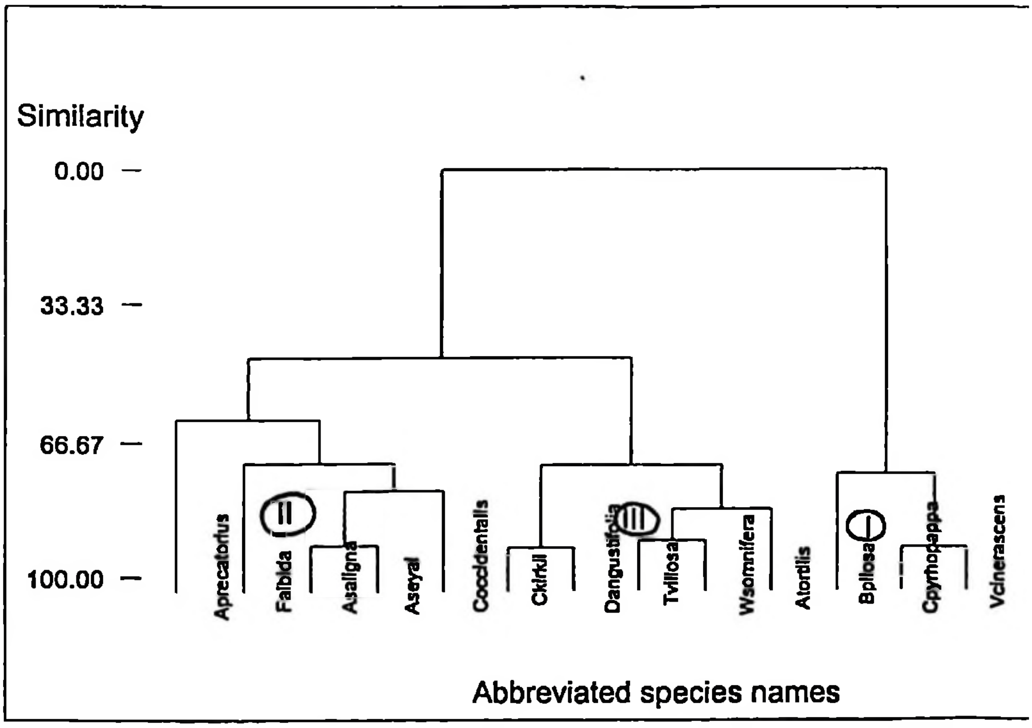

Figure 2. Dendrogram from hierarchical cluster analysis showing the three main clusters among the species studied. Group I are species with no seed dormancy, group II is an intermediate category of the two groups and group III are species with seed coat imposed dormancy.

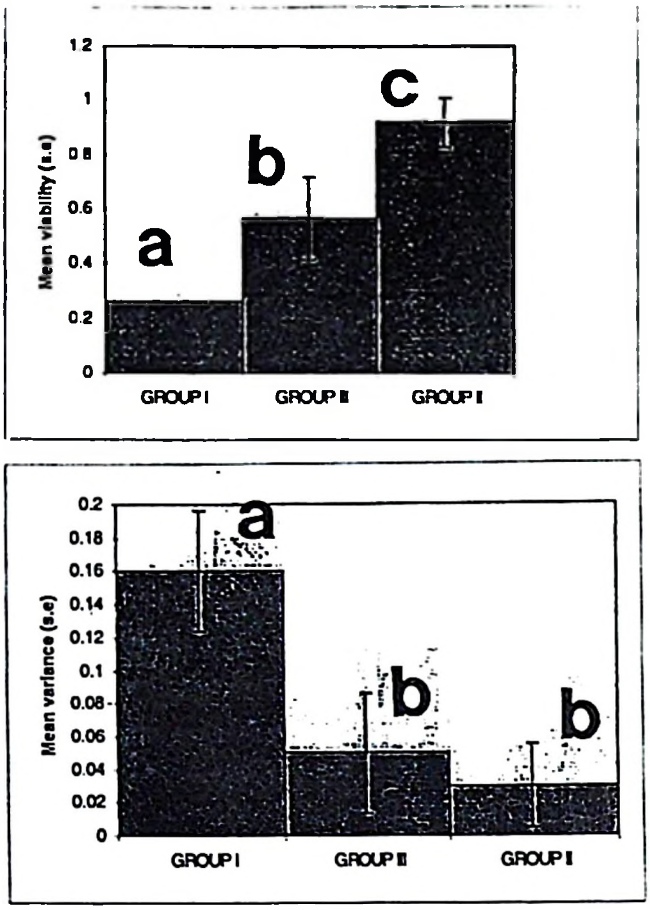

Figure 3. Duncan's Multiple Range Test comparison of group means (± s.e) for the viabilities and variances of the three groups. Different letters indicate significant variations among the means.

GROUP III- This is a group of three legumes, one species of Sapindaceae and one of Solanaceae. The seeds remained ungerminated in the soil and did not respond to wet conditions in the soil. However, in the greenhouse germination experiments, 100% germination of all seeds from members of this group could be achieved six months later when subjected to mechanical scarification (Fig. 4), indicating that they possess seed coat dormancy and therefore are able to form persistent seed banks. Both groups II and III have smooth seeds with no dispersal appendages. The allocation of *Cassia occidentalis* to group II of the hierarchical clusters is rather obscure because the seeds behaved more like group III species in the germination experiment.

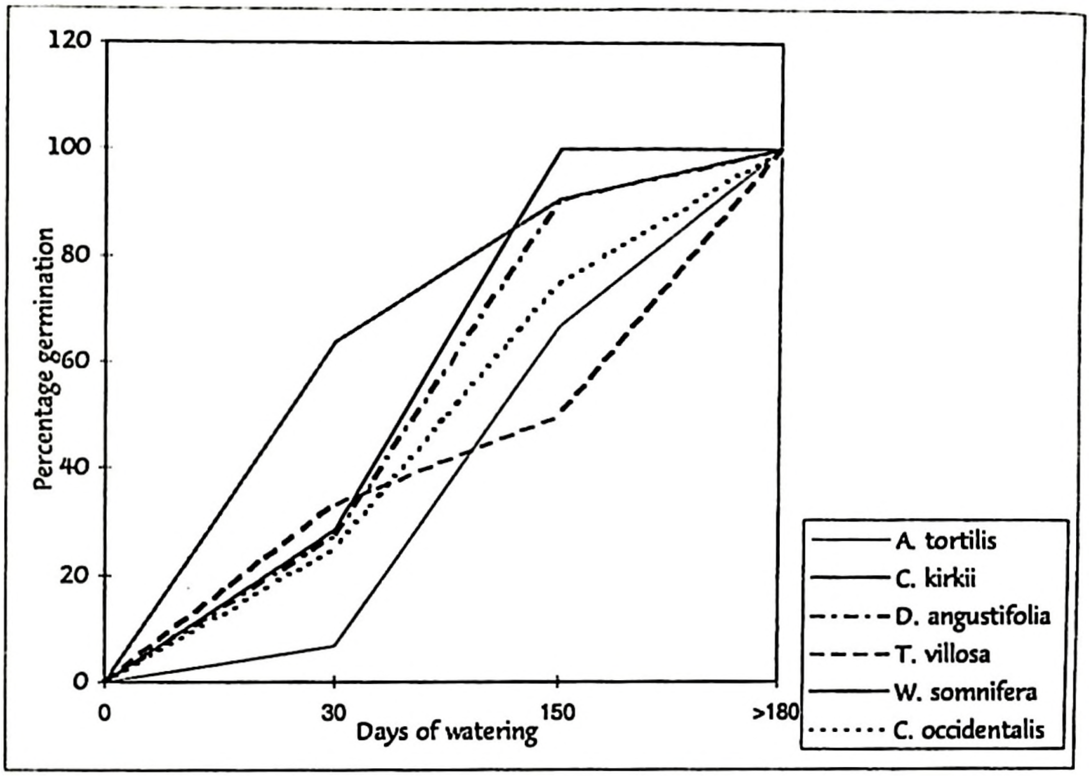

Figure 4. Timing of germination of the species shown to have seed coat imposed dormancy. The germination results are from seeds which have been buried in the soil for nine months. Except for *Withania somnifera*, all other seeds required scarification so as to attain 100% germination.

Seed survivorship versus seed decay patterns

For all species studied, Table 3 gives the constants (g) that determine rates of loss of seeds in the soil, their half-lifes and equations to estimate the number of seeds of a given species. Since it is assumed that seeds buried under natural conditions exhibit exponential decay in the soil, the parameter half-life quantifies the time required by viable seeds of any species to be reduced by half their original numbers. Species with persistent seed banks are associated with very low decay constants. The pattern of decay of seeds among the composites could not be established as no single seed survived burial conditions during the first three months. Group II species showed very little variations in their half-lifes but a remarkable difference in their rates of deterioration in the soil (Fig. 5). Group III species had a contrasting pattern to group II in terms of their decay constants and half-lifes. Four species, *Abrus precatorius*, *Acacia saligna*, *Acacia*

Table 3. Summarised information of species capable of surviving at least the first three months of burial, arranged in the decreasing order of their half-lifes. The decay constants ± s.e and half life of seeds in the soil were derived from the relationship $S = S_o e^{-rt}$ (Roberts and Dawkins 1967). nd stands for not determined. S predicts the number of seeds that will be viable at time t

Species name	Variance-	Decay constant	Half life days	Regression equation
Abrus precatorius	0.0	0.401 ± nd	52	$S = 20\,e^{-0.401t}$
Acacia saligna	0.04	0.257 ± 0.009	81	$S = 24.6\,e^{-0.257t}$
Acacia seyal	0.004	0.348 ± 0.029	63	$S = 26.3\,e^{-0.348t}$
Acacia tortilis	0.06	0.032 ± 0.001	662	$S = 19.9\,e^{-0.032t}$
Cassia occidentalis	0.08	0.186 ± 0.065	114	$S = 25\,e^{-0.186t}$
Crotalaria kirkii	0.002	0.055 ± 0.061	388	$S = 16.2\,e^{-0.055t}$
Dodonaea angustifolia	0.007	0.067 ± 0.005	340	$S = 20.3\,e^{-0.067t}$
Faidherbia albida	0.09	0.536 ± nd	41	$S = 20\,e^{-0.536t}$
Tephrosia villosa	0.03	0.054 ± 0.014	483	$S = 19\,e^{-0.054t}$
Withania somnifera	0.05	0.121 ± 0.023	187	$S = 21.7\,e^{-0.121t}$

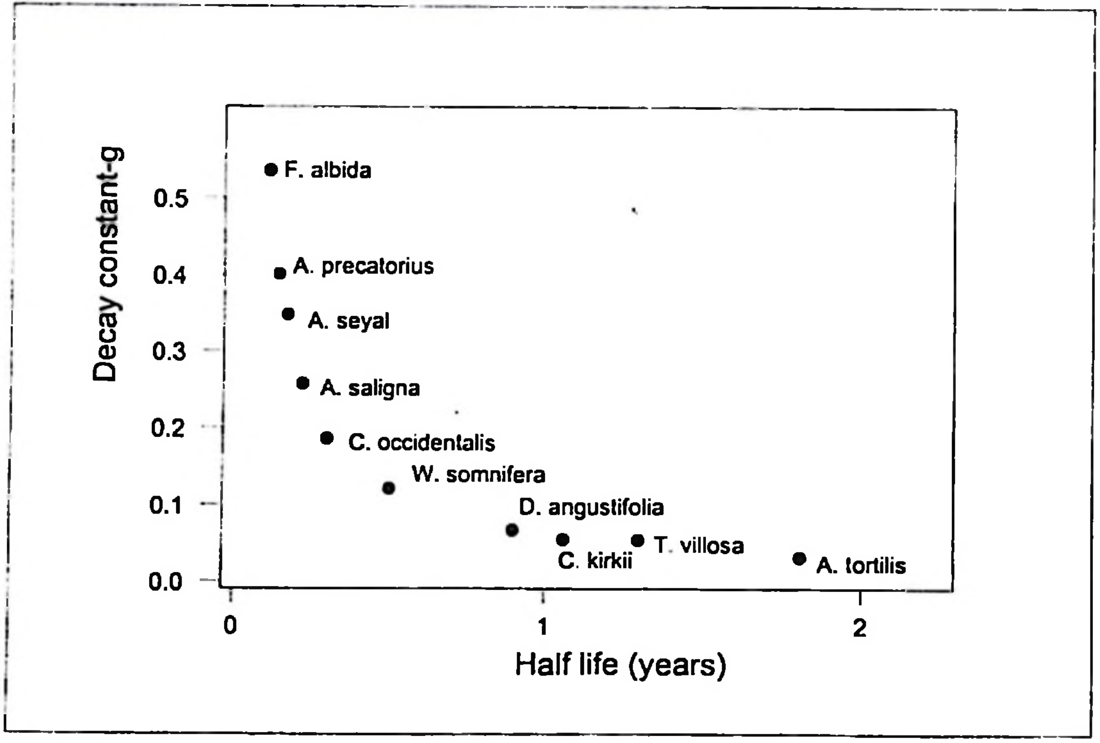

Figure 5. Graph to show the relationship between seed survival rate in the soil (g) and half-life (t_{50}) Of the studied species.

seyal and *Faidherbia albida*, conformed to the agreed pattern of exponential decay in the soil (Fig. 6). The species belong to group II of the cluster analysis and have short persistence in the soil. Species belonging to group III, i.e. *Acacia tortilis*, *Crotalaria kirkii*, survivorship patterns in the soil (Fig. 6), and for *Crotalaria kirkii* seeds the pattern is slightly different from the other two groups. Both *Withania somnifera* (from group III) and *Cassia occidentalis* (group II) slightly conform to the exponential seed decay pattern. Group III species have seed coat imposed dormancy in common, and consequently have long-term persistence in the soil.

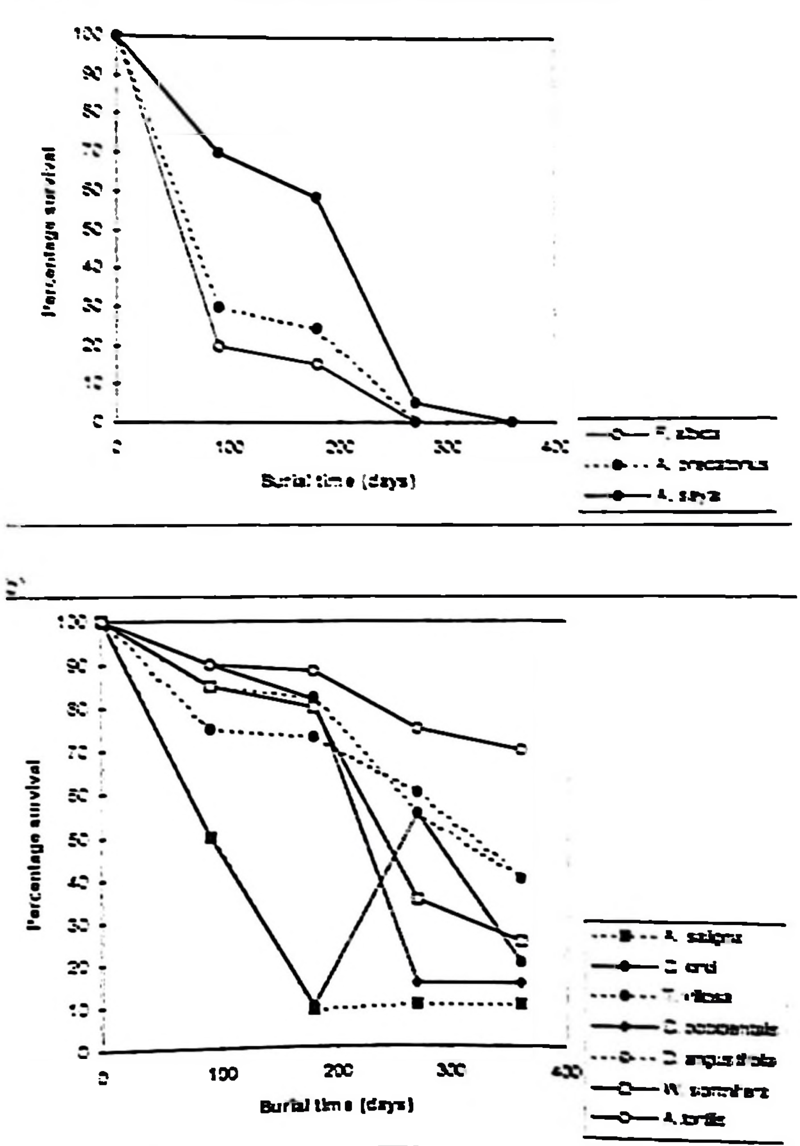

Figure 6. Survivorship curves of group II and group III species. Different species showed variations in their survival patterns, with some few species (i.e. short-lived species) conforming to the theoretical pattern of seed decay. Group I species did not survive burial conditions after three months.

Table 3. Summarised information of species capable of surviving at least the first three months of burial, arranged in the decreasing order of their half-lifes. The decay constants ± s.e and half life of seeds in the soil were derived from the relationship $S = S_o e^{-rt}$ (Roberts and Dawkins 1967). nd stands for not determined. S predicts the number of seeds that will be viable at time t

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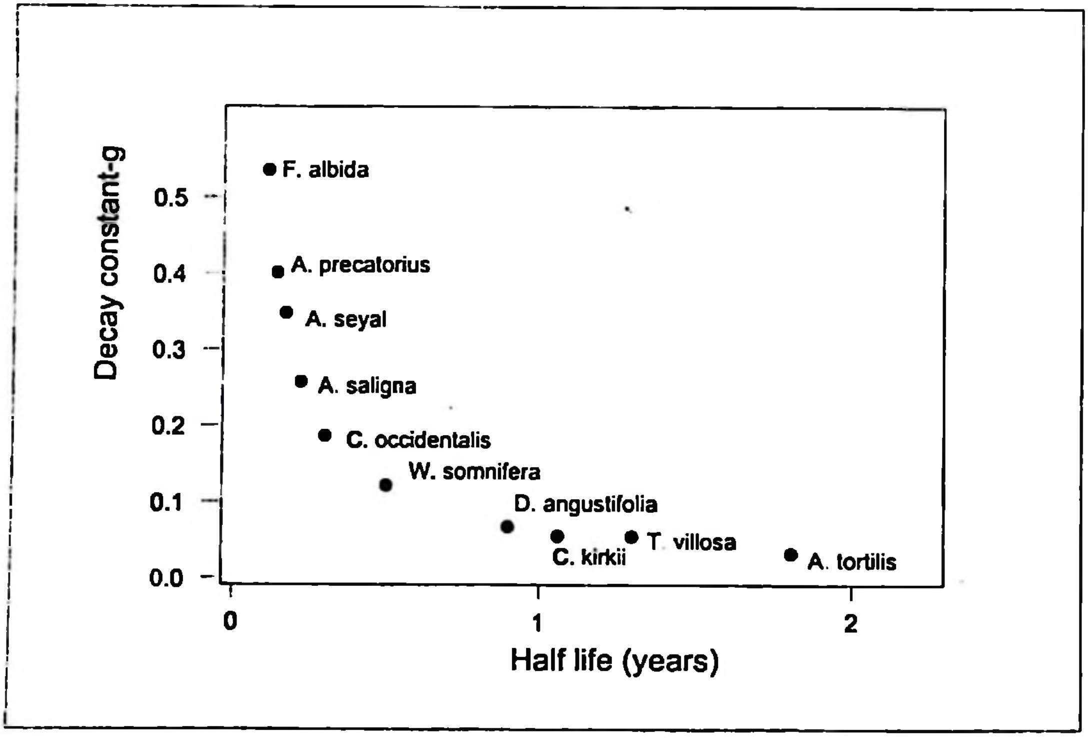

Figure 5. Graph to show the relationship between seed survival rate in the soil (g) and half-life (t_{50}) Of the studied species.

seyal and *Faidherbia albida*, conformed to the agreed pattern of exponential decay in the soil (Fig. 6). The species belong to group II of the cluster analysis and have short persistence in the soil. Species belonging to group III, i.e. *Acacia tortilis*, *Crotalaria kirkii*, survivorship patterns in the soil (Fig. 6), and for *Crotalaria kirkii* seeds the pattern is slightly different from the other two groups. Both *Withania somnifera* (from group III) and *Cassia occidentalis* (group II) slightly conform to the exponential seed decay pattern. Group III species have seed coat imposed dormancy in common, and consequently have long-term persistence in the soil.

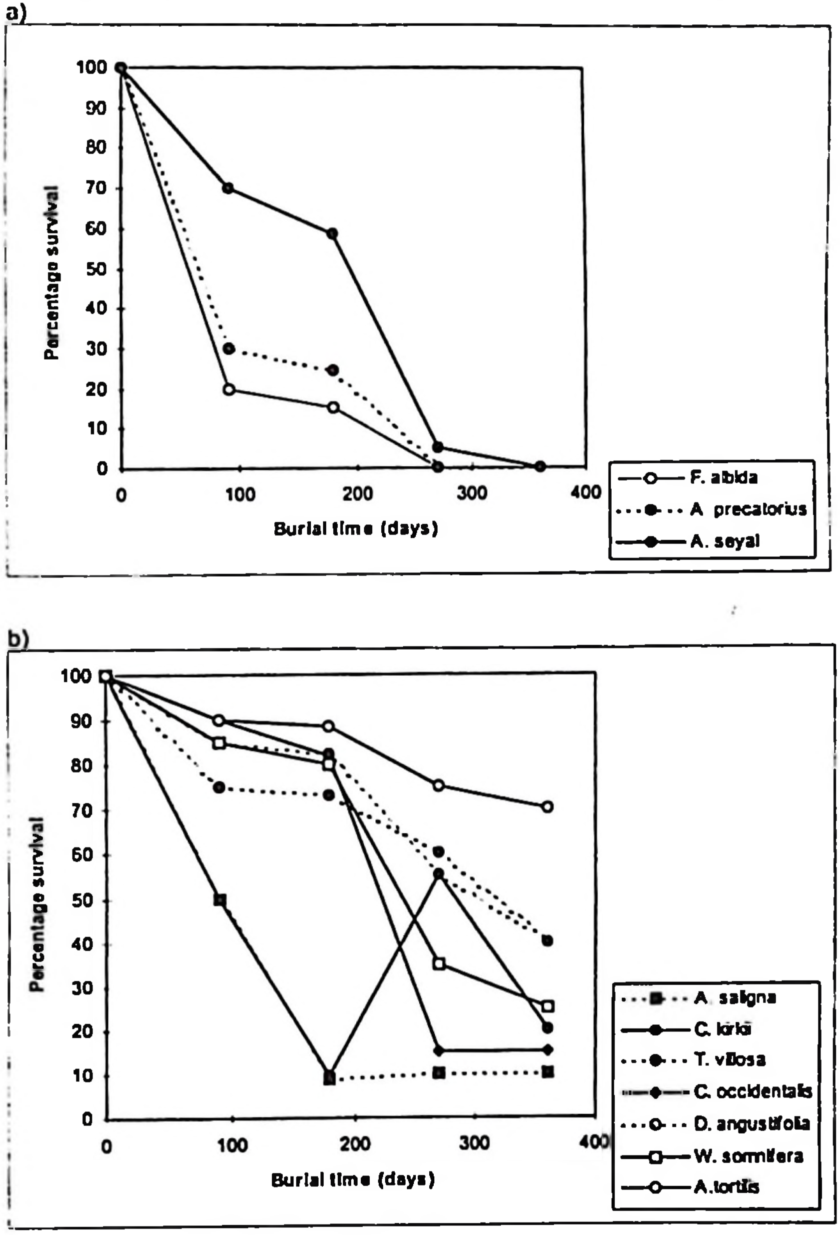

Figure 6. Survivorship curves of group II and group III species. Different species showed variations in their survival patterns, with some few species (i.e. short-lived species) conforming to the theoretical pattern of seed decay. Group I species did not survive burial conditions after three months.

Germination in the greenhouse

For the exhumed viable seeds of group III species (except *Withania somnifera*) to attain 100% germination in the greenhouse, the seeds had to be scarified mechanically. Seeds from most species reached 100% germination after 30 days. All species from group III (Fig. 4) showed intermittent and delayed germination owing to the differential permeability of their seed coats, and the same observation was made for *Cassia occidentalis* from group II.

Discussion

Causes of viability loss

Under natural conditions in the soil, seed longevity is a result of complex interaction between seeds and environmental factors such as light, moisture, temperature, carbon dioxide levels and oxygen (see Villiers 1973, Cook 1980 etc). Lethal or *in situ* germination, which was the most important cause of viability loss among the buried seeds of *Acacia seyal*, *Cassia occidentalis*, *Acacia saligna* and *Faidherbia albida*, is an indication that such seeds have enforced dormancy resulting from water stress, and that they quickly respond to germination in the presence of moisture. Although some seeds of *Cassia occidentalis* germinated promptly, a high proportion of seeds remain ungerminated for long periods of time, emphasizing the presence of individual variations in seed dormancy. Fenner (1985) reported 13% loss of buried seeds of *Bidens pilosa* due to lethal germination. Elsewhere, research has shown that lethal germination could account up to 85% mortality of buried seeds (Schafer and Chilcote 1970). The ecological interpretation of the behaviour of the four species is that they are unlikely to form persistent seed banks and therefore their survival is critically dependent on the longevity of the established vegetation, their annual seed production (O'Connor 1991) and other fates of seeds in the soil such as predation or consumption by ungulates. Environmental conditions strongly determine the recruitment probabilities from seeds among species, and species will respond timely to suitable germination cues. For unpredictable ecosystems such as that in the KIH, this implies that any major catastrophe that eliminates the established plants or untimely germination of seeds, may drive these species to extinction, assuming that no seeds are dispersed into the area.

Other losses due to insect infestation common among *Acacia tortilis*, *Crotalaria kirkii*, *Dodonaea angustifolia* and for all *Acacia* species worldwide (see Kaarakka 1996) have been reported in the literature, where bruchids are the dominant predators (see Ernst et al. 1989, Maxine 1994). The composites that did not survive burial conditions in the soil, i.e. *Abrus precatorius*, *Tephrosia villosa* and *Withania somnifera* succumbed to fungal infection and probably physiological ageing. Excessive soil moisture and high temperatures are conditions that are likely to promote fungal infection and rotting for any seed species.

Seed viability and cluster delimitation in relation to seed dormancy

The more spherical seeds had higher viabilities than elongated seeds, an observation that is in agreement with the hypothesis that seed longevity and possession of long-lived seed banks are properties associated with small and compacted seeds due to their ease of infiltrating into the soil (see Thompson et al. 1993).

Species from group I of the cluster analysis possess seeds without any kind of dormancy. The species are further characterised by production of numerous seeds having dispersal appendages as an adaptation to ensure effective dispersal and successful colonisation.

Seeds from groups II and III possess different levels of dormancy conferred by hard seed coats. Literature indicates that such type of dormancy is common among members of the families Leguminosae, Sapindaceae, Solanaceae, Geraniaceae etc. (see Murdoch and Ellis 1992). Although *Acacia saligna*, *Acacia seyal*, *Cassia occidentalis* and *Faidherbia albida* (group II) are hard-seeded, the fact that they responded to moisture during the rainy season by *in situ* germination implies that seed coat impermeability is not the cause of their delayed germination, but might be due to enforced dormancy imposed by water stress. Egley (1995) reports that in arid environments, for most species, it is rainfall rather than temperature fluctuations which is the most important determinant of seed condition. However, more research is needed to confirm this hypothesis. For group III species, hard-seededness that prevents seed imbibition is one of the regulators of viable seed populations in the soil. Many *Acacia* species are an important source of food for grazing ungulates and browsers during the dry season in savannas, where massive consumption of pods and seeds has been reported (Pellew & Southgate 1984, McNaughton & Georgiadis 1986, Ernst et al. 1989, Mwalyosi 1990, Miller 1994). The extent of removal of pods and seeds may greatly influence the dynamics of viable seeds in the soil. Their persistence in the soil makes this group the most reliable component of rehabilitating degraded savannas.

Germination in the greenhouse

Seeds within the same species in group III showed considerable variations in dormancy and that is why the germination of seeds was spread for more than six months in the greenhouse experiment. For *Cassia occidentalis*, which belongs to group II, having seeds which responded both to prompt germination (typical of group II species) and extended germination, just like group III species, signifies the existence of strong seed-to-seed variations in dormancy among the taxon. Such variations in germination pattern are ecologically important in unstable environments as the fraction of ungerminated viable seeds remaining in the soil serves as an insurance against extinction of species in cases of catastrophic pertubations. In other words, extended germination of seeds in the soil is associated with ability to persist longer in the soil.

Seed bank persistence among *Acacia* species

There is a lot of literature citing the ability of several species of *Acacia* to accumulate large seed banks which may persist for many years in semi-arid areas (see e.g. Milton 1980, Holmes 1989, Tybirk et al. 1994). However, the present study and other previous seed bank studies from the study area do not support these findings. For example, from 120 soil samples of 206 cm^3 each (sampled at 0 - 5 cm depth), studied using soil sieving and sorting technique, only one viable seed of *Acacia tortilis* was found (Skagerlund 1998). From another seed bank study using the seedling emergence method, (Lyaruu & Backéus unpublished data), no single *Acacia* seed was found in any of 540 soil samples of 206 cm^3 each (sampled at 0 - 5 cm depth). Therefore, it follows that, from the very low calculated values of seed half-lifes among *Acacia* species in this study, except for *Acacia tortilis* (Table 3), it is unlikely that *Acacia* seeds may remain viable in the soil for a long time. Both pre- and post-dispersal seed predation have been shown to account for huge losses of seed viability in the study area (Skagerlund 1998). Therefore even in the presence of dormancy among *Acacia* species, their possibility to accumulate large seed reserves in the soil in arid environments is unlikely due to heavy seed predation and severe losses of seeds incurred when pods and seeds are consumed by ungulates.

Conclusions

Presence of hard seed coats in most legumes does not necessarily guarantee seed dormancy among species. I have shown that the hard-seeded *Abrus precatorius*, *Acacia saligna*, *Acacia seyal*, and *Faidherbia albida* germinate promptly in the presence of moisture, indicating that they lack seed coat imposed dormancy. For species whose seeds are heavily predated, this may be interpreted as a survival strategy to avoid predation.

The extended distribution of germination in the soil shown by *Acacia tortilis*, *Cassia occidentalis*, *Crotalaria kirkii*, *Dodonaea angustifolia*, *Tephrosia villosa* and *Withania somnifera*, is explained by seed-to-seed variations in dormancy within the same species. This is an important strategy that prevents pre-emption of the seed bank through synchronous germination and is useful in maintaining uniform populations among species in the vegetation.

The ability of *Acacia* species to accumulate large seed banks in arid environments proposed earlier is doubtful. There is no evidence from the present study or from other previous seed bank studies conducted in the Kondoa Irangi Hills to support the idea that *Acacia* seeds form large persistent seed banks. Observations such as the existence of high levels of seed predation (Skagerlund 1998), relatively high decay rates, and prompt germination of seeds in response to rainfall, eliminate the possibility of seed persistence in the soil in this ecosystem for a long time. Moreover, *Acacia* pods and seeds are important components of the diet of many ungulates during the dry season.

Seed longevity results need to be interpreted cautiously taking into consideration the nature of the ecosystem where the study was conducted in relation to prevailing environmental and soil conditions.

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V

Soil amendments to facilitate regeneration of degraded hill slopes of Kondoa Irangi, central Tanzania

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ABSTRACT

A study was carried out in the degraded Kondoa Irangi Hills, central Tanzania, with an objective of finding out how various soil management practices could be used to improve productivity in this environment. At two sites, experiments were conducted in 1 m x 1 m plots; with fertilization, mulching, imported seed bank, seeding and seedlings as treatments in triplicates. The responses tested were seedling recruitment, total number of species, biomass, mortality, number of perennial species and recruitment of woody species and legumes. There were high significant correlations of 0.85 and 0.87 between seedling recruitment and mortality in both sites, indicating that other factors, probably aridity, rather than prevailing site conditions were likely to be important determinants of mortality. Inorganic fertilization was not an efficient means of improving short-term productivity, seedling recruitment or the number of species. Mulching treatment had an effect of increasing mortality of non-woody species and selectively favoring the establishment of woody species. The interactions between the seeding, seed bank and seedlings treatments increased the overall number of species in the study area. Direct sowing of seeds with desired traits into the soil to enhance seedling recruitment and increase species diversity is recommended over imported seed bank due to the costs involved in moving large volumes of soil as well as availability of proper seed bank soil. In oligotrophic savanna soils, nutrient-deficiency should be corrected naturally by fires and herbivores due to (1) high costs

associated with fertilization and (2) the deleterious effects of fertilizers to the soil.

INTRODUCTION

This study deals with degraded Kondoa Irangi Hills (hereafter called KIH) in central Tanzania where former land use practices resulted in severe soil erosion leaving some parts of the hills beyond recovery. The regeneration process in the hills has been very slow, considering a period of 25 years since activities such as grazing, tree-felling and hill slope cultivation were abandoned. Depending on the level of degradation, both primary and secondary succession proceed simultaneously in different parts of the hills. In principle, regeneration succession in severely degraded habitats generally begins with dispersal and establishment from seed of one or a few fast growing annual or perennial species. The further development is dependent on the outcome of three possible plant interactions, namely facilitation, competition and tolerance (Connell & Slatyer 1977). In facilitation, (see e.g. Glenn Lewin et al. 1992), first plants to be established in a site (also known as pioneer nurse plants) modify the microenvironment in such a way that it becomes more suitable for later successional species, which finally replace the pioneers. Contrary to this pattern, secondary succession often involves replacement of pre-existing vegetation following disturbance from its own seed or seedling bank. Disturbances influence the succession process by changing the levels of resources available and the efficiency of recruitment, and their magnitude will determine the succession path.

Another important factor which pre-determines the course of succession is whether the disturbance was accompanied by deterioration of soil quality, soil/water conditions and the microclimate. In savannas, availability of water is known to be the most important factor that governs the structure and functioning of the ecosystem (Noy-Meir 1982; Skarpe 1992), which is in turn dependent on soil properties. In such ecosystems, grasslands do not develop into second-growth forest because of frequent fires and the stiff competition for light tree seedlings face from established grasses (Ashton et al. 1997).

Degraded savanna ecosystems are in most cases characterized by soils of very low fertility (Högberg 1992), and most soil nitrogen exists in organic form which is not readily available to plants. Moreover, in semi-arid regions, nitrogen mineralization is limited by dry conditions (Booysen & Tainton 1984) and low levels of phosphorus (Högberg 1992); and therefore nitrogen fertilization may be essential to correct nutrient deficiencies in these soils. The importance of dryland fertilization is that it promotes root development so that soil water is used to greater depth, an advantage to woody species succession over grasses (Smith & Shackleton 1988). However, in drylands, the significance of fertilization on productivity is dependent on the balance between need and supply at critical phases of growth, and on the duration of soil water availability which is determined by the rainfall distribution.

Several approaches have been used to manipulate regeneration process in various environments to include nitrogen fertilization (Sandhu et al. 1992; Wilson & Gerry 1995; Chapman & Younger 1995), mulching (Smith & Shackleton 1988; Larsson et al. 1997), application of seed mixtures (Marquez & Allen 1996), planting seedlings (Whisenant et al. 1995, Gupta & Singh 1997) and enrichment of the soil with diaspores from imported seed bank.

Organic mulches are effective in improving soil moisture storage, thermal insulation, protection of the soil surface thereby improving infiltration and decreasing runoff as well as adding to the fertility of the soil (Bautista et al. 1996). Mulching is reported to increase the water-use efficiency of seedlings (Smith & Shackleton 1988), and to reduce soil surface crusting, thereby promoting seedling establishment (Hien et al. 1997). With termite activity, mulching is also known to improve humidification and water conservation in crusted soils of semi-arid regions (Mando et al. 1996).

Apart from altered nutrient levels, degraded savanna ecosystems are impoverished of seeds, and in the succession process, supplementing with seeds from other sources may be necessary. In some cases, seedlings have been planted in order to speed up the succession process (see e.g. Mbegu & Mlenge 1984). It has been shown that isolated trees and shrubs in savanna soils create fertile microsites in their vicinity (see Belsky et al. 1989; Vetaas 1992) which improve other ecosystem processes.

Objectives of the study

We assumed that regeneration succession in a landscape will result in an increased recruitment of individuals, particularly the perennial species and overall productivity. Specifically we wish to explore the possibility of speeding up the regeneration process in the hills by using different treatments such as fertilization, mulching, imported seed bank, seeding, seedlings and their combinations, and evaluate their effects on seedling recruitment, mortality, productivity, woody species recruitment as well as legumes. Finally, we wish to suggest a model that fits best the vegetation recovery exercise of the KIH. A good model in this case is the one which will maximize seedling recruitment, seedling survivorship and productivity and increase species diversity and the domination of perennial species.

Historical background and location of the study area

The KIH in central Tanzania have a long history of land degradation (Christiansson et al. 1991; see further Backéus et al. 1994; Lyaruu 1995). As a typical savanna ecosystem, KIH vegetation experiences one long rainy season every year, when phytomass accumulates to the maximum, followed by a prolonged period of drought which creates very harsh conditions and eventually the grass layer may burn. The average precipitation of KIH is 600 - 800 mm (Ngana 1992), but it exceeds 1000 mm in much more elevated parts of KIH.

The problem of land degradation in the hills started ca. 150 years ago when the Rangi people settled in the area. The main factors assumed to have caused land degradation in the hills included excessive tree cutting, uncontrolled grazing, hill slope cultivation and periodic fires all of which had a combined effect of depriving the soil of vegetation cover and making it more susceptible to sheet and gully erosion. Attempts to save the hills from further land degradation started with the formation of Hifadhi Ardhi Dodoma (HADO) or Soil Conservation Programme in Dodoma in 1973, a governmental organization responsible for reclamation of degraded semi-arid lands in the region. Among the measures taken by this organization to prevent further land degradation in KIH were (1) complete de-stocking of the hills in 1979, (2) ban on hill slopes cultivation, (3) introduction of stall-feeding practices, and (4) introduction of ecological engineering practices such as terracing, contour banding and tree planting.

At present, some parts of KIH vegetation have recovered sufficiently (see Backéus et al. 1994), but in others the process is still very slow.

Nomenclature follows the Flora of Tropical East Africa (Turrill & Milne-Redhead 1952-) for families treated therein, and Flora Zambesiaca (Exell & Wild 1960-) for other families.

MATERIAL AND METHODS

The experiment commenced in the field in KIH in March 1995 and was monitored up to December 1997. Two sites, Chakwe and Gubali, with different vegetation types and site characteristics were selected (see Table 1). The criterion used to select the sites was the homogeneity of the vegetation.

Table 1. Comparison of environmental attributes at the two sites studied. For soil analysis results, means ± s.ds ($n = 8$) are given. Differences between means are tested with a t- Test for pairwise comparison; and ns stands for not significant; * significant at $p < 0.1$; ** at $p < 0.05$ and *** at $p < 0.01$

Attribute	Chakwe	Gubali	t-value	significance
1. Moisture factor (%)	0.208 ± 0.008	0.508 ± 0.008	7.65	***
2. Soil texture (%)				
a) Gravel	34.30 ± 16.27	0.03 ± 0.02	9.83	***
b) Sand	62.14 ± 15.46	90.99 ± 0.71	6.95	***
c) Silt	2.89 ± 0.79	7.74 ± 0.42	8.04	***
d) Clay	0.32 ± 0.08	1.25 ± 0.43	15.14	***
3. Organic matter (%)	0.97 ± 0.21	1.73 ± 0.22	11.16	***
4. Hydrogen ion conc. (pH)	5.64 ± 0.01	6.11 ± 0.01	2.99	**
5. Exchangeable bases (Meq/100g soil)				
a) Ca^{++}	2.75 ± 0.58	5.19 ± 0.99	6.65	***
b) Mg^{++}	1.16 ± 0.07	2.91 ± 0.52	16.97	***
c) K^{+}	0.79 ± 0.32	1.79 ±0.46	10.72	***
d) Na^{+}	0.063 ± 0.008	0.078 ± 0.013	9.44	***
6. Cation exchange capacity (Meq/100g soil)	17.77 ± 2.64	19.83 ± 3.11	1.37	ns
7. Available phosphorus (mg/100g soil)	2.34 ± 0.32	2.76 ± 0.34	2.24	**
8. Total nitrogen (%)	0.08 ± 0.02	0.08 ±0.01	0	ns
9. Others				
a) Slope $^{(0)}$	10	5		
b) Altitude (m)	1530	1620		

The Chakwe site is characterized by shallow unmineralized soils, whereas Gubali site has deeper red soils. For comparison of other soil parameters refer to Table 1. The Chakwe site has been described as grassland on disturbed soil in Backéus et al. (1994) and Gubali is a grassland vegetation on transition to woodland (Lyaruu in press). Soil analysis and biomass determination were done in the laboratory at the University of Dar Es Salaam. In this study "site" refers to the area where the study was conducted and not the experimental plot only.

Experimental layout and design

A factorial design experiment in which five treatments and their combinations were replicated three times in a systematic manner in each site was conducted. For each site a total of 50 1m x 1m plots were established, 45 being treatment plots and 5 left without treatment to serve as controls. Before the experiment started, the sites were tilled and all plant material removed. The plots were fenced to exclude interference from people and wildlife, and fire breaks were created to protect the experimental plots from fire, which did not occur during the period of study. The treatments were applied only once at the beginning of the experiment. The treatments and their combinations were as follows: fertilization (coded FE throughout the text), mulching (MU), imported seed bank (SB), seeding (SD) and seedlings (SDL). Thus a combination of seed bank and mulching is denoted as SB + MU. In fertilization treatments, 100 g of inorganic fertilizer NPK (20% nitrogen, 10% phosphorus and 10% potassium) was applied once. Imported soil seed bank ca. 7 dm^3 (assuming bulky density of soil to be 1.5 g/cm^3) was thoroughly mixed with soil from seed bank experimental plots, and was evenly spread in each plot. A sufficient amount of mulch collected from seed-free broad leafed herbs and trees in the vicinity was applied to cover the mulched plots. For the seeding treatment, 20 seeds each from the five species *Acacia tortilis*, *Acacia saligna*, *Dodonaea angustifolia*, *Khaya nyasica* and *Psoropsis juliflora* were added to each plot. Both seeds and seedlings used in this experiment were obtained from the government nursery in Kondoa; only two seedlings were planted in order to minimize competition. Both the seeding and seedlings treatments utilized indigenous, exotic and naturalized species known to adapt well in arid environments. The exotic and naturalized species used were *Acacia saligna*, *Parkinsonia aculeata*, and *Psoropsis juliflora*, and the rest were the common indigenous species of savannas. Due to scarcity of seedlings from the nursery, only seedlings of *Acacia tortilis*, *Faidherbia albida*, and *Parkinsonia aculeata* were used.

In all plots, all emerging individuals were identified, counted and recorded in the first data collection after 3 months. In the subsequent recordings, species presence and/or absence were noted as well as new species unrecorded previously. Data were collected five times during the period of study, to include three rainy and three dry seasons. Species difficult to identify in the field were identified from available herbarium specimens and floras.

A total of four soil samples from each site were collected randomly at the beginning of the experiment from the untreated plots at a depth of 0 - 10 cm for laboratory analysis of soil texture, pH, total nitrogen (Kjeldahl), cation exchange capacity by displacing exchangeable cations following the procedures outlined in Metson (1956) and Tucker (1974).

Upon termination of the experiment, destructive sampling of dead and living plant material to include litter from each experimental plot was done for biomass determination. To minimize decomposition of the harvested material, pre-drying commenced in the field by spreading the material in the open air. The material was stored in plastic bags and transported to Dar Es Salaam, where it was carefully spread on newspapers in the greenhouse with mean temperature of $34 \pm 5\ ^0$C and dried to constant mass.

Data analysis

The data were more or less normally distributed and were therefore subjected to parametric statistical tests. Only the number of woody species were log-transformed using the relation $y' = \log_{10}(y + 1)$.

The GLM procedure for analysis of variance (ANOVA)

All statistical analyses were done using SAS statistical package (SAS Institute Inc. 1990). Seven responses were tested i.e. total seedling number, total species number, mortality (% of recruited seedlings), dry matter (biomass) production, number of perennial species, legumes recruitment and number of woody species. The sites were compared using paired t-tests and one way ANOVAs. The GLM procedure for multiple regression (SAS Institute Inc. 1990), was used to detect partial correlation and statistical differences ($p < 0.05$) between treatments and the dependent variables. Since the experiment did not have a full factorial design, only the main factors and their first order interactions were studied using the SAS GLM procedure for analysis of variance. When significant differences were found, ($p < 0.05$), Tukey's Studentized Range (HSD) Test was applied.

Multivariate analysis

In order to study the differences and similarities between treatments and their responses, multivariate analysis using the corrected version of the program CANOCO (ter Braak 1988-92) by Oksanen & Minchin (1997) was used and each site was treated separately. PCA was performed using species x treatment matrix. For the external variables, another matrix with information on seedling recruitment, mortality, total number of species recruited and biomass production x treatments was used.

Hierarchical clustering of the groups was performed using the program MINITAB version 10XTRA (1995) for dendrograms.

RESULTS

Results from treatments applied in this study and their interactions with site responses to overall seedling recruitment, mortality, number of species recruited and biomass are presented in Table 2.

Correlation between the dependent variables

Correlation analysis results for the two sites are presented in Tables 3a & b. In both sites, seedling recruitment and mortality showed highest significant positive correlation (0.85 and 0.87 for Chakwe and Gubali respectively). Seedling recruitment was positively correlated to the total number of species in both sites. For Gubali, there was a very significant positive correlation ($p < 0.001$) between total number of species recruited and woody species, and for Chakwe the number of species and mortality had significant positive correlation ($p < 0.001$).

Site comparison in responses

For all responses, only results from type I sum of squares ANOVA are used. Type I sum of squares explain better the results than type III sum of squares since there was no correlation between factors. Secondly, the order of entering the factors in the model did not influence the

Table 2. Summarized data showing the responses of the two sites (index 1 for Chakwe & 2 for Gubali) in terms of seedling recruitment, mortality, number of species recruited and biomass against the treatments applied. Mean (s.d.) of three replicates are included. SB stands for imported seed bank; MU for mulching; FE for fertilization; SD for seeding; SDL for seedlings and CONTR for untreated plots

Factor(s)	Seedling recruitment	Mortality	Species	Biomass(g.)
1. SB$_1$	372.3(4.1)	200.3(34.5)	10.0(1.4)	438.7(167.0)
SB$_2$	165.3(64.8)	79.3(35.0)	8.7(0.9)	141.3(86.0)
2. SB+MU$_1$	344.3(70.2)	226.0(79.0)	12.7(2.5)	363.0(15.0)
SB+MU$_2$	174.3(90.8)	116.7(81.3)	9.7(3.4)	165.7(141.7)
3. SB+FE$_1$	244.0(67.1)	131.3(46.0)	9.0(2.9)	325.7(112.5)
SB+FE$_2$	143.3(31.6)	59.3(2.6)	9.7(1.7)	105.5(84.5)
4. SB+SD$_1$	358.3(20.9)	247.0(34.2)	11.0(1.6)	434.7(83.8)
SB+SD$_2$	156.7(30.2)	54.6(6.1)	12.7(1.7)	117.0(11.4)
5. SB+SDL$_1$	365.7(112.9)	232.0(78.5)	12.7(1.7)	329.3(55.0)
SB+SDL$_2$	141.3(27.5)	70.3(26.0)	9.0(1.4)	159.3(116.5)
6. MU$_1$	344.0(75.4)	217.7(37.2)	11.7(2.9)	469.0(161.2)
MU$_2$	189.3(26.2)	99.0(42.2)	11.3(0.5)	141.3(34.4)
7. MU+FE$_1$	273.7(28.7)	168.7(18.4)	11.3(2.9)	433.3(205.0)
MU+FE$_2$	118.7(42.1)	62.7(26.9)	9.3(0.5)	76.0(13.4)
8. MU+SD$_1$	264.0(55.0)	164.7(34.0)	8.0(0.0)	391.7(184.9)
MU+SD$_2$	267.3(57.0)	168.0(37.4)	9.3(2.1)	170.0(79.7)
9. MU+SDL	268.3(45.6)	192.3(22.4)	9.0(0.8)	387.3(157.9)
MU+SDL	148.3(14.6)	91.3(18.7)	9.0(1.6)	236.7(130.8)
10. FE$_1$	232.3(45.1)	118.7(49.4)	10.3(1.7)	284.0(50.8)
FE$_2$	79.0(10.2)	42.0(14.4)	7.7(1.7)	71.0(36.3)
11. FE+SD$_1$	263.7(46.9)	152.0(73.4)	9.7(2.6)	452.0(104.3)
FE+SD$_2$	124.3(38.1)	67.7(9.3)	9.0(1.4)	207.3(85.9)
12. FE+SDL$_1$	262.7(54.0)	148.3(60.3)	10.0(3.7)	379.7(61.8)
FE+SDL$_2$	104.0(26.7)	48.0(16.8)	9.7(2.5)	218.7(222.3)
13. SD$_1$	330.7(74.0)	227.3(87.4)	10.7(2.5)	317.0(118.9)
SD$_2$	164.3(60.4)	93.3(29.8)	8.7(1.2)	205.7(124.8)
14. SD+SDL$_1$	318.7(68.2)	185.0(72.9)	11.7(0.5)	310.3(146.0)
SD+SDL$_2$	154.7(32.1)	77.7(23.9)	11.7(0.9)	165.3(69.6)
15. SDL$_1$	315.3(42.1)	181.0(63.8)	11.0(2.4)	241.7(56.2)
SDL$_2$	159.3(38.4)	95.3(27.6)	9.7(1.2)	135.6(51.1)
16. CONTR$_1$	246.0(67.3)	155.3(40.8)	11.7(1.9)	248.0(28.4)
CONTR$_2$	94.0(13.9)	36.6(5.0)	9.0(1.4)	98.7(26.9)

final probabilities or their significance levels. The overall model used in the analyses predicted quality of the site as the most important factor which accounted for variations in seedling recruitment, total number of species, mortality, biomass production and woody species recruitment (Table 4). The Chakwe and Gubali sites responded differently to various treatments and they differ in their recruitment ability, survivorship and biomass production. The two sites were significantly different in terms of total number of species recruited ($F_{(1,30)} = 51.5$, $p < 0.001$), seedling recruitment ($F_{(1,30)} = 494.2$, $p < 0.0001$), dry matter production ($F_{(1,30)} = 156.1$, $p < 0.0001$), life forms, woody species domination and survivorship (see also Tables 3a & b, Fig. 1). Whereas site 1 had the highest seedling and species recruitment, biomass and mortality, site 2 had the lowest mortality ($F_{(1,30)} = 12.75$, $p < 0.005$) among the seedlings recruited and highest recruitment of woody species ($F_{(1,30)} = 32.47$, $p < 0.0001$). The sites showed no significant differences in the recruitment of legumes, and there was no factor or any of its combination which significantly influenced recruitment of legumes at the two sites.

Table 3. Correlation analysis results of the dependent variables. Only variables with significant correlations ($p < 0.05$) are considered. Recruitment stands for overall seedling recruitment; turnover stands for total number of species recruited; perennial species for the number of perennial species and woody species for the number of woody species recorded

Factors	Pearson's Correlation Coefficient [r]	P
a) Chakwe		
1. Recruitment vs Mortality	0.85	0.0001
3. Recruitment vs Turnover	0.47	0.0007
4. Turnover vs Mortality	0.38	0.0071
5. Turnover vs Biomass	0.29	0.0447
6. Turnover vs Perennial species	0.31	0.0346
7. Perennial species vs Woody species	0.31	0.0298
b) Gubali		
1. Recruitment vs Mortality	0.87	0.0001
2. Recruitment vs Turnover	0.39	0.0050
3. Recruitment vs Biomass	0.39	0.0057
4. Turnover vs Woody species	0.38	0.0080
5. Mortality vs Biomass	0.40	0.0051
6. Perennial species vs Woody species	0.49	0.0004

Main factors with significant responses

FE and SB treatments were complimentary to each other in overall seedling recruitment and total number of species, with FE treatment having negative influence. They also differed in that FE treatment in addition decreased mortality and the number of perennial species (Table 4).

Table 4. ANOVA testing effects of fertilization, mulching, seed bank, seeding and seedlings and their interactions on seedling recruitment, total number of species, mortality, biomass production, woody species recruitment, legumes recruitment and perennial species recruitment. Only significant factors [Tukey's Studentized Range (HSD) Test] and interactions are shown. Degrees of freedom (df) error = 77, Model df = 18 for all responses

Source of variation	df	F	P	Result/Effect
		Seedling recruitment		
FE	1	12.14	0.0008	-
SB	1	7.94	0.0061	+
SITE	1	171.59	0.0001	SITE 1 > SITE 2
MUxSB	1	4.79	0.0316	+
		Mortality		
MU	1	6.66	0.0117	-
FE	1	10.43	0.0018	-
SITE	1	111.88	0.0001	SITE 1 > SITE 2
		Total number of species		
FE	1	6.41	0.0134	-
SB	1	14.68	0.0003	+
SD	1	7.26	0.0086	+
SITE	1	88.24	0.0001	SITE 1 > SITE 2
MUxSDL	1	4.92	0.0295	-
		Biomass production		
SITE	1	47.72	0.0001	SITE 1 > SITE 2
		Number of perennial species		
FE	1	4.93	0.0293	-
MUxSD	1	4.06	0.0474	-
		Number of woody species		
SD	1	4.87	0.0303	+
SB	1	4.11	0.0460	+
SITE	1	7.99	0.0060	SITE 2 > SITE 1

In terms of seedling establishment, FE significantly increased survivorship of seedlings, whereas the effect of mulching was to increase seedling mortality only at Gubali, (Table 5). At Chakwe, FE treatment alone decreased seedling recruitment by ca. 20%, but at Gubali the decrease was even much higher to ca. 27%. SB treatment increased seedling recruitment and the number of species in both sites (Table 5). Both SD and SDL treatments were more important to Gubali site than to Chakwe site in that they increased woody species recruitment and the turnover of perennial species. This finding reflects on the differential capabilities of the two sites of seedling recruitment and successful establishment from seed.

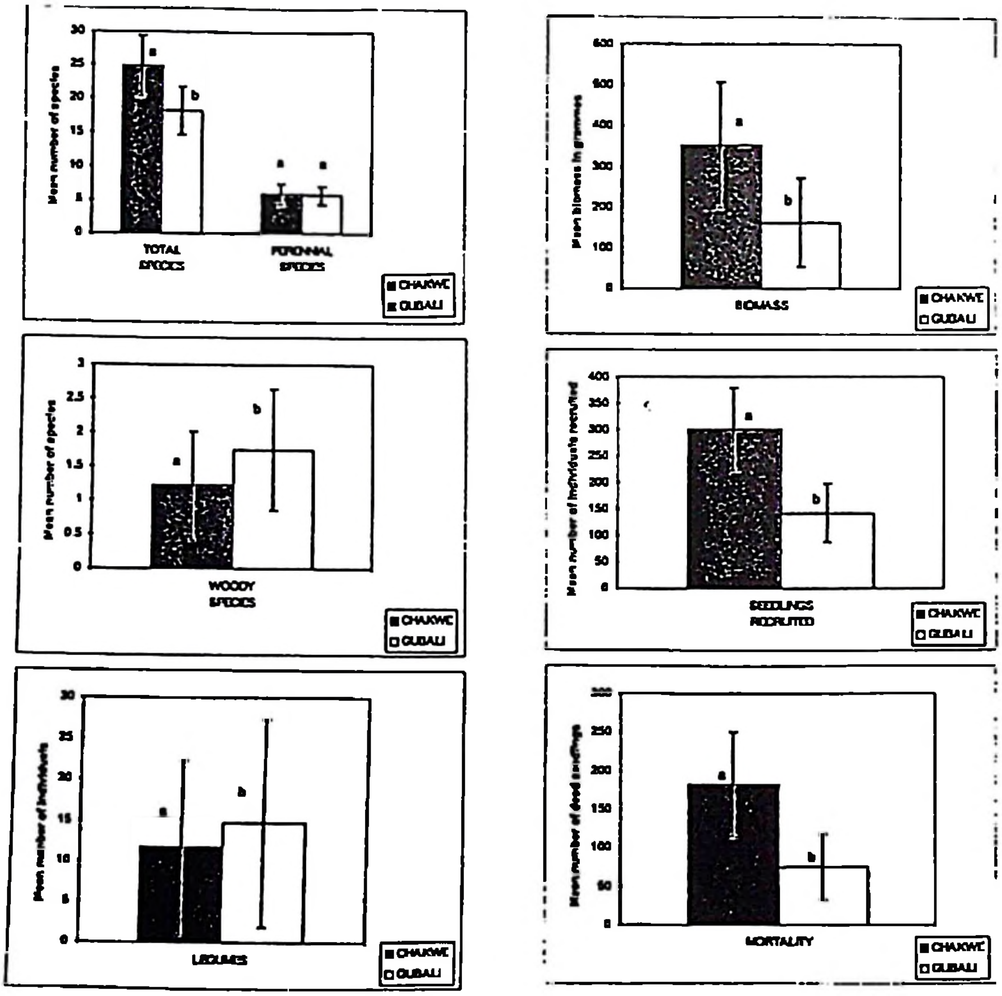

Figure 1. Site comparison (mean ± s.d.) of the responses to treatments. With exception of the number of legumes recruited and perennial species, all attributes compared are significantly different (Tukey's Studentized Range (HSD) Test & paired t-test, and are indicated by two different letters.

Table 5. Overall treatment effect of factors at two levels (i.e. present = 1, absent = 0) on seedling recruitment, total number of species, mortality, number of woody species and number of perennial species. Statistical analyses consists of one-way ANOVA, followed by Tukey's Studentized Range (HSD) Test among treatments. Mean values designated with the same letter are not significantly different ($p < 0.05$). Only factors with statistically different means from at least one site are considered. Site 1 = Chakwe & site 2 = Gubali

Factor	Level	Site 1	Site 2	(Sites 1 + 2)
		Seedling recruitment		
FE	0	321.2±77.5a	155.6±57.0a	238.4±67.3a
FE	1	256.3±57.1b	113.2±40.6b	133.8±48.9b
SB	0	284.5±68.6a	135.8±54.1a	210.2±61.4a
SB	1	337.1±85.3b	156.7±57.0b	246.9±71.8b
		Total number of species		
FE	0	25.9±4.43a	18.6+3.7a	22.3±4.04a
FE	1	22.5±3.8b	17.4±3.3a	20.0±3.5b
SB	0	23.9±4.4a	17.4±2.9a	20.6±3.6a
SB	1	27.0±4.1b	20.1±4.2b	23.6±4.2b
SD	0	24.1±4.5a	17.9±3.8a	21.0±4.1a
SD	1	26.5±4.2b	19.0±3.0a	22.8±3.6b
		Mortality		
FE	0	199.8±64.7a	83.8±47.4a	141.8±56.1a
FE	1	144.3±59.8b	55.3±20.5b	99.8±40.2b
MU	0	176.4±73.7a	64.9±29.4a	120.7±51.6a
MU	1	195.6±52.1a	96.9±58.6b	146.3±55.4b
		Number of woody species		
SDL	0	1.3±0.9a	1.6±0.8a	1.4±0.9a
SDL	1	1.1±0.7a	2.1±1.1b	1.6±0.9a
SD	0	1.2±0.8a	1.5±0.9a	1.4±0.9a
SD	1	1.2±0.9a	2.3±0.9b	1.7±0.9a
SB	0	1.1±0.8a	1.7±1.0a	1.4±0.9a
SB	1	1.6±0.8a	1.9±0.9a	1.8±0.9b
		Number of perennial species		
SDL	0	5.9±1.5a	5.5±1.3a	5.4±1.4a
SDL	1	5.9±1.5a	6.4±1.4b	6.2±1.4a
FE	0	6.2±1.5a	6.0±1.4a	6.1±1.5a
FE	0	5.5±1.5a	5.2±1.1b	5.3±1.3b

Significant interactions

The combination of MU and SB significantly increased total seedling recruitment in the study area as revealed by the significant interaction (Table 4).There was a significant reduction in the total number of species recruited by the interaction between MU and SDL (see Table 4). Likewise interaction between MU and SD reduced the number of perennial species recruited. By treating the two sites independently, SB x SDL interaction enhanced the recruitment of perennial species at Gubali, and SDL x SD interaction increased species diversity at Chakwe (Table 6). This implies that SDL treatment is important means of increasing species diversity of the study area.

Table 6. ANOVA results comparing responses Chakwe and Gubali sites to fertilization, mulching, seed bank, seeding and seedlings effects with their interactions on seedling recruitment, total number of species, mortality, biomass production, woody species recruitment, legumes recruitment and number of perennial species. Only factors and interactions which are significantly different are shown. Degrees of freedom (df) error = 32, Model df = 15 for all responses

Site	Source of variation	df	F	P	Effect
		Seedling recruitment			
SITE 1	FE	1	5.91	0.0209	-
	SB	1	5.14	0.0303	+
SITE 2	FE	1	3.86	0.0583	-
		Mortality			
SITE 1	FE	1	4.84	0.0352	-
SITE 2	MU	1	5.96	0.0204	+
		Total number of species			
SITE 1	FE	1	7.92	0.0083	-
	SB	1	8.00	0.0080	+
	MUxSD	1	7.38	0.0106	-
	SDxSDL	1	10.83	0.0024	+
SITE 2	SB	1	6.02	0.0198	+
		Number of woody species			
SITE 2	SD	1	11.64	0.0018	+
		Number of perennial species			
SITE 2	SDL	1	4.45	0.0428	+
	SBxSDL	1	7.67	0.0093	+
	FE	1	4.13	0.0504	-

Multivariate analysis

In both sites, axes 1 & 2 in the PCA (Figs. 2a & b) accounted for observed differences in terms of seedling recruitment, total species number, mortality and biomass production. Seedling recruitment is explained by axis 2 at Chakwe (eigenvalue: 0.19) and axis 1 at Gubali (eigenvalue: 0.67). Mortality is explained by axis 1 at Chakwe (eigenvalue: 0.49) and by axis 3 at Gubali (eigenvalue: 0.086), and total species number is accounted more by axis 2 at Chakwe and by axis 1 at Gubali. Seedling recruitment increased with introduction of seed bank, seeding and by planting seedlings, results which are confirmed by ANOVA (see Tables 4, 5 & 6). Biomass increased at Gubali when planted seedlings were mulched, but it was fertilization and seeding which increased biomass at Chakwe. These results are accounted by site differences in terms of mineralization and seed dynamics. Species which are associated with different treatments in both sites from ordination results are summarized in Figs.2a & b.

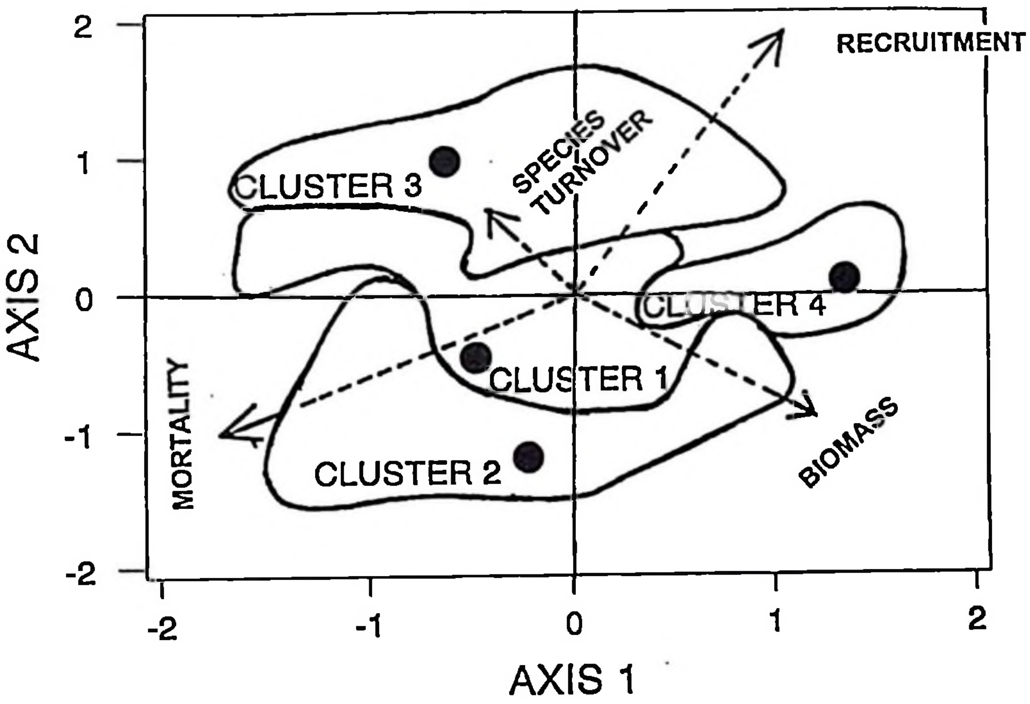

Figure 2a. Position of clusters as derived from species associations with treatments of axes 1 and 2 in the PCA diagram for Chakwe site. CLUSTER 1 (associated with seed bank treatments with strong influence on all variables)- *Vernonia perrottetii*, *Polygala erioptera*, *Triumfetta dekinditiana*, *Aloteropsis cimicina*, *Rhus natalensis*, *Tridax procumbens*, *Tephrosia villosa*, *Thunbergia alata*, *Crabbea velutina*, *Solanum incanum*, *Oxygonum sinuatum*, *Eragrostis congesta*, *Ormocarpum kirkii*, & *Laurnea cornuta*. CLUSTER 2 (associated with mulching and fertilisation with strong influence on biomass and mortality)- *Tephrosia pumila*, *Indigofera volkensii*, *Bulbostylis burchellii*, *Crotalaria microcarpa*, *Heteropogon contortus*, *Microchloa kunthii*, *Blepharis affinis*, *Schizachryium sanguineum*, *Harpachne schimperi*, *Senecio abyssinica*, & *Setaria sphacelata*. CLUSTER 3 (associated with seeding and seedlings with strong influence on species turnover and recruitment)- *Stylosanthes fruticosa*, *Indigofera cuneata*, *Wahlenbergia denticulata*, *Pogonarthria squarossa*, *Portulaca oleracea*, *Polygala liniflora*, *Sessamum angustifolium*, *Cassia mimosoides*, *Aristida adoënsis* & *Hyparrhenia filipendula*. CLUSTER 4 (associated with fertilisation and seeding influencing strongly biomass)- *Rhynchelytrum repens*, *Acacia senegal*, *Acacia seyal* & *Spermacoce senensis*.

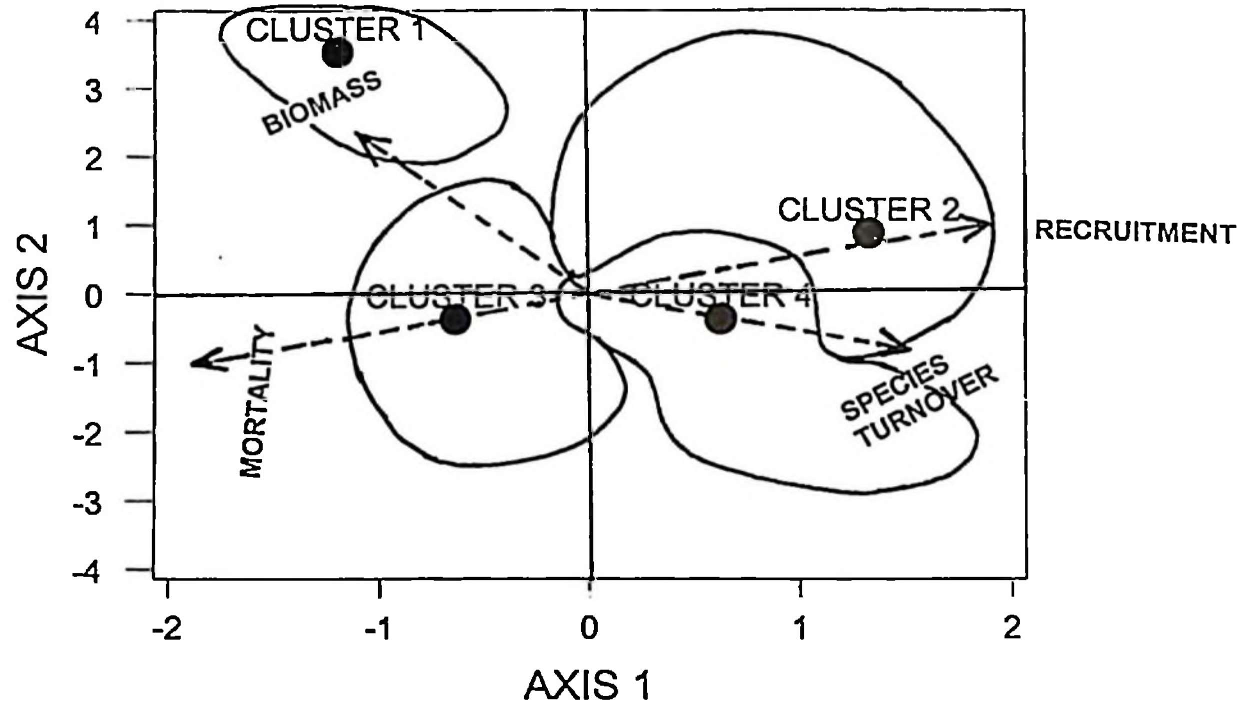

Figure 2b. Position of clusters as derived from species associations with treatments of axes 1 and 2 in the PCA diagram for Gubali site. CLUSTER 1 (associated with seed bank and mulching with strong influence on biomass)- *Stylosanthes fruticosa* & *Senecio abyssinica*. CLUSTER 2 (associated with seeding and seedlings with strong influence on recruitment and species turnover)- *Indigofera cuneata*, *Wahlenbergia denticulata*, *Triumfetta dekindítiana*, *Digitaria rivae*, *Rhynchelytrum repens*, *Hyparrhenia filipendula*, *Bulbostylis burchellii*, *Kohautia coccinea*, *Vernonia poskeana*, & *Waltheria indica*. CLUSTER 3 (associated with fertilisation and mulching and strongly influencing mortality and biomass)- *Dodonaea angustifolia*, *Triumfetta rhomboidea*, *Cassia mimosoides*, *Tephrosia villosa*, *Sporobolus panicoides*, *Spermacoce senensis*, *Harpachne schimperi*, *Laurnea cornuta*, *Psychotria kirkii*, *Hirpicium diffusum*, *Acacia saligna*, *Faidherbia albida*, *Aeschynomene abyssinica*, *Indigofera astragalina*, *Heteropogon contortus*, *Emilia javanica*, *Crotalaria iringana*, *Aristida adoēnsis*, *Vernonia glabra*, *Monsonia angustifolia*, *Cyperus rotundus* & *Ormocarpum kirkii*. CLUSTER 4 (associated with seeding and fertilisation with strong influence on species turnover)- *Crotalaria bernieri*, *Acacia tortilis*, *Pogonarthria squarossa*, *Eragrostis congesta*, *Spermacoce chaetocephala*, *Oxygonum sinuatum*, *Tephrosia pumila*, *Crotalaria cylindrostachys*, *Zornia glochdiata*, *Schizachryium sanguineum*, *Crotalaria tenuirostrata* & *Zornia setosa*.

DISCUSSION

Limitation of the results

The time lag between successive data collections could have influenced overall results. Some plant species found in this area such as *Biophytum abyssinica, Cassia mimosoides and Iphigenia oliveria* etc. are ephemerals and could have germinated and died before they could be counted. As an example, *Iphigenia oliveria* takes less than three weeks to complete its life cycle. Another problem was that it was difficult to ascertain whether an individual recorded in the previous data (especially among the perennial grasses) was the same which was recorded in the subsequent data.

Seedling recruitment and total number of species

The differences in seedling recruitment and survivorship between Chakwe and Gubali sites can be explained in terms of seed dynamics of the KIH ecosystem. Previous research (Lyaruu in press) indicates that grassland sites at Chakwe had much higher seed rain density than Gubali site (1667 and 230 seeds/m^2 over 8 months period respectively). The seed bank density is also higher at Chakwe (2185 seeds/m^2) than at Gubali (1842 seeds/m^2). The seed bank is more diverse at Gubali than at Chakwe (11.5 ± 2.5 and 8.7 ± 3.95 species respectively). The implication is that for some areas which are still in the early stages of recovery, seed bank enrichment may be an appropriate solution to increase species diversity. The presence of many seeds which readily germinate in response to amenable conditions during the rainy season, account for higher seedling recruitment at Chakwe. The significantly higher mortality recorded at Chakwe than at Gubali can be explained in terms of increased competition for nutrients, light, space and probably less favorable soil conditions for establishment (see Table 1) among the seedlings. The very high positive correlation between seedling recruitment and mortality in both sites (0.85 and 0.87) suggests that soil moisture availability in the study area accounts for seedling mortality rather than site conditions. Establishment from seed seems to be more difficult at Chakwe than at Gubali, where no seedling (i.e. from seeding treatment) survived to be enumerated at least twice. On the other hand, most seedlings from the seeding treatment at Gubali and the transplants survived for a much longer time; and seedlings of *Acacia saligna* grew 1.5 m high during the period of study.

Treatment effects and their relevance to succession

Inorganic fertilization is not an efficient means of improving short term productivity, seedling recruitment and increasing species number in the study area. Instead, fertilization increases the potential for environmental stress by limiting water availability and consequently increasing mortality among the individuals recruited. In some occasions fertilization may prove useful especially if combined with other treatments such as seeding, but still not a useful means of manipulating regeneration. Importantly, fertilization is deleterious to soil quality because it depletes the soil organic matter, the reservoir of plant available nitrogen and phosphorus in weathered tropical soils (Goladi & Agbenin 1997).

Mulching is a useful treatment which increases seedling recruitment and total number of species and biomass, especially when combined with seed bank. Mulching applied alone has an effect of increasing mortality of the non-woody species but increase survivorship among woody species. For KIH ecosystem, this is desirable especially when the ultimate goal is to restore the original woody vegetation. In the study area, addition of imported seed bank, is an effective means of increasing species and seedling recruitment, regardless of the nature of the site.

Two models or statements can be proposed on the manipulation of regeneration process of the two sites studied based on results obtained in this study:

1) For early succession category, which includes areas where the disturbance agents are still operative such as the Chakwe site, it is desirable to enhance recruitment of woody species and perennial species in general. From this study, it was apparent that selective seeding and transplanting of seedlings increased the two properties above. Combination of the two treatments with mulching maximized biomass production, possibly through increased water and nutrient-use efficiencies.

2) For the second category which represents advanced mid-succession stage such as the Gubali site, only imported seed bank was necessary to

increase woody species diversity. From this study, mulching application was useful to eliminate the non-woody species and favor the more stable perennial woody-species vegetation, through elimination of water competition from the shallow rooted species.

Nutrient stress, fires and herbivory in savanna ecosystems

Savannas are a result of interactions between soil water and nutrient availability with fire and grazing acting as ecosystem modifiers (Sarmiento 1992). Fire can be used in grazed savannas to regulate vegetation composition and to maintain succession to a certain stage (Booysen & Tainton 1984). Direct additions of inorganic fertilizers to savanna soils is not recommended in that it depletes the soil organic matter thereby alleviating the problem of plant nitrogen and phosphorus availability and reducing the cation exchange capacity of the soil. This implies that nutrient deficiency has to be corrected by other means. Herbivores and fire are known to speed up the nutrient turnover rates in savannas (see e.g. Booysen & Tainton 1984, Ruess & McNaughton 1987, Skarpe 1992). For semi-arid ecosystem such as KIH where grazing animals were evicted ca. 25 years ago, low nitrogen mineralization and water stress are agents which slow the succession process, although other limiting conditions such as seeds could be present. It is on this understanding that any model developed for speedy vegetation recovery of KIH should take into account the influence of grazing and fires which are integral part of savanna ecosystems.

Main factors in succession dynamics

Among factors used in this experiment, fertilization is the most outstanding factor. It negatively affects seedling recruitment, total number of species, mortality and biomass. The implication is that fertilization is not an effective means of speeding up the vegetation recovery process in this savanna ecosystem, where moisture is the most important factor known to limit germination and establishment (see Walker & Noy-Meir 1982, Pandey & Singh 1992, Sarmiento 1992, Egley 1995). Moreover, it will be practically impossible to carry out inorganic fertilization of the whole KIH. If inorganic fertilization is considered in arid environments, then it has to be supplemented with other treatments such as mulching which buffer their effect. The effect of mulching differs depending on the soil conditions of a given habitat. As an example, in this study, mulching significantly increased mortality in site 2 but in site 1 the increase was not significant. The practical utility of mulching is to change the organic composition of the soil as well as increasing the water-use efficiency of seedlings growing under mulch, properties which favor selective establishment of woody species. On the other hand, mulching is important to preserve soil moisture (Sandhu et al. 1992, Smith & Shackleton 1988). Woody species will utilize this advantage by growing fast and developing deep penetrating roots which will enable them to extract water below from which competition with shallow rooted annuals or grasses is avoided. Probably increased seedling mortality of non-woody species observed in mulched plots could be attributed to mulch-decomposing termites.

Application of imported seed bank and seeding are important in KIH in that they significantly increase seedling recruitment and total number of species and biomass production. All these are desired qualities needed for speedy recovery of disturbed vegetation, where probably the disturbance agent have impoverished the soil seed bank. As a measure to increase species diversity and recruitment, introduction of seeds with desired qualities, planting seedlings and soil enrichment with imported seed bank are necessary.

CONCLUSIONS

This study has shown that seed bank enrichment in form of imported seed bank or direct sowing of seeds improved seedling recruitment and increased total number of species including number of perennial species in the study area. Direct addition of seeds of desired quality could be more appropriate than imported seed bank, due to technicalities involved in moving large volumes of soil, and most important, the availability of proper seed bank soil. The study also showed that planting seedlings was another option to increase species diversity.

Bearing in mind that the oligotrophic savanna soils are nutrient-deficient and that the existence of savanna ecosystems is dependent on herbivory and fire; then nitrogen deficiencies can be corrected naturally by fires and grazing animals and not by inorganic fertilization. This takes into consideration the shortcomings associated with usage of inorganic fertilizers as well as the cost effectiveness. This suggests re-introduction of livestock into the hills (see also Lyaruu in press), assuming that the cattle will add more (dung) than they remove (grazing).

In severely degraded areas still in the early stages of succession, introduction of seeding and transplants increased seedling recruitment and promoted co-existence of species. The above treatments when applied with mulching maximized biomass production, probably due to increased water and nutrient-use efficiencies. For areas which are in mid stages of succession, the study showed that only imported seed bank was necessary to correct seed deficiencies in the soil; and mulching of these relatively deep soils seemed to favor the establishment of woody species over non-woody species.

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