

## RESEARCH ARTICLE

# Recovery of Plant Species Richness and Composition in an Abandoned Forest Settlement Area in Kenya

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## Abstract

Cultivation of annual crops in the initial stage of reforestation has been commonly practiced in the tropics. In recent decades, however, cultivation of such areas has been discontinued, resulting in widespread abandoned settlements. In this article we used a former forest village settlement in Kenya, which had been cleared, cultivated and then abandoned, to study how natural vegetation recovers after such disturbances. Species richness, abundance, and composition of tree seedlings, saplings, adult trees, shrubs, and herbs were recorded in different zones, from a heavily degraded zone in the center of the settlement, through less disturbed transition zones (TZs), and in the surrounding secondary forest (SF). Species richness and abundance of tree seedlings, saplings, and adult trees increased gradually from the heavily degraded zone to the SF, whereas

shrub and herb richness were the same for TZs and SF and abundance was lowest in the SF. Total species richness was highest in the SF. Some pioneer tree species were highly associated with the TZs, whereas sub-canopy tree species were associated with the SF. A group of tree species were not particularly associated with any of the four zones. Thus, these species might have good potential as restoration species. The results of our study contribute to the knowledge of natural regeneration in general, and of individual species characterizing the different stages of recovery of abandoned settlements in particular. Such information is urgently needed in designing ecologically sound management strategies for restoring abandoned forest settlements in tropical areas.

**Key words:** forest degradation, restoration species, species diversity, tree recruitment.

## Introduction

Degradation of natural forests is widely acknowledged to be a serious problem that causes rural poverty, destruction of water catchments, loss of biodiversity, and increases in carbon emissions (Barnes 1990; FAO 2005). Degraded landscapes are expanding in the tropics as forests are converted to unsustainable pasture or cultivation and then abandoned (FAO 1978; Nair 1984; Bussmann 2004). In the 1940s, the forest village scheme (taungya system) was introduced to stop further spread of deforestation in tropical Asia and Africa. The scheme became widespread in various countries, such as Uganda, Gabon, India, Thailand, Cambodia, and Kenya, the study area of this article (Boonkird et al. 1984; Oduol 1986; Samapuddhi 2009). The system envisaged the sustainable use of forest land for food production by landless people who would otherwise be engaged in forest destruction to obtain food and cash.

A forest village was established by giving each farmer a plot to construct a house, develop a home garden, and raise livestock. Cultivation proceeded until tree seedlings were big enough to shade and inhibit growth of annual crops, usually within 3–5 years. With increased population density and decreases in natural forest resources, forest village systems have proved expensive and are either facing slow growth or are being discontinued (Lamb & Tomlinson 1994).

The initial floristic composition (IFC) hypothesis (Egler 1954 see also van Breugel et al. 2007) is applicable to tropical post-agricultural succession where previous land use is of low intensity and seed sources are available in nearby natural forests, conditions typical of abandoned forest villages. The hypothesis proposes a sequential floristic or life form dominance of species. Early after abandonment, light-demanding species will dominate, but will eventually be replaced by shade-tolerant species due to differences in growth rate, longevity, and shade-tolerance among tree species that colonize an abandoned site. Several studies support the validity of the IFC hypothesis under different scenarios, such as these on fallows of contrasting duration since abandonment (Swaine & Hall 1983; Uhl et al. 1988; Chazdon 2003; Duncan & Chapman 2003), where some clear patterns have emerged. For instance, rates of recovery are accelerated if prior land use intensity was low, if the area of disturbance is small, and if there are remnant forest areas nearby (Swaine & Hall 1983;

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Uhl et al. 1988; Guariguata & Ostertag 2001; Chinaea 2002; Chazdon 2003; Duncan & Chapman 2003). For East African montane forests, however, only a few studies have been conducted on the impact of human use of vegetation resources (Bussmann 1996; Mathoko & Kariuki 2000; Bussmann 2002; Bussmann 2003; Bussmann 2004), regeneration after disturbance (Hitima et al. 2004; Farwig et al. 2006; Baldyga et al. 2007), and forest composition after abandonment (Kigomo et al. 1990; Duncan & Duncan 2000; Mwima & McNeillage 2003).

Various forms of *taungya* have been reported for Kenya (Oduol 1986), Tanzania (Chamshama et al. 1992), and Uganda (Chaudry & Silim 1980). For instance, in 1981–1983 an average of 413 households with a mean of 2,072 farmers was engaged in the *shamba* system (a form of *taungya*), which covered a total area of 5,831 hectares in 20 forest stations in Kenya (Oduol 1986), and 533 farmers were engaged in Northern Kilimanjaro in Tanzania (Chamshama et al. 1992). However, in later years of the twentieth century, the *shamba* system was discontinued in the region and forest settlements were vacated (Witcomb & Dorward 2009), chiefly due to increases in human population density and illegal activities (clearing, poaching, hunting). Abandoned forest settlements vary in size, which has resulted in discrete degraded areas that now dominate the Kenyan forest landscape. They form mosaics that comprise a range of habitat types, such as pastures, old plantations, and abandoned fallows left to succession with no management intervention. However, in Kenya, active restoration is being initiated by planting indigenous tree species to restore forests for soil protection, production, biodiversity conservation, and carbon sequestration (KEFRI, unpublished data). The restoration efforts are, however, hampered by inadequate understanding of silvicultural management and ecological requirements of many of the tropical tree species used (Wass 1995; Kinyamario et al. 2008). The results of our study will contribute to the knowledge of natural forest establishment after settlement abandonment, and will identify species that may be useful in active restoration of such sites and other disturbed areas in tropical forest ecosystems. Such information is urgently needed to design ecologically sound management strategies for restoration of abandoned settlements arising from failed forest village systems, which have become common since the late 1980s in tropical Asia and Africa, including Kenya (Samapudhi 2009; Witcomb & Dorward 2009). Our study was carried out in Mau forest where about 15 hectares of forest was cleared and cultivated for 11 years and then abandoned 19 years ago. The *shamba* system is representative of land uses in the region, and Mau forest is a case study from which we might make references about the larger geographic area.

In this article we describe plant species richness, abundance, and composition in the previous settlement area and of the surrounding secondary forest (SF) to obtain an understanding of the natural recovery of degraded forest ecosystems in this area. In addition, we examined natural tree recruitment by recording tree seedling and sapling species composition in the different disturbance zones to better understand the colonization processes and to identify potential species for active

restoration of abandoned areas. This article addresses the following questions: (1) How do species richness, abundance, and composition of different growth forms (herbs, ferns, lianas, shrubs, and tree seedlings, saplings, and adult trees) vary among degraded forest areas of different disturbance levels and in the SF? (2) How do ongoing disturbances such as grazing and human activities (selective logging, firewood collection) affect forest recovery? (3) Based on the species composition of different growth forms in the disturbed zones and in the SF, is colonization a function of surrounding vegetation or long distance dispersal? and (4) Which tree species may be suitable for active restoration of abandoned areas in the study site?

## Methods

### Study Area

Mau forest, which is divided into seven blocks, is the largest remaining near-continuous indigenous montane forest in East Africa. Since its designation as a Forest Reserve in 1964, Mau forest has lost almost 34,000 hectares of primary forest, or 9% of the original area. By 1999, the forest covered 360,000 hectares and comprised over 25% of Kenya's forest cover. The forest is one of the major water catchment areas in Kenya. Our study was conducted in a degraded site within the southwest forest block of Itare. The 83,395 hectares block is composed of natural forests, swamps, grasslands, fallows, and regenerating forests. The study area is at 2,120 m elevation, with an annual rainfall around 2,000 mm. Mean annual temperatures range from 12 to 16°C and potential evapo-transpiration varies between 1,400 and 1,800 mm (Jackson & McCarter 1994). The natural forest consists of Afromontane bamboo forest at higher elevations and secondary plant communities derived from logged rainforest at lower elevations. The forest has high biodiversity and hosts indigenous tree species, such as *Olea europaea* (Oleaceae), *Dombeya torrida* (Sterculiaceae), and various bamboo species. The forest is the home of the largest group of forest dwellers in Kenya, the Ogiek (Jackson & McCarter 1994).

Within the forest block, 15 hectares of previously cleared, cultivated, and then abandoned area surrounded by SF was chosen for this study. Detailed information on the history of land use was collected from Kenya Forest Service (KFS) records and by interviewing local people. The settlers removed all trees, logs and stumps, and hoed the soil by hand. They practiced a mixed crop system (corn, beans, and potatoes) during the 11 consecutive years that the settlement was active. Each year before planting, the area was burned and hoed to remove weedy grasses and herbs. Two plantings were made each year. Outside the village, the settlers partially removed trees to allow for grazing and some farming activities. The intensity of tree cutting in the surrounding area decreased with increasing distance from the village. The village was vacated and the land abandoned in 1987, except for periodic grazing by cattle, donkeys, and goats thereafter.

Nineteen years after abandonment, the site consists of three zones of recovery due to different degrees of degradation before abandonment, and continued grazing, selective logging, and firewood collection thereafter. Thus, the degradation is a combined effect of deforestation by clear cutting and selective logging, and overexploitation of the vegetation by grazing animals. In the area where the village was situated, there is a heavily degraded zone dominated by grasses and forbs, here termed the grass zone (GZ). Outside this zone, there is a less disturbed zone consisting of early colonizing shrubs and a few tree seedlings, termed transition zone I (TZI). Further out and closest to the SF, there is a zone of lesser degradation with shrubs, tree seedlings, tree saplings, and adult trees, termed transition zone II (TZII). Due to past selective logging, the SF is dominated by pioneer species (gap species) like *Tabernaemontana stapfiana* (Apocynaceae), *Celtis gomphophylla* (Ulmaceae), *Suregada procera* (Euphorbiaceae), *Xymalos monospora* (Monimiaceae), *Cassipourea malosana* (Rhizophoraceae), and *Fagaropsis angolensis* (Rutaceae). In addition, the presence of *Ehretia cymosa* (Boraginaceae), and *Achyranthes aspera* (Amaranthaceae) in the forest suggests that the Itare block is a SF (Mathoko & Kariuki 2000).

#### Data Collection

Data were collected in November 2006 in the middle of the dry season, and in March 2007 at the beginning of the rainy season. Each zone was divided into four sections along the cardinal directions. We randomly selected 40 plots within the different zones as follows: six plots in GZ, ten in TZI, ten in TZII and fourteen plots in SF. Each section of GZ, TZI, TZII, and SF had 1–2, 2–3, 2–3, and 3–4 plots, respectively. The plots in the SF were located at least 200 m away from the edge of the closest plot in TZII. We used plots of 5 × 30-m in GZ and TZI and 10 × 30-m in TZII and SF. We used larger plots in TZII and SF in order to capture the variation in species richness, abundance, and composition in these zones, where the species–area relationship differed from the other zones due to a greater number of larger trees. Each plot was divided into 6 subplots (for the 5 × 30-m plots) and 12 subplots (for the 10 × 30-m plots), and each subplot had a 1 × 1-m quadrat in its center. Adult trees and lianas (taller than 1.3 m and dbh > 10 cm) were counted in all subplots. Tree saplings (young trees with dbh < 10 cm and height > 1.3 m) and shrubs were counted in every other subplot. Tree seedlings (< 1.3-m height), ferns and herbs (percent cover) were recorded in every quadrat within each subplot. To enable comparison between the different plot sizes, corrections were done before data analyses. For the species abundance data, we divided abundance within the 10 × 30-m plots by 2. For the species richness data, we calculated the mean number of species within each of the two 5 × 30-m plots of a 10 × 30-m plot and used the mean of these plots in the analyses. We also collected information on environmental variables that could potentially explain the variation in species composition and richness among plots. As indicators of grazing pressure and

human disturbance, we counted all animal droppings (cow and donkey) inside each of the plots and measured the length of human/animal paths crossing the plots, as described by Silori (2001) and Silori and Mishra (2001). A taxonomist assisted by local para-taxonomist and KFS staff identified the plant species. All unidentified species were deposited at the National Herbarium of Kenya for identification and voucher species were kept there. Nomenclature follows Agnew and Agnew (1994) and Beentje (1994).

#### Statistical Analyses

We used repeated-measures analyses of variance (ANOVAs) to examine how species richness and abundance of herbs, ferns, lianas, and tree seedlings (dependent variables) differed between GZ, TZI, TZII, and SF (zone, fixed factor) and between dry and wet seasons (season repeated measures variable). Because we did not expect any of the following groups to be affected by season, we used one-way ANOVAs to examine how shrubs, tree saplings, adult trees, and the total species richness (dependent variables) differed between GZ, TZI, TZII, and SF (zone, fixed factor). We used Bonferroni post hoc tests to determine if dependent variables differed significantly between zones. To test for spatial autocorrelation, that is, whether the data points represented statistically independent sample units, we used two-way ANOVAs that included “section” and season as fixed factors, and species richness and mean abundance of species as response variables. Species–area relationships were examined by generating species accumulation curves for each growth form and within each zone with the program EstimateS (v.8.2.0), (Colwell 2009), and “true” species richness values were estimated using the Mao Tau estimator. These analyses showed that our plots did not capture the real species richness in the area, and the estimated “true” species richness was therefore used in the ANOVAs. R 2.10.0 (R Development Core Team 2009) was used for the species richness ANOVAs, and SYSTAT 10 for windows was used for the remaining analyses.

We used multivariate analyses to examine how species composition differed among zones (GZ, TZI, TZII, and SF, defined as dummy variables), and along gradients of animal grazing, and human disturbance. Detrended Correspondence Analysis (ter Braak & Prentice 1988; Eilertsen et al. 1990) was used to assess gradient length. Due to large variation in the species composition data (total variation > 4.0 SD) for all growth forms, Canonical Correspondence Analyses (CCA, ter Braak 1986; ter Braak 1987; Leps & Šmilauer 2005) were used to ordinate species composition of the different growth forms (separate analysis for each group) and environmental variables (zone, section, animal droppings, path length). We tested each environmental variable by forward selection, using 999 permutations with all variables included. For growth forms whose composition did not differ between seasons, namely saplings, adult trees, and shrubs, we present results only from the wet season. For those growth forms that differed in species composition between seasons, namely tree seedlings and herbs, we analyzed and present the data from wet and the dry seasons

separately. For each analysis, we tested the significance of all canonical axes with 999 unrestricted permutations in a Monte Carlo test. We conducted all ordinations by using default settings in CANOCO 4.5 and used CanoDraw to produce ordination diagrams (ter Braak & Smilauer 2002).

## Results

### Species Richness and Abundance

Repeated-measures ANOVA showed that species richness of tree seedlings differed significantly between zones and between seasons (Table 1). In both seasons, richness was significantly highest in the SF, intermediate in the transition zones (TZs), and lowest in the GZ (Fig. 1a). ANOVAs showed that tree sapling and adult tree species richness were lowest in GZ and highest in the SF (Table 1; Fig. 1b & 1c). Species richness of herbs was significantly lower in GZ than in all the other zones, with significantly more species in the wet season in the zones (Table 1; Fig. 1d). Shrub species richness was higher in both TZs and in SF than in the GZ (Table 1; Fig. 1e). Liana species richness was higher in SF and TZII, compared to TZI and GZ in both seasons (Table 1). Species richness of ferns was higher in SF than in all other zones in the wet season (Table 1). TZI and TZII had higher total species richness than GZ, but lower than SF (Table 1; Fig. 1f).

Mean abundance of tree seedlings was higher in SF than in the other zones, but only in the wet season (Table 1; Fig. 1g).

Abundance of tree saplings and adults was higher in SF than in both TZs, and higher in TZII compared to GZ (Table 1; Fig. 1h & 1i). Herb species cover was not significantly different in TZII compared to GZ or TZI in the dry season, but it was in the wet season (Table 1; Fig. 1j). The abundance of shrubs was higher in the TZs than in both GZ and SF (Table 1; Fig. 1k). Liana species abundance was higher in SF and TZII compared to TZI and GZ in both seasons (Table 1). The abundance of fern species was higher in SF than in all other zones in the wet season (Table 1). The ANOVA with section as a factor showed that there was no effect of section on species abundance or richness, suggesting that there was no spatial autocorrelation of species richness or abundance within the zones.

### Species Composition

The position of plots among different "sections" did not affect species composition, suggesting lack of autocorrelation within the zones. The relationships between species composition and the different zones, human and animal disturbances are shown in CCA biplot ordination diagrams of species and environmental variables (Figs. 2 & 3). The whole CCA model was significant for the species composition of tree seedlings in the wet season, and for herbs and lianas (not shown) in both seasons (Figs. 2 & 3). The first canonical axis explained a large part of the variation in species composition of tree saplings, shrubs, herbs, and lianas. The CCA model was only close to significant for adult tree species composition

**Table 1.** Repeated-measurement ANOVAs of Mao Tau estimated species richness and mean abundance of tree seedlings, herbs, lianas, and ferns (dependent variables) in four different disturbance zones (zone; fixed factor) and in the wet and the dry season (repeated measure factor) and ANOVAs of Mao Tau estimated species richness and abundance of tree saplings, adult trees, shrubs, and all plants (dependent variable) in the four disturbance zones in Mau forest, Kenya.

	Zone		Season		Zone × Season	
	F	p	F	p	F	p
<b>Repeat-ANOVAs</b>						
<b>Richness</b>						
Tree seedlings	32.01	<0.001	514.74	<0.001	1.56	0.214
Herbs	17.40	0.362	49.89	<0.001	1.69	0.185
Ferns	56.12	<0.001	54.482	<0.001	3.26	0.092
Lianas	15.30	<0.001	488.53	<0.001	1.36	0.174
<b>Abundance</b>						
Tree seedlings	5.312	0.004	22.56	<0.001	6.57	<0.001
Herbs	38.07	<0.001	1.32	0.258	7.98	<0.001
Lianas	17.10	<0.001	7.09	0.011	1.87	0.153
Ferns	12.49	<0.001	18.21	<0.001	11.00	<0.001
<b>ANOVAs</b>						
<b>Richness</b>						
Saplings	307.54	<0.001				
Adult trees	492.54	<0.001				
Shrubs	249.14	<0.001				
All plants	331.55	<0.001				
<b>Abundance</b>						
Saplings	16.922	<0.001				
Adult trees	24.563	<0.001				
Shrubs	10.50	<0.001				

F and p values are shown.

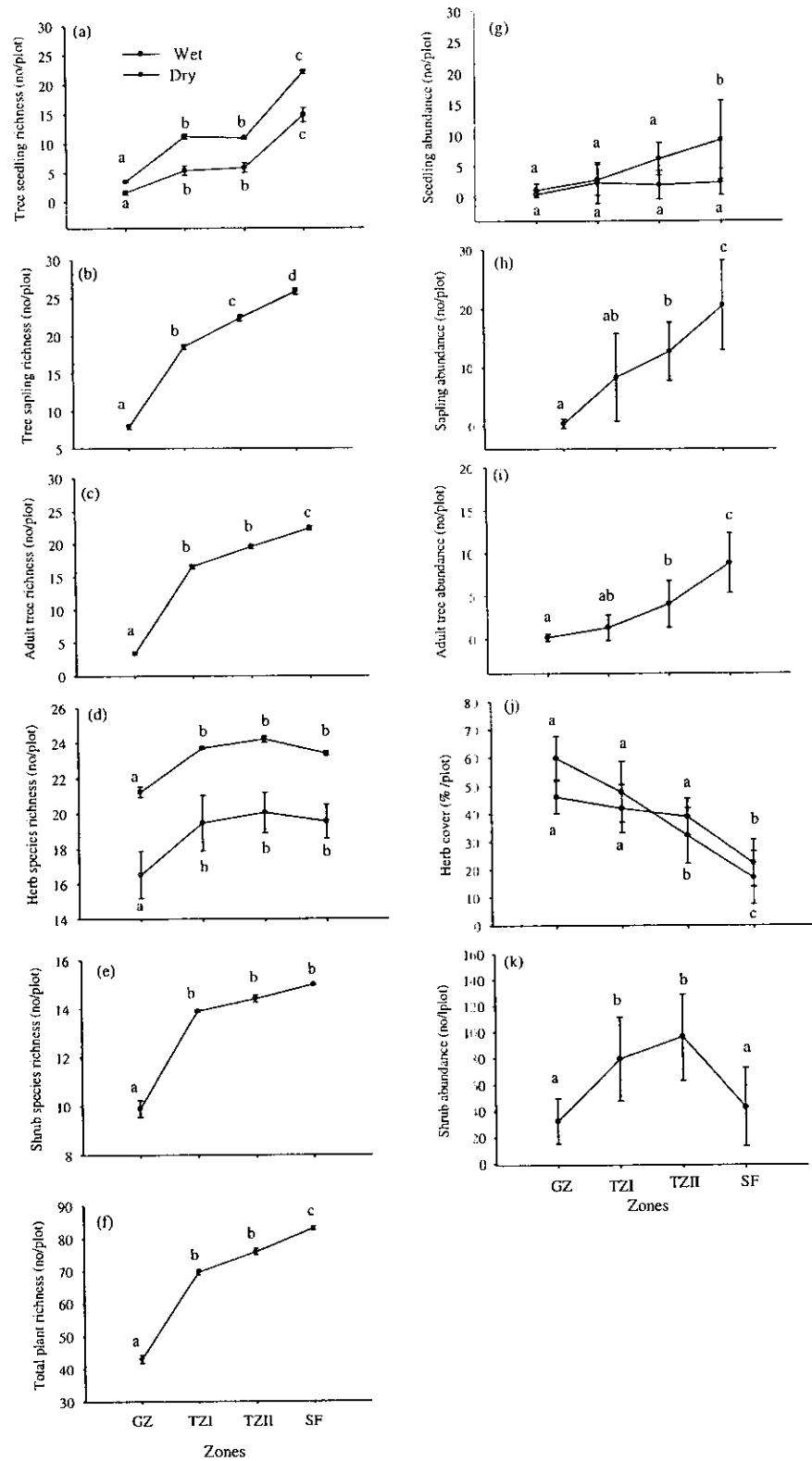


Figure 1. Mao Tau estimated species richness (mean  $\pm$  SE) of (a) tree seedlings, (b) tree saplings, (c) adult trees, (d) herbs, and (e) shrubs, and (f) total species richness, and abundance (mean  $\pm$  SE) of (g) tree seedlings, (h) tree saplings, (i) adult trees, (j) herbs, and (k) shrubs in different zones of disturbance; GZ, TZI, TZII, SF in Mau forest, Kenya. Both wet and dry season are shown for tree seedlings and herbs. Different letters indicate significant difference using Bonferroni pair wise mean comparison post hoc test. Only one set of letters is shown where there was no significant difference between the seasons.

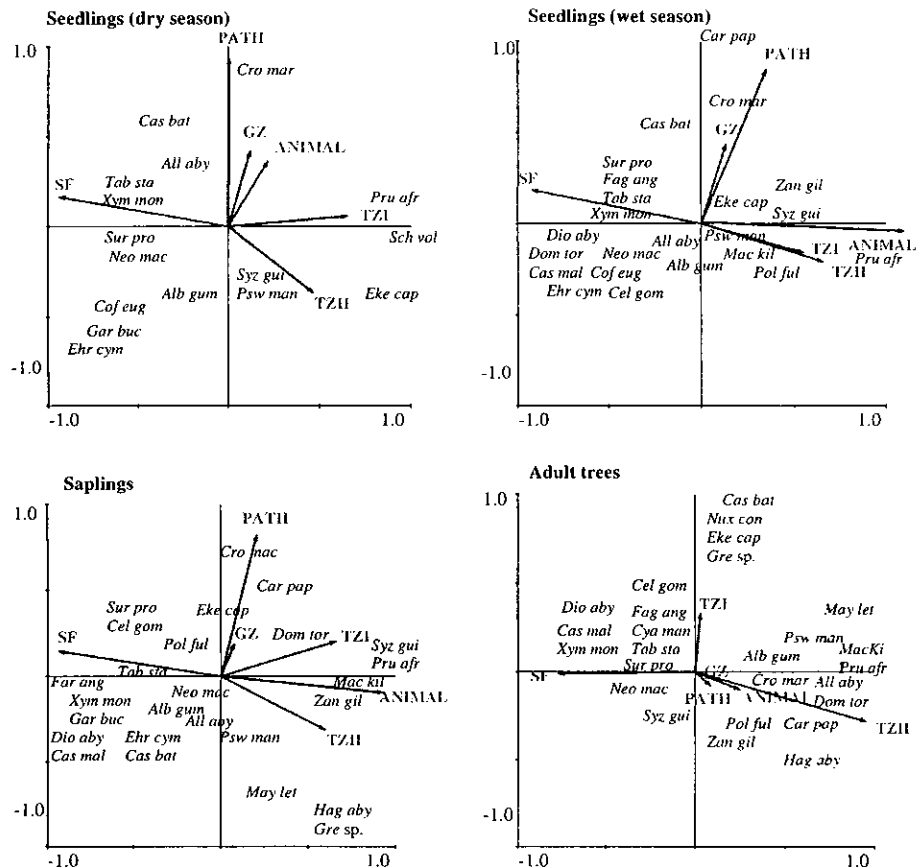


Figure 2. CCA ordination of seedlings, saplings, and adults of tree species, including six environmental variables in Mau forest, Kenya. Cro mac, *Croton macrostachyus*; Cas bat, *Casearia battiscombei*; Cas mal, *Cassipourea malosana*; All aby, *Allophylus abyssinicus*; Tab sta, *Tabernaemontana stapfiana*; Xym mon, *Xymalos monospora*; Sur pro, *Suregada procera*; Neo mac, *Neoboutonia macrocalyx*; Ehr cym, *Ehretia cymosa*; Gar buc, *Garcinia b Buchananii*; Cof eug, *Coffea eugenioides*; Alb gum, *Albizia gummifera*; Psy mah, *Psychotria mahonii*; Syz gui, *Syzygium guineense*; Eke cap, *Ekebergia capensis*; Pru afr, *Prunus africana*; Sch vol, *Schefflera volkensii*; Car pap, *Carica papaya*; Fag ang, *Fagaropsis angolensis*; Cel gom, *Celtis gomphophylla*; Dio aby, *Diospyros abyssinica*; Dom tor, *Dombeya torrida*; Zan gil, *Zanthoxylum gillettii*; Pol ful, *Polyscias fulva*; Mac kil, *Macaranga kilimandscharica*; May het, *Maytenus heterophylla*; Gre spp., *Grewia* species; Hag aby, *Hagenia abyssinica*; Nux con, *Nuxia congesta*; Cya man, *Cyathea manniana*. Only well-fitting species are shown in the figure.

( $p = 0.058$ ,  $TI = 5.631$ ,  $Var. Exp. = 1.081$ , Table 2; Fig. 2,  $TI$  [Total inertia] = the total variation of data;  $Var. Exp.$  = total variation explained of the  $TI$  by the environmental variables). The tree seedling species composition differed significantly between the SF and the other zones in both seasons ( $p = 0.004$ ,  $TI = 3.969$ ,  $Var. Exp. = 1.000$ , Table 2; Fig. 2). The species composition of tree saplings ( $p = 0.002$ ,  $TI = 2.632$ ,  $Var. Exp. = 0.685$ ) and adult trees ( $p = 0.002$ ,  $TI = 1.436$ ,  $Var. Exp. = 0.718$ ) differed significantly between the SF and the other zones, but did not differ between the TZs and the GZ (Table 2; Fig. 2). The herb species composition differed significantly between GZ and the SF and TZII, both in the wet ( $p = 0.002$ ,  $TI = 2.007$ ,  $Var. Exp. = 0.974$ ) and the dry season ( $p = 0.002$ ,  $TI = 2.768$ ,  $Var. Exp. = 0.878$ , Table 2; Fig. 3). The species composition of shrubs ( $p = 0.002$ ,  $TI = 2.163$ ,  $Var. Exp. = 0.898$ ) differed significantly between the TZII and the other zones and between the SF and the other zones (Table 2; Fig. 3). The CCA clearly showed

that species composition differed between TZs and the SF for tree seedlings and saplings. However, only a few of the seedling and sapling species already occurred in the SF as adult trees, e.g. *Syzygium guineense* (Myrtaceae) and *Neoboutonia macrocalyx* (Euphorbiaceae) (Appendix).

Tree species composition of all life stages were well separated among the zones (Fig. 2). In the dry season, seedlings of *Prunus africana* (Rosaceae) and *Schefflera volkensii* (Araliaceae) were associated with TZI and *S. guineense* and *Psychotria mahonii* (Rubiaceae) were associated with TZII (Fig. 2). In the wet season, seedling species of *Macaranga kilimandscharica* (Euphorbiaceae), *Polyscias fulva* (Araliaceae), and *P. africana* occurred in both TZI and TZII. *Syzygium guineense* was associated with high grazing pressure in the wet season while *Croton macrostachyus* (Euphorbiaceae) was associated with animal and human paths in both seasons (Fig. 2). As opposed to the species mentioned above, some species, such as *Allophylus abyssinicus*

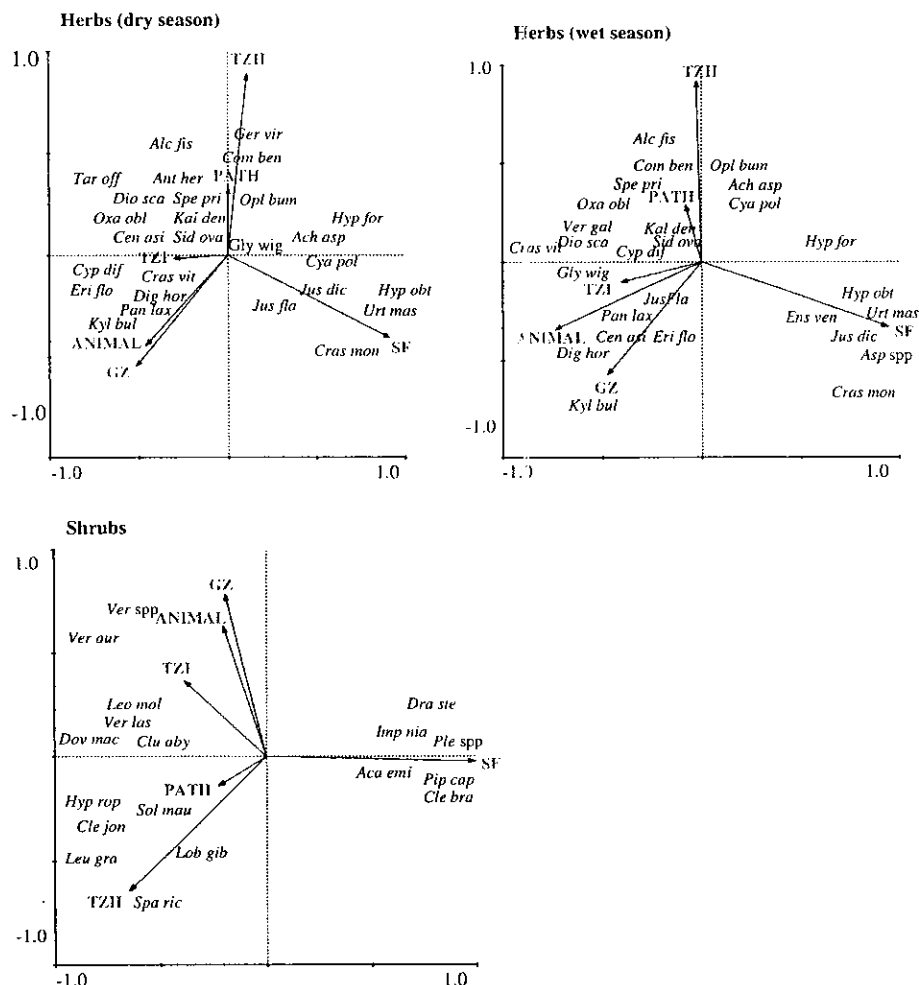


Figure 3. CCA ordination of herb and shrub species, including six environmental variables in Mau forest, Kenya. Vero spp., *Vernonia* species; Ver aur, *Vernonia auriculifera*; Leo mol, *Leonotis mollissima*; Hyp rop, *Hypericum rooperanum*; Sol man, *Solanecio mannii*; Cle joh, *Cleidodendrum johnstonii*; Leu gra, *Leucas grandis*; Spa ric, *Sparmannia ricinocarpa*; Lob gig, *Lobelia gibberoa*; Pip cap, *Piper capense*; Aca emi, *Acanthus eminens*; Cle bra, *Clematis brachiata*; Ple spp., *Plectranthus* species; Dov mac, *Dovyalis macrocalyx*; Dra ste, *Dracaena steudneri*; Imp nia, *Impatiens niarniamensis*; Ger vir, *Gerbera viridifolia*; Com ben, *Commelina benghalensis*; Alc fis, *Alchemilla fischeri*; Ant her, *Anthospermum herbaceum*; Opl bum, *Oplismenus burmannii*; Kal den, *Kalanchoe densiflora*; Tar off, *Taraxacum officinale*; Sid ova, *Sida ovata*; Dio sca, *Diodia scandense*; Oxl obl, *Oxalis obliquifolia*; Cen asi, *Centella asiatica*; Cyp dif, *Cyperus difformis*; Gly wig, *Glycine weightii*; Cra mon, *Crassocephalum montuosum*; Eri flo, *Erigeron floribundus*; Pan lax, *Panicum laxum*; Dig hor, *Digitaria horizontalis*; Kyl bul, *Kyllinga bulbosa*; Jus fla, *Justicia flava*; Ach asp, *Achyranthes aspera*; Hyp for, *Hypoestes forskalei*; Cya pol, *Cyathula polycephala*; Jus dic, *Justicia diclipteroidea*; Hyp obt, *Hypoxis obtusa*; Urt mas, *Urtica m issaica*; Ens ven, *Ensete venricosum*

(Sapindaceae), *P. mahonii*, *Ekebergia capensis* (Meliaceae), *N. macrocalyx* (Euphorbiaceae), and *Albizia gummifera* (Fabaceae), had seedlings that were not associated with any zone.

Saplings of *Zanthoxylum gilletti* (Rutaceae) and *M. kilimandscharica* were closely associated with high grazing pressure (Fig. 2). A group of species, namely *P. mahonii*, *A. abyssinicus*, *A. gummifera*, *N. macrocalyx* and *P. fulva*, had saplings that were not associated with any zone or environmental variable. Adult trees of *Nuxia congesta* (Loganiaceae), *E. capensis*, and *Casaria battiscombei* (Flacourtiaceae) were strongly associated with TZI (Fig. 2). TZII was characterized

by adult tree species of *Dombeya torrida*, *C. macrostarchyus*, *S. guineense*, *P. fulva*, and *Hagenia abyssinica* (Rosaceae).

## Discussion

Plant species richness, abundance, and composition differed substantially between zones in the Itare block of Mau Forest. The CCA ordinations showed that species composition of the different functional groups remained fairly well-separated among degradation zones, mainly because several species were strictly associated with the different zones. This supports previous findings that after establishment, species form distinct

**Table 2.** *F* and *p* values of environmental variables tested by forward selection in CCA in relation to the species composition of tree seedlings, tree saplings, adult trees, shrubs, herbs, and lianas in the wet and the dry (in parentheses) season in Mau forest, Kenya.

Environmental Variable	Tree Seedlings		Saplings		Adult Trees	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Secondary forest	4.62 (2.62)	0.002 (0.002)	5.92	0.002	3.81	0.002
Transition zone II	2.35 (2.00)	0.022 (0.070)	1.54	0.128	1.71	0.086
Transition zone I	0.39 (1.33)	0.988 (0.208)	1.55	0.102	1.71	0.086
Grass zone	1.51 (0.23)	0.208 (0.706)	0.57	0.806	1.64	0.112
Path	0.84 (0.43)	0.506 (0.860)	0.87	0.868	0.54	0.790
Animal dung	0.39 (0.44)	0.988 (0.828)	0.33	0.970	0.12	0.954

	Shrubs		Herbs		Lianas	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Secondary forest	14.81	0.002	20.44 (9.42)	0.002 (0.002)	18.81 (10.44)	0.002 (0.002)
Transition zone II	3.25	0.002	8.11 (3.59)	0.002 (0.002)	2.75 (9.78)	0.008 (0.002)
Transition zone I	2.13	0.174	3.12 (6.31)	0.544 (0.752)	0.67 (0.54)	0.768 (0.202)
Grass zone	1.77	0.146	2.19 (1.30)	0.024 (0.200)	0.42 (0.65)	0.982 (0.758)
Path	1.36	0.222	1.45 (0.87)	0.140 (0.506)	1.85 (1.23)	0.098 (0.124)
Animal dung	0.39	0.878	0.84 (0.76)	0.428 (0.590)	0.16 (0.44)	1.000 (0.904)

combinations, depending on the suitability of small-scale environmental conditions (Brown & Lugo 1994; Myster 2004). The gradual increase in species richness and abundance of tree seedlings, saplings and adult trees from the heavily degraded GZ to the SF is a good indication of the rate of forest regeneration after abandonment.

Muniz-Castro et al. (2006) found that sapling density decreased gradually with increasing distance from potential seed sources in the forest. We found a similar pattern in Mau forest, although a direct distinction between the effects of distance to the seed source and disturbances cannot be drawn, as the distance to the seed source correlated with the degree of disturbance, which likely explained most of the variation in species richness, abundance, and composition between the different zones (GZ, TZI, TZII, and SF). However, our results show that only a few of the seedlings and saplings species colonizing the TZs occurred in the SF as adult trees, suggesting that colonization of the site is a function of both neighbor vegetation and long distance dispersal. It is, however, worth noting that the fact that only a few of the tree seedling and sapling species found in TZs also occurred as adults in the SF may be a result of inadequate sampling.

The presence, abundance, and species composition of tree saplings are good indicators of recovery trends in degraded natural forest as they indicate how species composition and diversity may develop in the future (Duarte et al. 2006). Our results show that there were significant differences in sapling richness and abundance between the zone of lowest disturbance (TZII) and the SF. However, species richness and abundance of adult trees were high in both TZs and the SF, suggesting that previously disturbed areas transition toward a forest structure and composition that resembles, but is not necessarily identical to, SF. The TZs and SF had higher species richness of shrubs and herbs than GZ, but GZ and SF had lower abundance of shrubs than TZs, probably

because of a higher light availability and more intense grazing pressure, which both benefit shrubs over trees (Piggot & Taylor 1994; Ostertag & Verville 2002). In general, 19 years after cessation of cultivation, the tree seedling and sapling richness were highest close to the SF edge and lower further away. This pattern agrees with other studies suggesting that species richness of woody seedlings and saplings can recover within 15–20 years in post-agricultural SFs that are close to mature forest areas (Guariguata & Dupuy 1997). In addition, previous studies of post-agricultural recovery in tropical forests have shown that recovery of species richness is far more rapid than recovery of species composition (Chazdon 2003), which is also suggested by our results. Overall, the observed forest regeneration trends in the Itare forest block shows that recovery to a closed forest canopy does not occur within 19 years. Species richness and abundance in the less disturbed zones were considerably lower than in the SF. Furthermore, species composition differed substantially between the SF, the transitional zones and the GZ.

Regeneration is a central process of forest ecosystem dynamics (Grubb 1977), and sustainable forest restoration is only possible if adequate information on regeneration of species is available. Unfortunately, this has been difficult to achieve because of propagation difficulties of many tropical hardwood tree species (Boots & Gullison 1995) and inadequate knowledge of their ecological requirements (Engel & Poggiani 1992). Consequently, it has been difficult to identify suitable tree species (early or late pioneers) for active restoration that could accelerate succession in degraded tropical forest systems (Wass 1995; MacDonald et al. 2003; Bussmann 2004). The presence of tree species in the different degradation zones of our study site could be one criterion used to identify species suitable for restoration. Our study identifies a group of tree species that appear to have relatively low affiliation with any zone (i.e. they occur close to the center



in the ordination diagrams), suggesting that these species are habitat-generalists with few requirements for specific environmental conditions that change during succession. Such species may be particularly suitable for active restoration because they may germinate under most conditions and may persist for long periods during succession. The species that most clearly exhibited these characteristics in our study were *Psychotria mahonii*, *Allophylus abyssinicus*, *Albizia gummifera*, *Neouboutonia macrocalyx*, *Polyscias fulva*, *Dombeya torrida*, and *Ekebergia capensis*. These species may have potential for restoration of degraded tropical forests in areas where they occur naturally because they have the ability to establish as seedlings and survive as saplings in sites with different degrees of degradation. We propose that further studies should focus on the reproduction, dispersal, colonization, and abundance of various life-stages of these species under contrasting environmental conditions, and on how they influence recruitment and establishment of other species during succession.

The constraints on vegetation recovery from disturbances caused by the previous settlement are evident from the present plant species richness, abundance, and composition in Mau forest. All tree cover and most tree stumps were removed. Regeneration from the soil seed bank and/or through stump sprouting likely did not occur. This, together with the current grazing pressure and the distance from current seed source, may explain the low tree regeneration rate in the central GZ. Grazing has continued after abandonment of the settlement and is likely to impact soil and above-ground vegetation, which may significantly impede forest regeneration, particularly recovery of species composition. For example, Haggard et al. (1997) and Posada et al. (2000) reported that severe reduction in regeneration of trees and shrubs in pastures was due to intensive browsing by livestock. Intensive grazing, trampling, and uprooting by both large and small domestic herbivores in these grass/forb areas have perpetuated dominance by perennial grasses, such as *Digitaria horizontalis*, *Kyllinga bulbosa*, and *Panicum laxum* that are all abundant in the heavily degraded grasslands in Itare.

Recovery of degraded forest areas after agriculture is important for climate change mitigation, biodiversity conservation, rural development, and poverty reduction in Africa. Our study shows that 19 years are not sufficient for a degraded tropical forest site to recover to levels of species diversity and composition similar to a SF. However, the relatively high species richness and abundance of adult trees and saplings in the zone of lowest disturbance and closest proximity to the SF suggests that the site is in a transitional phase toward a structure that resembles a SF. The generality of our results may be limited as our study was conducted at a single abandoned settlement. Nevertheless, we believe our results are representative of recently abandoned settlements in East Africa, because management history and the forest landscapes are similar across the region (Chaudry & Silim 1980; Chamshama et al. 1992; Witcomb & Dorward 2009). Additional studies are needed both in comparable sites in the region and in other parts of the tropics to confirm whether our results are applicable elsewhere.

### Implications for Practice

- Successful tropical montane forest restoration requires use of habitat generalist indigenous tree species.
- Because successional processes decline with increasing distance (20–170 m) from the forest edge, active restoration should be carried out about 100 m away from the SFs.
- Although regenerating forest on former settlement areas can rarely deliver all attributes of a primary forest, these forests are ecologically more valuable than single-species plantations. As such these forests require silvicultural management to promote the natural development of diverse SFs.

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**Appendix.** Plants species sampled in grass zone (GZ), transition zones I and II (TZI and TZII) and secondary forest (SF) at Itar, Mau forest, Kenya.

Scientific Name	Family	Life Form	Zone
<i>Cyperus alterniflorus</i> Schwein.	Cyperaceae	Grass	GZ
<i>Kyllinga bulbosa</i> P. Beauv.	Cyperaceae	Grass	GZ
<i>Digitaria horizontales</i> Henrard	Poaceae	Grass	GZ
<i>Panicum laxum</i> Sw.	Poaceae	Grass	GZ
<i>Scadoxus multiflorus</i> (Martyn) Raf.	Amaryllidaceae	Herb	GZ
<i>Erigeron floribundus</i> (Kunth.) Sch. Bip.	Asteraceae	Herb	GZ
<i>Plectranthus barbatus</i> Andrews	Lamiaceae	Herb	GZ
<i>Alchemilla fischeri</i> Engl.	Rosaceae	Herb	GZ
<i>Cissampelos pareira</i> L.	Menispermaceae	Liana	GZ
<i>Vernonia</i> spp.	Asteraceae	Shrub	GZ
<i>Cyperus difformis</i> L.	Cyperaceae	Grass	TZI
<i>Centella asiatica</i> (L.) Urb.	Apiaceae	Herb	TZI
<i>Crassocephalum viellinum</i> (Benth.) S. Moore	Asteraceae	Herb	TZI
<i>Gerbera viridifolia</i> (Dc.) Sch. Bip.	Asteraceae	Herb	TZI
<i>Taraxacum officinale</i> F.H. Wigg.	Asteraceae	Herb	TZI
<i>Cynoglossum coeruleum</i> A.DC.	Boraginaceae	Herb	TZI
<i>Kalanchoe densiflora</i> Rolfe	Crassulaceae	Herb	TZI
<i>Sida ovata</i> Forssk.	Malvaceae	Herb	TZI
<i>Oxalis obliquifolia</i> Steud. ex A. Rich.	Oxalidaceae	Herb	TZI
<i>Glycine wightii</i> (Taub.) Verdc.	Papilionaceae	Herb	TZI
<i>Solanum indicum</i> L.	Solanaceae	Herb	TZI
<i>Solanum nigrum</i> L.	Solanaceae	Herb	TZI
<i>Diodia scandens</i> Hutch. & Dalziel	Rubiaceae	Herb	TZI
<i>Clusia abyssinica</i> Jaub. & Spach.	Euphorbiaceae	Liana	TZI
<i>Vernonia auriculifera</i> Hiern	Asteraceae	Shrub	TZI
<i>Vernonia lasiopus</i> O. Hoffm.	Asteraceae	Shrub	TZI
<i>Vernonia</i> spp.	Asteraceae	Shrub	TZI
<i>Solanecio mannii</i> (Hook. f.) C. Jeffrey	Euphorbiaceae	Shrub	TZI
<i>Indigofera volkensii</i> Taub.	Fabaceae	Shrub	TZI
<i>Leonotis mollissima</i> Gurke.	Labiatae	Shrub	TZI
<i>Grewia</i> spp.	Malvaceae	Shrub	TZI
<i>Dovyalis macrocalyx</i> (Oliv.) Warb.	Silicaceae	Shrub	TZI
<i>Nuxia congesta</i> R.Br. ex Fresen	Stilbaceae	Shrub	TZI
<i>Polyscias fulva</i> (Hiern) Harms	Araliaceae	Tree	TZI
<i>Schefflera volkensii</i> (Engl.) Harms	Araliaceae	Tree	TZI
<i>Maytenus heterophylla</i> N. Robson	Celastraceae	Tree	TZI
<i>Neoboutonia macrocalyx</i> Pax	Euphorbiaceae	Tree	TZI
<i>Albizia gummifera</i> (J.F. Gmel.) C.A. sm.	Fabaceae	Tree	TZI
<i>Ekebergia capensis</i> Sparm.	Meliaceae	Tree	TZI
<i>Oplismenus bumbanii</i> P. Beauv.	Poaceae	Grass	TZII
<i>Achyranthes aspera</i> L.	Amaranthaceae	Herb	TZII
<i>Cyathula polycephala</i> Baker	Amaranthaceae	Herb	TZII
<i>Vernonia galamensis</i> (Cass.) Less.	Asteraceae	Herb	TZII
<i>Commellina benghalensis</i> Forssk.	Commelinaceae	Herb	TZII
<i>Kalanchoe densiflora</i> Rolfe	Crassulaceae	Herb	TZII
<i>Sida ovata</i> Forssk.	Malvaceae	Herb	TZII
<i>Oxalis obliquifolia</i> Steud. ex A. Rich.	Oxalidaceae	Herb	TZII
<i>Anthospermum herbaceum</i> L.f.	Rubiaceae	Herb	TZII
<i>Spermacoce princeae</i> (K. Schum) Verdc.	Rubiaceae	Herb	TZII
<i>Clusia abyssinica</i> Jaub. & Spach.	Euphorbiaceae	Liana	TZII
<i>Ipomoea hildebrandtii</i> Vatke	Convolvulaceae	Liana	TZII
<i>Scutia myrtina</i> (Burm.f.) Kurz.	Rhamnaceae	Liana	TZII
<i>Rubus steudneri</i> (Olive.) R.A. Graham	Rosaceae	Liana	TZII
<i>Physalis minima</i> C.H. Wright	Solanaceae	Liana	TZII
<i>Sparmannia ricinocarpa</i> (Eckl. & Zeyh.) Kuntze	Tiliaceae	Liana	TZII
<i>Cyphostemma orondo</i> (Gil & M. Brandt) Desc.	Vitaceae	Liana	TZII
<i>Acanthus eminens</i> C.B. Clarke	Acanthaceae	Shrub	TZII
<i>Launaea cornuta</i> C. Jeffrey	Asteraceae	Shrub	TZII
<i>Lobelia gibberoa</i> Hemsl.	Campanulaceae	Shrub	TZII
<i>Hypericum roeperianum</i> Schmp. ex A. Rich.	Hypericaceae	Shrub	TZII
<i>Leucas grandis</i> Vatke	Labiatae	Shrub	TZII

## Appendix. Continued

<i>Hibiscus ludwigii</i> Eckle. & Zeyh.	Malvaceae	Shrub	TZII
<i>Rumex usambarensis</i> Dammer	Polygonaceae	Shrub	TZII
<i>Solanum mauritianum</i> Scop.	Solanaceae	Shrub	TZII
<i>Solanum</i> spp.	Solanaceae	Shrub	TZII
<i>Solanum terminale</i> Forssk.	Solanaceae	Shrub	TZII
<i>Triumfetta rhomboidea</i> Jacq.	Sterculiaceae	Shrub	TZII
<i>Clerodendrum johnstonii</i> Oliv	Verbenaceae	Shrub	TZII
<i>Polyscias fulva</i> (Hiern) Harms.	Araliaceae	Tree	TZII
<i>Carica papaya</i> L.	Caricaceae	Tree	TZII
<i>Croton marcrostachyus</i> Hochst.ex Delile	Euphorbiaceae	Tree	TZII
<i>Macaranga kilimandscharica</i> Pax	Euphorbiaceae	Tree	TZII
<i>Neoboutonia macrocalyx</i> Pax	Euphorbiaceae	Tree	TZII
<i>Albizia gummifera</i> (J.F. Gmel.) C.A.sm.	Fabaceae	Tree	TZII
<i>Dombeya torrida</i> Bamps.	Malvaceae	Tree	TZII
<i>Ekebergia capensis</i> Sparm.	Meliaceae	Tree	TZII
<i>Hagenia abyssinica</i> J.F. Gmel.	Rosaceae	Tree	TZII
<i>Prunus africana</i> (Hook.f.) Kalkman	Rosaceae	Tree	TZII
<i>Psychotria mahonii</i> C.H. Wright	Rubiaceae	Tree	TZII
<i>Allophylus abyssinicus</i> P. Beauv.	Sapindaceae	Tree	TZII
<i>Ensete ventricosum</i> (Welw.) Cheesman	Musaceae	Grass	SF
<i>Justicia diclipteroides</i> Lindau	Acanthaceae	Herb	SF
<i>Justicia flava</i> (Forssk.) Vahl.	Acanthaceae	Herb	SF
<i>Crassocephalum montousum</i> (S.Moore) Milne-Redh.	Asteraceae	Herb	SF
<i>Impatiens niamniamensis</i> Gilg.	Balsaminaceae	Herb	SF
<i>Kalanchoe densiflora</i> Rolfe	Crassulaceae	Herb	SF
<i>Hypoxis obtusa</i> Burch.	Hypoxidaceae	Herb	SF
<i>Sida ovata</i> Forssk.	Malvaceae	Herb	SF
<i>Urtica massaica</i> Mildbr.	Urticaceae	Herb	SF
<i>Cyathea</i> spp.	Amaranthaceae	Liana	SF
<i>Landolphia buchananii</i> (Hallier.f.) Sapf.	Apocynaceae	Liana	SF
<i>Periploca linearifolia</i> Quart.-Dill. & A. Rich.	Apocynaceae	Liana	SF
<i>Zehneria scabra</i> (L.f.) Sond.	Cucurbitaceae	Liana	SF
<i>Gouania longispicata</i> Engl.	Rhamnaceae	Liana	SF
<i>Galium aparine</i> L.	Rubiaceae	Liana	SF
<i>Galium scioanum</i> Chiov.	Rubiaceae	Liana	SF
<i>Keetia guenzi</i> (Sond.) Bridson	Rubiaceae	Liana	SF
<i>Pauridiantha paucinervis</i> (Hiern) Bremec	Rubiaceae	Liana	SF
<i>Rubia cordifolia</i> L.	Rubiaceae	Liana	SF
<i>Toddalia asiatica</i> (L.) Lam.	Rutaceae	Liana	SF
<i>Smilax anceps</i> Willd.	Smilacaceae	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
<i>Cyphostemma orondo</i> (Gil & M.Brandt) Desc.	Vitaceae	Liana	SF
<i>Rhoicissus tridentata</i> (L.f.) Wild & R.B.Drumm.	Vitaceae	Liana	SF
<i>Dracaena steudneri</i> Engl.	Asparagaceae	Shrub	SF
<i>Asplenium</i> spp.	Aspleniaceae	Shrub	SF
<i>Pteris catoptera</i> Kunze	Cyatheaaceae	Shrub	SF
<i>Erythrococca bongensis</i> Pax	Euphorbiaceae	Shrub	SF
<i>Plectranthus</i> spp.	Labiatae	Shrub	SF
<i>Clematis brachiata</i> Thumb.	Ranunculaceae	Shrub	SF
<i>Tabernaemontana stapfiana</i> Britten	Apocynaceae	Tree	SF
<i>Spilanthes mauritiana</i> (A.Rich.ex Pers) DC.	Asteraceae	Tree	SF
<i>Ehretia cymosa</i> (R.Br.ex Fresen.) Brenan	Boraginaceae	Tree	SF
<i>Celtis gomphophylla</i> Baker	Cannabaceae	Tree	SF
<i>Garcinia buchananii</i> Baker	Clusiaceae	Tree	SF
<i>Diospyros abyssinica</i> (Hiern) F.White	Ebenaceae	Tree	SF
<i>Neoboutonia macrocalyx</i> Pax	Euphorbiaceae	Tree	SF
<i>Suregada procera</i> Croizat	Euphorbiaceae	Tree	SF
<i>Albizia gummifera</i> (J.F. Gmel.) C.A.sm.	Fabaceae	Tree	SF

## Appendix. Continued

<i>Trichilia emetica</i> Vahl	Meliaceae	Tree	SF
<i>Bersama abyssinica</i> Verdc.	Melanthaceae	Tree	SF
<i>Xymalos monospora</i> (Harv.) Baill.ex Warb.	Monimiaceae	Tree	SF
<i>Ficus capensis</i> Hiern	Moraceae	Tree	SF
<i>Syzygium guineense</i> F. White	Myrtaceae	Tree	SF
<i>Olea capensis</i> L.	Oleaceae	Tree	SF
<i>Olea europea ssp africana</i> (Mill.) P.S. Green	Oleaceae	Tree	SF
<i>Coffea eugeniioides</i> S. Moore	Rubiaceae	Tree	SF
<i>Heinsenia diervilleoides</i> K. Schum.	Rubiaceae	Tree	SF
<i>Fagaropsis angolensis</i> (Engl.) Dale	Rutaceae	Tree	SF
<i>Tectea nobilis</i> Delile	Rutaceae	Tree	SF
<i>Casearia battiscombei</i> R.E. Fr.	Salicaceae	Tree	SF
<i>Allophylus abyssinicus</i> P. Beauv.	Sapindaceae	Tree	SF
Unknown tree species	Unknown	Tree	SF