

Factors Influencing Succession of Kakamega Forest Grasslands

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ABSTRACT Forty-seven patches of termite mounds were sampled in Kakamega forest grasslands with a view to assessing forest succession, forest species diversity, tree species-area relationships and species associations of forest and grassland tree species. These grasslands have been subjected to burning and grazing by people for a long period of time. The objective was to assess forest succession of grasslands by determining regeneration strategies of both forest and grassland tree species, and the role of termite mound patches in this process. This would then explain the mechanisms of forest succession in grasslands. A total of 34 tree species occurred in patches whose areas ranged from 0.5m² to 1880m². Sixty-eight per cent of these species were forest tree species while the rest were grassland tree species. There was a varied response of regeneration to increasing termite mound patch size. While grassland tree species showed a strong correlation with increasing termite mound patch size, forest tree species correlated less. There was a significant variation in species richness with termite mound patch age between forest and grassland tree species. Termite mound patch age correlated positively with forest species richness than did grassland tree species. There was a strong positive association between the presence of forest species and established grassland tree species. This appears to imply that successful establishment of forest tree species depends largely on the presence of a grassland tree species on the termite mound. Understanding mechanisms that maintain grasslands is crucial to understanding forest succession of the Kakamega forest grasslands. This knowledge can be used as a management tool in managing forest expansion into the grasslands without artificial reforestation.

INTRODUCTION

Kakamega Forest in western Kenya (Tsingalia and Kassilly 2009) is dotted with a number of varied grasslands that range in area from 10ha to 200ha. There are over 25 documented grasslands in the Kakamega forest alone and about five in the nearby Kisere forest (a 500ha fragment to the north of the main Kakamega forest, (Tsingalia 1988; Doute et al. 1981)). Collectively, these grasslands represent a substantial percentage of the total forest area. Kakamega Forest was gazetted in 1932 with an area of 140km² of which indigenous forest rainforest comprises 15,480ha, plantation forest 1592ha and the rest is grasslands (Mutangah 1996; Lung and Schaab 2006; Wass 1995).

The origins of Kakamega forest grasslands have been discussed extensively by Tsingalia and Kassilly (2009). These grasslands have been subjected to burning and grazing by the local people from time immemorial and this has greatly influenced their structure and composition. Burning as a management tool was used to stimulate new grass for cattle and other domestic herds (Tsingalia and Kassilly *in press*) and repeated grazing is used to regulate the use of fires (Pasada et al. 2000; Zimmerman and

Neuenschwander 1984). This has in turn influenced the interaction between them and the surrounding forest. The effects of burning and grazing can be seen in the size of the ecotone. In grasslands that are subjected to infrequent burning and high intensity of grazing, the ecotone is wide and is successfully being colonized by the forest. In grasslands that are subjected to frequent burning and grazing, the ecotone is narrow and open with no evidence of forest invasion except for scattered clumps of fire-resistant shrubs and trees.

An interesting feature of Kakamega forest grasslands is the presence of termites. These termites form scattered mounds of varied sizes inside the grasslands. Six species that belong to four genera *Odontotermes*, *Cubitermes*, *Macrotermes* and *Sphaerotermes* have been identified. *Odontotermes* builds large mounds with wide tunnels while *Cubitermes* builds relatively low, hard brown mounds. *Macrotermes* builds extremely large and extensive mounds while *Sphaerotermes* builds soft cone-shaped mounds. It is on termite mound patches that small forest fragments can be seen (Tsingalia 1988) especially in grasslands that are subjected to least burning and grazing. These termite mounds form

epicentres from which forest invades the grasslands.

Densities of termite mounds differ significantly from grassland to grassland. This difference appears to be influenced by burning and grazing regimes (Benzie 1986). This can be seen in the differences between Kakamega and Kisere forest grasslands. In Kakamega forest, grasslands are burned more frequently than in Kisere forest. Consequently, Kisere forest grasslands have a significantly higher density of termite mounds than Kakamega grasslands. *Odontotermes* occurs in higher densities in Kakamega forest and is absent in Kisere forest while *Macrotermes* is found only in Kisere forest.

Termite mound patches appear to confer to grasslands, characteristics that distinguish them from such other grasslands within the forest. It is, for instance around the termite mound patches that establishing forest tree species occur. These develop further into tiny forest islands and later act as centres from which the forest will spread out to colonize the remaining grasslands given the right conditions. These islands or patches of forest are important in shaping the interaction between the forest and the grasslands. The presence of termite mounds appears to be a function of fire, people and grazing. Termite mound patches were investigated with a view to (i) determining their plant species composition, (ii) determining presence or absence of forest tree species. The objective was to determine the characteristics that would explain how species whose fruits could not be dispersed by wind occur in grasslands far away from the forest where the parent trees grow. It was hoped that information on patch size, frequency and abundance of species within the patches would provide a clue as to the mode of regeneration and the identity groups of forest species that use these patches as safe sites for regeneration (Tsingalia 1989; Fowler 1988; Janzen 1971). Data from this study were to provide information on groups of grassland tree species that characterize such patches.

STUDY METHODS

The study methods were structured to address, (a) grasslands and termite mounds patches and (b) interaction between the forest and the grasslands.

The density of the termite mound patches was determined using 10 quadrats measuring 50m by

50m that were established randomly in the grasslands. Grasslands were selected randomly in Kakamega Forest, while in Kisere Forest, they were selectively chosen because the invading forest seemed to kill the termites. Grasslands that exhibited the least forest invasion were therefore selected. Two grasslands were chosen in Kisere, while four grasslands were selected in the Kakamega Forest.

In each quadrat, a complete census of all termite mound patches was made. For each mound patch, the area, all tree species including seedlings, sapling and adults were inventoried. All forested patches present in the selected grasslands were sampled. For each patch, the area was determined using a standard tape measure. Since most of the patches were more or less rectangular in shape, width and length of the patches was sufficient for the determination of area. Absolute count of adult trees together with their Dbh (diameter at breast height), seedlings and saplings was made for each patch. Patches were also categorized on the basis of relative age. Patch age was determined by examining canopy development, presence of an old adult tree that is typical of grasslands and the presence of a well-defined buffer zone of *Acanthus arboreus*.

For each species whose seedlings/saplings were present in each patch, dispersal mode was determined by examining the type of fruit from the nearest adult of the same tree species (Dansereau and Lems 1957). Dispersal was classified as animal, wind or both. Using morphological characteristics of young plants, the mode of regeneration, whether from seed, coppice or suckering was determined. Species-area relationships were used to determine the response of regeneration of trees species to increasing patch size. Species normal and inverse analysis (Greig-Smith 1983) was used to define groups of species with similar stand occurrences in order to determine whether stand species had similar ecological characteristics.

Species were categorized as forest or grassland. Forest species were those whose adults were typically found inside the forest. Grassland species were those whose adults occur outside the forest in open areas like grasslands or forest edges but never inside the forest.

RESULTS

Thirty-four species were identified in forty-

seven termite mound patches whose area ranged from 0.5m² to 880m². About 67.6 per cent of these species (23 spp.) were forest while 32.4 per cent of the species (11 spp.) were grassland species. Of the grassland species, one species was a fern (subphylum: *Pteropsida*; Class: *Filicinaceae*).

With the exception of one species, *Chaetacme aristata*, an under storey forest shrub, all seedlings in the grasslands were of canopy trees in the forest. They occurred as seedlings and/or saplings in all the patches examined in the grasslands.

Of the forest species, about 22 per cent were wind dispersed while 78 per cent were animal dispersed. Examination of the general fruit morphology revealed that 17 per cent were berries, 72 per cent were drupes while 11 per cent were capsules.

The size of the fruits was also significant in dispersal. All forest tree species, except for *Maesopsis eminii*, and all grassland tree species had small fruits (< 1cm in length and < 5gms in weight). All grassland tree species had fruits with animal dispersed characteristics. Sixty-seven per cent were drupes, 22 per cent were berries, while 11 per cent were capsule.

Basal sprouting with varying degrees of vigour occurred in all grassland species and in about 70 per cent of the individuals in the termite mound patches. This form of growth varied with different species. In *Bridelia micrantha* for instance, stumps sprouted with one or two of the sprouts becoming dominant and grew into mature trees. In *Maesa lanceolatum*, stumps sprouted into several stems of roughly equivalent sizes, usually with many small branches to produce a dense rounded crown. Seedlings of forest tree species did not have basal sprouting.

Seedlings of canopy trees were by far the most abundant vascular recruits. Relatively few of the herbaceous or scandent species present in the neighbouring forest were represented in these patches. Notably absent were seedlings of under storey species from the forest.

None of the species occurring in the termite mound patches were pioneers species typical of the surrounding forest, indicating that dispersal into these patches was directed. Grassland species on the other hand occurred in mixtures of pioneer species like *Acanthus spp.*, and *Maesa lanceolatum*, and later successional species like *Bridelia micrantha* and *Erythrina abyssinica*.

Species – Area Relationship

Responses of species to regeneration with increasing patch size varied for each category of species examined. Grassland species showed a strong positive correlation with increasing patch ($r=0.706$, $p<0.001$, $n=44$; Fig. 1). Forest species correlated less strongly with increasing patch size (Spearman, $r=0.307$, $p<0.043$; Fig. 2).

Results of analysis of covariance on the influence of patch age on species richness for forest and grassland tree species showed significant differences in regression slopes. The regression line for older patches had a significantly steeper slope ($b=0.0146$) than that for younger patches ($b=0.0011$; $F [1, 40] = 65.46$, $p<0.001$; Fig. 3). Consequently, differences in intercepts could not be analyzed statistically. A closer examination of figure 3 reveals that older patches had more forest tree species than younger patches.

In contrast, the slope of the same relationship for grassland tree species did not vary with the age of the patch (Fig. 4 older patches, $b=0.0038$; young patches, 0.0008 ; $F [1, 41] = 4.831$, $p<0.034$), indicating that older patches of a given area did not support more grassland tree species than younger patches of the same size. Old patches were those that did not show disturbances by people, fire or cattle. These were patches that had developed a fire buffer zone of prickly *Acanthus spp.* that made penetration into them by people and cattle difficult. With a well established canopy, herbaceous species suitable for grazing including grasses were absent.

When all patches were plotted against the total number of species present (grassland and forest), the correlation between species and area not only decreased below that of grassland trees species (from $r=0.740$ to $r=0.550$) but also the resulting curve conformed to the general species – area curve (Fig. 5; McArthur and Wilson 1967; Greig – Smith 1983). The number of species increased with increasing patch size, reaching the asymptote at about 1000m².

Overall, regeneration of forest species was abundant in older than in younger larger patches. With the exception of *Prunus africana* which is mainly an edge species. Seedlings of forest tree species were restricted in their distribution among patches (Table 1). Both seedlings and saplings of *Prunus africana* were found in 72.7 per cent of all the patches sampled, exceeding all other forest

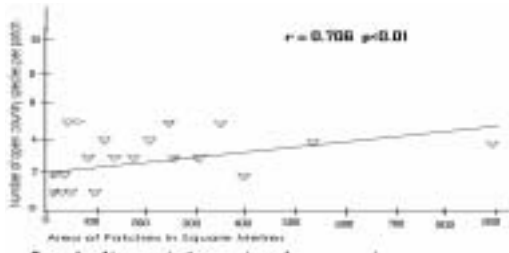


Fig. 1. Changes in the number of open-country species in relation to changing patch area.

Fig. 2. Relationship between forest species and patch area in Kakamega Forest.

Fig. 3. Relationship between forest free species and patch area and age in Kakamega Forest

tree species for the regeneration of many forest tree species in the grasslands. Patch size did not limit the regeneration of grassland tree species. *Bridelia micrantha* was the most widely distributed grassland species, occurring in all patches sampled, while *Erythrina abyssinica* and *Maesa lanceolatum* occurred in 50 per cent of all the patches, being the second and third largest in abundance of the grassland species (Table 2).

Fig. 4. Species response to patch size as a function of patch age

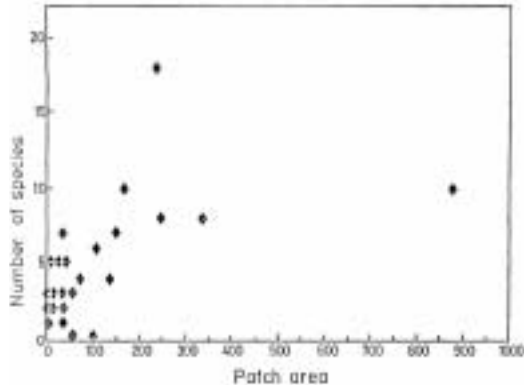


Fig. 5. Species-area relationship in termite mound patches in grasslands in the Kakamega Forest.

Species – Associations

Patches in which regenerating species were found occurred on grounds that were raised relative to the surrounding area. These raised patches were dead termite mounds. Active mounds were in most cases not colonized by trees. Colonization of mounds by trees was evident on dormant mounds and/or dying mounds. Dying or dead termite mound patches were therefore the centre of focus for the regeneration of many forest tree species. Could there be a relationship between grassland tree species and their saplings, and the forest tree species on the mounds?

There were similarities between fruits types and sizes of the two categories of species. Of interest was the small size of fruits of most of the tree species. Notable among these were *Prunus africana*, *Bridelia micrantha*, and *Maesa*

Table 1: Forest tree species occurring as seedlings in patches in study grasslands in Kisere forest.

Species	Mean mound patch size in m ²	Number of seedlings	Fruit type	Dispersal Mode	
				Animal	wind
<i>A. fraxinifolius</i>	170	2	capsule	no	yes
<i>A. grandibracteata</i>	64	4	capsule	no	yes
<i>A. gummifera</i>	170	1	capsule	no	yes
<i>A. phoberos</i>	238	32	drupe	yes	no
<i>A. toxicaria</i>	220	15	drupe	yes	no
<i>C. aristata</i>	238	32	drupe	yes	no
<i>C. Africana</i>	6	4	drupe	yes	no
<i>C. battiscombe</i>	280	10	drupe	yes	no
<i>C. macrostchyus</i>	320	5	capsule	yes	no
<i>F. varucarpa</i>	238	3	berry	yes	no
<i>E. mildabraedi</i>	238	8	drupe	yes	no
<i>E. macrophylla</i>	170	1	drupe	yes	no
<i>F. angolensis</i>	110	11	drupe	yes	no
<i>F. latifolia</i>	175	26	capsule	yes	no
<i>Blighia</i> sp.	238	9	drupe	yes	no
<i>O. welwitschii</i>	36	4	drupe	yes	no
<i>P. fulva</i>	420	9	capsule	no	yes
<i>P. Africana</i>	150	1509	drupe	yes	no
<i>M. eminii</i>	70	39	drupe	yes	no
<i>S. ellipticum</i>	310	33	drupe	yes	no
<i>Maesa</i> sp.	238	8	drupe	yes	no
<i>S. gigantum</i>	238	28	berry	yes	no
<i>T. roka</i>	210	21	capsule	yes	no
<i>V. apiculata</i>	250	12	drupe	yes	no

Table 2: Number of seedlings of open-country species, patch size, fruit type and dispersal modes in patches in Kakamega forest grasslands.

Tree Species	Mean mound patch size in m ²	Number of seedlings	Fruit type	Dispersal Mode	
				Animal	wind
<i>A. monticola</i>	267	61	drupe	yes	no
<i>Acanthus</i> spp.	135	1000	drupe	yes	no
<i>B.micrantha</i>	235	256	drupe	yes	no
<i>Dombea</i> spp.	392	298	drupe	yes	no
<i>E. abyssinica</i>	280	37	capsule	yes	no
Fern spp.	132	700	unknown	-	-
<i>P. guajava</i>	88	11	berry	yes	no
<i>H. madascariensis</i>	36	149	drupe	yes	no
<i>M.lanceolatum</i>	281	41	drupe	yes	no
“Shilindula”	22	4	drupe	yes	no
<i>V. fischeri</i>	33	19	unknown	-	-
Vine	300	1	unknown	-	-

lanceolatum. These tree species have very small fruits which are drupes. In addition, *Prunus africana* and *Bridelia micrantha* co-occurred significantly in about 70 per cent of the patches of all the tree species examined than would have been expected by chance ($\chi^2 = 4.36, p=0.045$).

All seedlings of forest tree species were found on mounds. Such mounds always had an adult *Bridelia micrantha* and/or *Erythrina abyssinica*. Occasionally, *Acacia* spp., *Maesa lanceolatum* and *Harungana madascariensis*

co-occurred with the former. Since forest tree species on the mounds were seedlings or saplings, there appeared to be a relationship between grassland tree species and forest tree species that were regenerating on these mounds.

There was a positive association between presence of seedlings of forest species and established adults of grassland tree species ($\chi^2 [0.05, 1] = 4.137, p < 0.05$). Regeneration of forest tree in these patches appeared to follow the establishment of adult grassland tree species.

This relationship was, however, not species specific because the establishment of forest tree species on mounds was independent of the species of the adult grassland tree established on the mound.

DISCUSSION

These results clearly demonstrate the importance forest grasslands in the regeneration of forest canopy trees. This role is further reinforced by the presence of termite mound patches that provide safe havens for seed germination and growth of tree species (Augspurger 1983, 1984; Janzen 1970, 1971). Termite mounds are raised grounds that are devoid of grass. They therefore do not attract grazers that are mainly cattle ensuring safety for the regenerating species from which new forest spreads. The size and age of the termite mound patch also greatly influences the type of tree species that will regenerate. Older mound patches appear to provide condition that allow for easier regeneration of forest tree species. Larger termite mound patches resemble large forest gaps that allow for establishment of colonizing species (Augspurger 1984). In addition, mounds contain abundant nutrients that make them provide optimal habitats for growth of trees (Bagine 1982; Lamotte 1982; Woods and Sands 1978). Mounds therefore appear to be centres of regeneration of forest tree species. The events that shape forest invasion of the grasslands are initiated on the mounds when they begin to die or become dormant.

The establishment of a grassland tree species appears to precede establishment forest tree species. The commonest grassland tree species on the mounds is *Combretum molle*, which is a wind dispersed species, *Bridelia micrantha* and *Maesa lanceolatum* both of which are animal dispersed. These are used by animal dispersers that make incursions into the forest to feed on fruits of sizes similar to those found in the grasslands. These dispersers appear to be mainly birds that perch on these trees more so, during termite swarming (Tsingalia 1988). It appears like these bird species establish the link between the forest and the grasslands. That animal dispersal is important can be seen in the number of animal dispersed tree species on the mounds.

The effect of patch area on the number of regenerating tree species clearly shows the differences in requirements of forest and grassland

tree species (Brokaw 1987; Condit et al. 1999, 2000). Forest trees respond better to patch age than area because older patches appear to possess characteristics that are necessary for the regeneration of forest tree species. This explains why they are less sensitive to patch area. Thus large older patches will have more forest tree species than smaller older patches. Reasons for this discrepancy are yet to be investigated and therefore call for future research.

Evidence of basal sprouting is demonstration of the effects of fire in these grasslands. It is an adaptation of regeneration of plants that are subjected to fires and grazing. This mode of regeneration was clearly absent in forest tree species.

CONCLUSIONS AND RECOMMENDATIONS

It appears that regulated burning and the cutting of grass by people, and grazing by cattle does not impede forest succession of grasslands. This has great implications on the roles of the communities that surround the forest in conservation efforts. Forest grasslands have traditionally been used by the local communities as sources of grass and grazing for their cattle. Conservation efforts that strike a positive balance between grazing and cutting of grass, and forest regeneration in the grasslands will maintain a cordial relationship between these local communities and conservationists. A total ban on grazing and grass harvesting that is sometimes advocated by conservationists can only exacerbate conservation efforts.

Kakamega Forest with its many types of grassland is managed by two institutions – Kenya Wildlife Service (KWS) and the Kenya Forest Service (KFS). Each organization has a deferent approach to conservation with Kenya Wildlife Service advocating for a total ban while the Kenya Forest Service allows limited use of the forest by the local communities. These two differing approaches have greater ecological implications for the dynamics of both the forest and the grasslands. A detailed study of the effects these approaches have on conservation efforts is therefore recommended.

The canopy forest trees that regenerate in older termite mound patches in the grasslands do not regenerate easily inside the forest. This appears to suggest that grasslands provide safe sites in which seeds of these canopy dominants

escape seed predation. But these sites are useless unless seed dispersers that utilize both the forest and the grasslands are present. A study on the differences in the conservation and management styles may reveal how these dispersers respond to changing conditions. In addition, these management styles are likely to have large impacts on important mound building termite species.

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