Thicket clumps: A characteristic feature of the Kagera savanna landscape, East Africa

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Abstract

Question: What are the genesis and development of thicket clumps within a savanna landscape at geomorphically different locations and what are the driving forces?

Location: The Kagera Region, in the border area of Rwanda, Uganda and Tanzania.

Methods: The vegetation of 32 dry evergreen thicket clumps and their surrounding savannas have been analysed at different geomorphic locations. At each vegetation plot Na^+, K^+, Mg^{2+}, Ca^{2+}, Al^{3+}, $Fe^{2+/3+}$, H^+, P, C, N, bulk density and particle size were determined for each soil horizon. The impact of soil and termite mounds on thicket clump dynamics on seasonally waterlogged plains, gentle slopes and stony hillsides were assessed.

Results: Thicket clumps and their surrounding savannas have a distinct structure and floristic composition. They also have distinct soil properties although parent materials are the same. On seasonally waterlogged plains, new thicket clumps can develop on *Macrotermitinae* mounds; on stony hillsides, *Trinervitermes* and *Macrotermes* show a uniform distribution pattern and may initiate the genesis of thicket clumps.

Conclusions: Geomorphology broadly determines the significance and interactions of the main factors affecting site-specific vegetation dynamics. On seasonally waterlogged plains, thicket clumps are restricted to termite mounds. Since intra-species competition dictates a minimal distance between neighbouring *Macrotermitinae* colonies, thicket clumps do not coalescence. By contrast, on stony hillsides, the vegetation mosaic is highly dynamic and determined by the interplay of several factors. The growth of thicket clumps is mainly a function of the fire regime and the browsing intensity. At the present time, frequent cool, early dry season fires and the near absence of large browsers have favoured the advance and coalescence of thicket clumps and forest patches on stony hillsides.

Keywords: Browsing; Dry evergreen forest; Ecosystem dynamics; Termitarium; Vegetation mosaic.

Nomenclature: Troupin (1978, 1983, 1985, 1988) for grasses and forbs; Beentje (1994) for woody plants; Pearce (1997) for termites.

Introduction

Savannas of varying physiognomy cover about 20% of the Earth's land surface and about 40% of Africa (Cole 1986; Scholes & Walker 1993; Mistry 2000). They embrace the larger part of the world's undeveloped and underdeveloped lands and are of great importance for the livelihood of rural communities mainly for subsistence farming and animal husbandry. Better understanding of the driving forces of savanna dynamics is essential for sustainable management. Water and nutrient availability, fire and herbivores are considered as the main determinants in the distribution, structure and function of savannas while the relative importance of these interactive determinants depends on geomorphology (Walker 1987; Furley et al. 1992; Skarpe 1992; Scholes & Walker 1993; Archer 1995). Savanna landscapes are composed of a highly variable mosaic of vegetation patches of different size having distinct tree-grass ratios caused by such varied local features as animal waste, trails, presence of perennial plants producing clonal areas, burrows, tree shading, termite mounds, erosion, sodic patterns, inselbergs, gullies and watercourses, as well as slope and drainage (Belsky 1989).

Thicket clumps and small forest patches of various shapes and sizes are often irregularly dispersed within the savanna vegetation and are important elements of the landscape. So far, the dynamics of these formations including the pivotal role of nucleus trees in the genesis of thicket clumps have been studied only to a limited extent mainly along the rain forest-savanna boundary e.g., Central and South America (Kellman 1979; Furley et al. 1992), southwestern India (Puyravaud et al. 2003), and northern Australia (Bowman et al. 1990). However, little is known about the dynamics of dry evergreen thicket clumps within savanna landscapes with no or very low affinities with rain forest like those of the Kagera region of East Africa (Bloesch 2002). Only Liben (1961), Troupin (1966) and Runyinya (1979) analysed the dynamics of the Kagera thicket clumps and forest patches to some extent

but they did not consider the role of termite activities and geomorphology. To understand vegetation patterns in savanna landscapes, it is necessary to study vegetation dynamics at a range of spatial scales, over long periods (Gillson 2004) and on different geomorphologic positions (Cole 1986; Bloesch & Klötzli 2005).

In the present study, a landscape approach has been used, concentrating on the geomorphology and spatial distribution, soil properties and large termitaria as possible driving forces of thicket clump dynamics. The additional factors climate, fire and mammalian herbivory were addressed by Bloesch (2002) and are shortly considered in the Discussion and Conclusions only.

Two main hypotheses are put forward and tested: firstly, that thicket clumps within a grass savanna matrix on seasonally waterlogged plains are usually restricted to termite mounds, remain apart rather than amalgamate, and the vegetation mosaic stays relatively static; secondly, that thicket clumps on stony hillsides, which are irregularly distributed in shrub savannas, tend to spread and fuse forming small, dry evergreen forest patches, and the vegetation mosaic is relatively dynamic.

Study areas

The Kagera Region (of which the administrative *Kagera Region* in Tanzania is a part) lies in the border area of Rwanda, Uganda and Tanzania (Fig. 1) and forms a geographical and ecological unit with common socio-cultural roots (Bloesch 2002). The region is named after
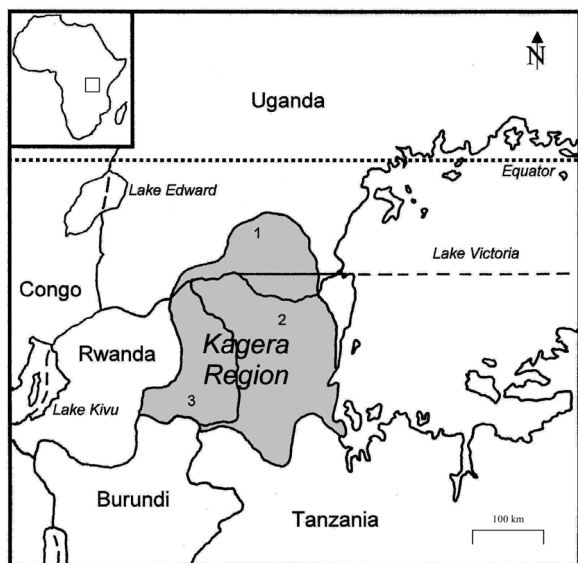
Fig. 1. The Kagera Region. 1. Lake Mburo National Park (0°37' S, 30°39' E); 2. Kikulula Ranch (1°28' S, 31°13' E); 3. Karama ISAR research site (2°11' S, 30°17' E).

the Kagera River (Nyabarongo and Akagera in Rwanda), which is the upper part of the White Nile system. The Kagera savanna landscape covers ca. 30 000 km^2 of variable geomorphology of the Great Rift Valley System, between 1142 and 1800 m a.s.l. The predominant soil types are dystric Planosol with vertic characteristics on seasonally waterlogged plains, Ferralsol on gentle slopes and dystric Leptosol on stony hillsides (FAO/UNESCO/ISRIC, Anon. 1988).

The rainfall pattern is typically bimodal near the equator having a major peak in March-May, and a second peak in (October) November-December. The main dry season from mid-May-August normally lasts about 100 days (Troupin 1966). Annual rainfall ranges from 650 mm to about 1000 mm and is quite unpredictable and remarkably irregular in time and space, the coefficient of variation being ca. 20-25% (Bloesch 2002). Mean annual temperature is about 21 °C with daily temperatures fluctuate between 12 and 34 °C. The climate type in the Köppen system is Aw (Köppen 1931). Thicket clumps and small, variably-sized forests on stony hillsides are a peculiar trait of this savanna landscape (Figs. 2 and 3). Thicket clumps are defined as: Dry, evergreen formations, with a mean height of the dominant trees of 8 to 10 m, containing dense clusters of gnarled, much-branched, often armed trees and shrubs, thickly interlaced with climbers and almost impenetrable. Succulents are often present and there is a very sparse herbaceous layer.

Methods

Three study areas, the Kikulula cattle ranch (Tanzania), the ISAR (*Institut des Sciences Agronomiques du Rwanda*) research site at Karama (Rwanda) and Lake Mburo National Park (Uganda) were selected (see Fig. 1) on the basis of two criteria: (1) the areas contain typical thicket clumps at different geomorphic locations and (2) the vegetation pattern illustrates different successional stages, allowing study of the dynamic processes.

Vegetation

Vegetation structure and floristic composition of 32 sites as listed below were analysed using the phytosociological methods outlined by Braun-Blanquet (1932):

8 sites on seasonally waterlogged plains at Kikulula and Lake Mburo National Park;

12 sites on gentle slopes at Lake Mburo National Park and Karama;

12 sites on stony hillsides at Kikulula and Karama.

Each surveyed site comprised two sampling plots, one in the core part of the thicket clump and one in each of the surrounding savanna types, ca. 20 m from the

thicket edge (64 plots in all). Since eight thicket clumps are surrounded by two different savanna types, 72 plots were surveyed in total.

At each plot, the herb layer was studied using a subplot of 5 m × 5 m (thicket) or 8 m × 8 m (savanna), and the tree/shrub layer by a subplot of 25 m × 25 m (thicket) or 50 m × 50 m (savanna), following consideration of the appropriate minimal area. On seasonally waterlogged plains and gentle slopes, due to the sizes of thicket clumps (20-150 m²) the whole thicket clump was sampled in order to record the tree/shrub layer and, for the herb layer, the sampling was restricted to the core part, thereby excluding any ecotone effect. The cover-abundance value (Braun-Blanquet 1932) of all species was recorded separately for each layer.

Vegetation surveys were conducted mainly in the first half of the dry season, before general burning started. At this time many plants are flowering, aerial shoots of geophytes are present, and the grasses still have their inflorescences, facilitating species identification. All vascular plants have been recorded and at least one specimen per species has been collected and stored in a herbarium. The herbaria of the *Institut National de Recherche Scientifique* in Butare (Rwanda), of the University of Makerere in Kampala (Uganda) and of the *Jardin Botanique National de Belgique* in Meise (Belgium) were consulted for identification of uncertain species.

Out of the 32 sampled thicket clumps, two mature thicket clumps on seasonally waterlogged plains, stony hillsides and smooth rounded hilltops respectively, and one on gentle slopes were analysed using a modified line-intercept method (Buell & Cantlon 1950), together with a belt-transect. A belt-transect 2 m wide and 25 to 55 m long (according to the size of the thicket clump) was taken through the thicket, extending into open savanna on either side. This approach allows good assessment of the spatial variation (horizontal and vertical structure) across the thicket clumps and their ecotone (Mühlenberg 1993).

The floristic similarity (β-diversity) of thicket clumps and their surrounding savannas has been assessed using the community coefficient C_j of Jaccard (1928). One of the great advantages of the Jaccard index is its simplicity, though the cover-abundance value of species is not included (Magurran 1988).

Soil

For each of the 72 vegetation plots a soil pit was excavated for the description of the soil profile and for chemical and physical analysis. In total, 231 samples were taken from the topsoil and subsoil and air-dried. The samples were collected at the beginning of the dry season before the savannas had been burnt. The savanna soil samples were taken at least 10 m from the nearest tree in order to avoid its effect on the soil properties (Kellman 1979; Weltzin & Coughenour 1990; Belsky & Amundson 1992). Topsoil values correspond to samples of the A-horizon or samples taken at 15 - 20 cm depth (if there was no clear horizon boundary); subsoil values correspond to the average value of B- and C-horizons or were taken at around 50 cm depth (if no clear horizon boundary). The chemical parameters have been determined following standard methods (Anon. 1996). To measure pH, sub-samples were determined after standing overnight in H_2O; a replicate set of pH readings was measured in 0.01 M $CaCl_2$ (1:2.5). For cation determination (Na^+, K^+, Mg^{2+}, Ca^{2+}, Al^{3+}, $Fe^{2+/3+}$), the soil was extracted with NH_4-acetate and EDTA at pH 4.65. The soil suspension was shaken, filtered and the cations were subsequently determined by atomic absorption spectrometry (Varian, Spectr AA-400). Exchangeable H^+ was determined by combining a soil suspension (20 g soil, 20 ml H_2O) with a buffer solution of pH 8 (20 ml). Readily available P was determined after extraction with NH_4-acetate and EDTA at pH 4.65, and measured colorimetrically (λ = 690 nm). The measurement of total carbon and nitrogen content used a fully automatic CN-Analyser (LECO, CNS-2000). Bulk density was measured using a cylinder method (Anon. 1996), except on stony hillsides where this method is not suitable. Particle size was analysed using the pipette method.

The soil data for Kikulula on seasonally waterlogged plains and stony hillsides as well as for Lake Mburo National Park on gentle slopes were analysed by a two-way analysis of variance (ANOVA) with interactions between vegetation and relief types, stratified by topsoil and subsoil (though for technical reasons not all the analytical data could be used). If normality of residuals was not obtained for a parameter ($p \le 0.05$), ANOVA used a logarithmic distribution. Texture was not included in the two-way analysis of variance since the analysed samples were not taken from exactly the same sites.

Termites

Mound-building termites have been studied since they may offer favourable conditions for the growth of woody plants. At all sites, the species were identified and their feeding behaviour recorded. The mound characteristics (population, structure, height, diameter, and number per ha) and their vegetation cover were noted. The dispersion pattern of termitaria is an important criteria for coalescence of thicket clumps. *Macrotermes* mounds, both bare and vegetated, have been mapped on two seasonally waterlogged plains, at Kikulula and Lake Mburo National Park, having areas of 2.5 and 6.7 ha respectively. The dispersion pattern of *Trinervitermes* mounds at Kikulula

has been analysed on three stony hillsides (areas of 0.2, 0.3 and 0.5 ha) using orthophotographs. A grid has been put on these maps to count the number of mounds per grid. The three basic types of pattern and their variance-to-mean relationships followed the definitions of Ludwig & Reynolds (1988).

Results

Vegetation

Mature thicket clumps on seasonally waterlogged plains and on gentle slopes mostly measure 100 - 150 m² in area (Fig. 2) and even large ones do not usually exceed 400 m². On stony hillsides, thicket clumps may be of much larger size (Fig. 3). The mean species number of thicket clumps is 29 (sd = 7) and considerably higher than that of savannas with a mean species number of 19 (sd = 6); but note the differences in size of the respective minimal areas sampled.

Thicket clumps and their surrounding savannas are separated from one another by a sharp ecotone, which is usually less than 2 m broad and mainly composed of climbers and heliophilous savanna species (Figs. 2 and 3). The two plant communities have a distinct structure and floristic composition. In total 183 species were found in 32 thicket clump plots; 192 species occur in 40 savanna plots, with 52 species common to both vegeta-

tion types. Jaccard's index is 16% (when comparing all thicket clumps with all savanna sites), a relatively high beta-diversity.

If the ecotone is excluded in the comparison, the floristic difference between thicket clumps and savannas becomes very obvious (data from belt-transects). Only six identical plant species, whereof three are forbs, are found in the core part of seven thicket clumps and in their adjacent open savannas. *Rhus natalensis* is the only woody plant that occurs frequently as an adult plant in both plant communities. *Carissa edulis* and *Psydrax schimperiana*, both typical woody thicket clump species, only occur transiently as seedlings in the adjacent savanna as do some other forest species.

The ubiquitous species *Rhus natalensis*, *Grewia trichocarpa* and *Teclea nobilis* are important elements for the structure of thicket clumps on all types of relief (see Table 1). Further woody species with a high degree of cover are *C. edulis* and *Albizia petersiana* (only at Kikulula) on seasonally waterlogged plains, the wild olive (*Olea europaea*) on gentle slopes, and *Haplocoelum gallaense*, a sciaphilous tree reaching ages of over 500 years, on stony hillsides. From the 33 common thicket clump woody plants (occurring in at least 20% of the sampling plots, see Table 1), only *G. trichocarpa*, *Pappea capensis*, *Euphorbia candelabrum* and the already mentioned *R. natalensis*, also occur frequently in savannas mostly on barely vegetated termitaria.

Lianas are abundant in the herb and tree/shrub layer
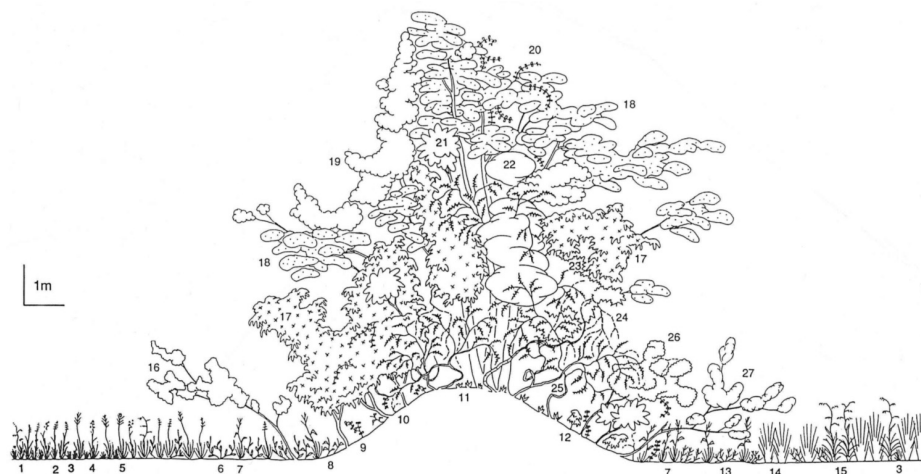
Fig. 2. Profile diagram of thicket clump on termitarium, Kikulula plain (drawn by D. Berner)
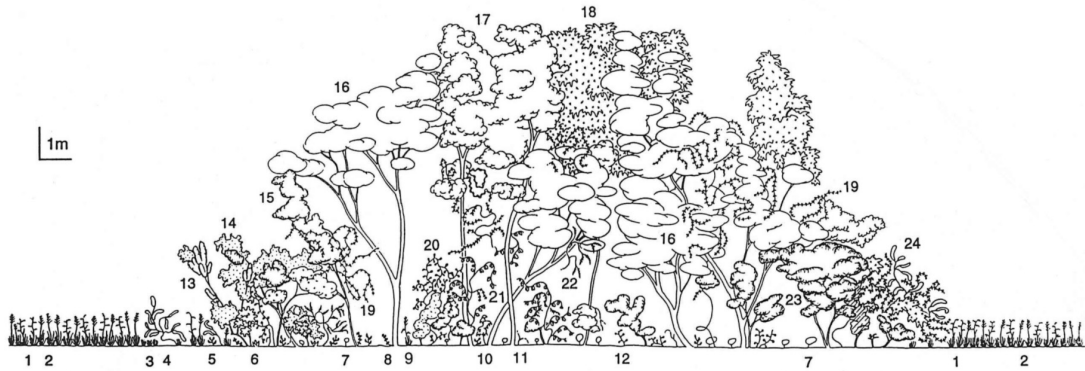
Herb layer
1	*Hyparrhenia filipendula*	9	*Jasminum schimperi*	
2	*Sporobolus pyramidalis*	10	*Cissus quadrangularis*	
3	*Fimbristylis complanata*	11	*Sansevieria parva*	
4	*Themeda triandra*	12	*Teclea nobilis*	
5	*Loudetia simplex*	13	*Cynodon dactylon*	
6	*Brachiaria decumbens*	14	*Miscanthus violaceus*	
7	*Panicum maximum*	15	*Hyparrhenia diplandra*	
8	*Setaria kagerensis*			

Tree/shrub layer
16	*Pittosporum spathicalyx*	23	*Allophylus ferrugineus*
17	*Teclea nobilis*	24	*Cissus quadrangularis*
18	*Albizia petersiana*	25	*Capparis erythrocarpos*
19	*Ficus glumosa*	26	*Carissa edulis*
20	*Jasminum schimperi*	27	*Rhus natalensis*
21	*Grewia trichocarpa*		
22	*Haplocoelum gallaense*		

Fig. 3. Profile diagram of thicket clump on a stony hillside (slope 45%), Kikulula (drawn by D. Berner).

Herb layer		Tree/shrub layer	
1 *Hyparrhenia newtonii*	7 *Haplocoelum gallaense*	13 *Rhus natalensis*	19 *Ancylobotrys amoena*
2 *Loudetia simplex*	8 *Jasminum schimperi*	14 *Harrisonia abyssinica*	20 *Blepharispermum pubescens*
3 *Cyperaceae*	9 *Panicum maximum*	15 *Psydrax schimperiana*	21 *Strychnos lucens*
4 *Rhynchosia resinosa*	10 *Teclea nobilis*	16 *Haplocoelum gallaense*	22 *Capparis erythrocarpos*
5 *Commelina* spec.	11 *Cissus quadrangularis*	17 *Drypetes gerrardii*	23 *Canthium* spec. 2
6 *Sansevieria parva*	12 *Blepharispermum pubescens*	18 *Canthium* spec. 1	24 *Rhynchosia resinosa*

Table 1. Common woody plants of thicket clumps on different topography at Kikulula, Karama and Lake Mburo National Park.

Species	Life form	Plains (n = 8) (mean cover degree)	Gentle slopes (n = 12) (mean cover degree)	Stony hillsides (n = 12) (mean cover degree)	Relative constancy (%)
Rhus natalensis	s	**16.6**	**5.7**	**7.5**	88
Grewia trichocarpa	t/s	**13.4**	**17.1**	**10.9**	84
Jasminum schimperi	l	3.5	**5.1**	1.9	84
*Teclea nobilis**	t	**6.3**	**8.0**	**6.9**	84
*Cissus quadrangularis**	l	2.3	1.4	1.0	78
Euclea racemosa	t/s	4.3	0.8	1.0	75
*Haplocoelum gallaense**	t	2.5	4.0	**15.5**	75
Capparis erythrocarpos	l	**9.7**	2.4	2.8	72
Scutia myrtina	s	**6.9**	**5.8**	0.7	72
*Olea europaea**	t	3.5	**22.1**	2.7	69
Carissa edulis	s	**13.1**	0.9	2.1	66
Allophylus ferrugineus	t	1.0	1.2	1.1	63
Canthium lactescens	t	-	2.4	2.2	56
Acokanthera schimperi	s	0.9	1.3	1.6	53
Coffea eugenioides	t/s	0.3	**5.7**	4.0	53
Psychotria kirkii	s	0.1	1.2	2.4	53
Asparagus falcatus	l	1.0	1.9	0.2	44
*Psydrax schimperiana**	t	-	**7.6**	**7.6**	44
Flacourtia indica	s	0.4	0.5	0.7	44
Pappea capensis	t	1.1	3.4	0.1	41
Pittosporum spathicalyx	t	**5.0**	-	1.3	41
Euphorbia candelabrum	t	4.8	**5.1**	-	38
Grewia similis	s	**5.3**	4.2	1.5	38
Ancylobotrys amoena	l	0.3	-	**7.6**	34
Strychnos lucens	s/l	0.3	0.2	**6.2**	34
Harrisonia abyssinica	s	2.2	-	0.1	28
Jasminum fluminense	s/l	3.1	-	0.3	28
Albizia petersiana	t	**13.4**	-	1.3	25
Blepharispermum pubescens	l	0.1	-	2.5	25
Triumfetta cordifolia	s	0.4	0.2	0.7	25
Clausena anisata	s	1.3	-	0.3	22
Maytenus arguta	s	0.3	-	0.3	22
Microglossa pyrifolia	s/l	0.3	0.3	0.3	22

Species of the core part of thicket clumps which are typical sciaphilous are marked with an asterisk. Relative constancy refers to the number of *relevés* in which a given species occurs, expressed in percentage of the total number of relevés. The mean cover degree (Knapp 1971) is the conversion of the Braun-Blanquet cover-abundance values into cover percentages; mean cover degrees ≥ 5 in bold. Life forms: t = tree, s = shrub, l = liana.

and they are a typical feature of thicket clumps (see below). The herb layer is usually sparse and not continuous, and only abundant in gaps including the constant species *Asystasia gangetica*, *Achyranthes aspera* and *Setaria kagerensis* as well as the more sporadic *Erythrococca bongensis*, *Fuerstia africana* and the succulents *Sansevieria parva* and *Sarcostemma viminale*.

The floristic composition of thicket clumps is very uniform with 21 constant woody species (constancy value higher than 40%, see Table 1) despite the heterogeneous stratification of the woody layer, the diverse topography and the considerable distance of about 220 km between Lake Mburo National Park in the north and Karama in the south of the Kagera Region as shown by Jaccard's similarity index:

Seasonally waterlogged plain ($n = 8$) – gentle slope ($n=12$): $C_j = 70\%$
Gentle slope ($n = 12$) – stony hillside ($n = 12$): $C_j = 73\%$
Seasonally waterlogged plain ($n = 8$) – stony hillside ($n = 12$): $C_j = 91\%$

On the other hand, the floristic composition of savannas is highly heterogeneous varying strongly with the landform. Only five species are constant within savannas, namely one woody plant (*Rhus natalensis*), two grasses (*Loudetia simplex* and *Sporobolus pyramidalis*) and two forbs (*Vernonia schweinfurthii* and *Spermacoce pusilla*).

Nucleus tree species being essential for genesis and development of thicket clumps as personally observed over the years are mostly found in all three study areas, but only *G. trichocarpa* and *O. europaea* play the same important dynamic role in all areas (see Table 2). *A. petersiana* and *Maytenus heterophylla* having a limited geographical distribution may act as nucleus species only in Kikulula and Lake Mburo National Park, respectively. Shrubs may play an important role in the genesis of thicket clumps as well, preceding tree growth. *R. natalensis* not only plays an essential role in the thicket genesis but, as a typical ecotone species, may also favour the extension of thicket clumps. *C. edulis* (at Kikulula on seasonally waterlogged plains), *G. similis* and *Scutia myrtina* (both at Lake Mburo seasonally waterlogged plains) are important pioneer shrubs of thicket clump genesis and development, but were only located in one of the studied sites. *Capparis erythrocarpos* frequent on all landforms may also initiate the growth of a thicket clump. It has the life form of a subshrub if isolated in the savanna matrix, but takes the life form of a liana within a thicket. At a later successional stage, *Ancylobotrys amoena* (mainly on stony hillsides), *Blepharispermum pubescens* (mainly Kikulula) and the more sporadic *Microglossa pyrifolia*, may form a dense 'curtain' around the thicket clump, while the ubiquitous *Jasminum schimperi* is frequent in the herb layer and shrub layer. *Asparagus falcatus*, *Cissus quadrangularis*, *Dioscorea* spp. and *Sarcostemma viminale* are typical lianas of the core part of mature thicket clumps. The abundance of lianas in the core part becomes reduced in larger thicket clumps (diameter > 30 m, only occurring on stony hillsides).

Soil

The results of the two-way analysis of variance show significant differences for most soil properties between thicket clumps and savannas (see Table 3a and 3b), the differences being slightly more pronounced for topsoil. Both tables are a summary of the complete two-way analysis of variance (ANOVA) displaying only the main effects for vegetation. Significant differences are shown with asterisks when the interactions between relief and vegetation were not significant at the 1% level. Differences for the relief types are for most parameters significant but are not shown since they are outside of the scope of this study. Most parameters, with the exception of Na, K and P, vary relatively little, as reflected in the low standard error.

The pH value of thicket clump soil on seasonally waterlogged plains and on gentle slopes is higher than the

Table 2. Constant nucleus trees of thicket clumps.

Seasonally waterlogged plains		Gentle slope		Stony hillside
Kikulula ($n = 6$)	Lake Mburo ($n = 2$)	Lake Mburo ($n = 6$)	Karama ($n = 6$)	Kikulula ($n = 6$)
Albizia petersiana	***Euphorbia candelabrum***	***Olea eurpaea***	*Olea europaea*	***Euclea schimperi*** *
Euclea schimperi *	*Grewia trichocarpa* *	*Grewia trichocarpa* *	***Grewia trichocarpa*** *	*Boscia angustifolia* *
Grewia trichocarpa *	*Maytenus heterophylla* *	*Maytenus heterophylla* *	*Boscia angustifolia* *	*Grewia trichocarpa* *
Olea europaea	*Olea europaea*		*Euphorbia candelabrum*	*Olea europaea*
Pittosporum spathicalyx *			*Pappea capensis* *	*Parinari curatellifolia* *
				Pappea capensis *
				Pittosporum spathicalyx *

Typical pioneer species are marked with an asterisk; Most frequent nucleus trees are written in bold; Nucleus trees in thicket clumps on stony hillside from Karama could not been determined as they have been cut.

Table 3a. Chemical and physical properties of the topsoil at Kikulula and Lake Mburo National Park.

Vegetation type	pH (H₂O) **	pH (CaCl₂) ***	CEC***	Base saturation	Na	K**	Mg	Ca	Al***	H-ions	C***	N***	C/N-ratio***	Fe	P***	Bulk density ***	Texture
			mmol/100g soil	(%)	mg/100g soil	mg/100g soil	mg/100g soil	mg/100g soil	mg/100g soil	mmol/100g soil	mg/100g soil l	mg/100g soil		mg/100g soil	mg/100g soil	g/dm³	clay: silt: sand (%)
Thicket clumps on plains (n = 6)	5.7	5.1	19.16	67.7	5.33	72.28	61.22	121.76	11.65	4.67	2608	338	7.6	18.4	0.528	899	35:46:19
	(0.21)	(0.24)	(1.24)	(3.79)	(1.79)	(22.83)	(8.32)	(12.13)	(1.79)	(0.32)	(272.2)	(25.1)	(0.29)	(3.34)	(0.092)	(33.9)	
Savannas on plains (n = 6)	4.8	4.0	12.57	28.0	15.47	6.50	15.38	29.95	23.22	6.39	1583	237	6.7	60.8	0.176	1216	20:43:37
	(0.15)	(0.05)	(0.71)	(1.83)	(8.48)	(0.31)	(1.86)	(5.03)	(1.73)	(0.37)	(76.5)	(7.6)	(0.17)	(7.91)	(0.023)	(18.2)	
Thicket clumps on gentle slopes (n = 6)	5.9	5.3	12.06	60.4	0.01	42.63	28.64	79.03	10.25	3.53	1838	337	5.4	16.2	0.256	1218	17:12:71
	(0.25)	(0.24)	(0.55)	(4.03)	(0.00)	(6.06)	(2.95)	(10.06)	(0.97)	(0.26)	(172.6)	(11.9)	(0.32)	(1.79)	(0.072)	(24.8)	
Savannas on gentle slopes (n = 6)	5.1	4.4	8.49	20.2	2.47	17.95	7.15	11.68	23.00	4.20	958	256	3.7	13.6	0.096	1468	19:7:74
	(0.15)	(0.14)	(0.28)	(4.09)	(2.35)	(3.07)	(1.75)	(3.59)	(2.15)	(0.13)	(75.3)	(7.6)	(0.20)	(1.17)	(0.013)	(24.8)	
Thicket clumps on stony hillsides (n = 3)	4.4	3.8	17.25	14.2	0.61	23.73	10.84	18.96	61.63	7.93	3310	360	9.2	76.0	0.293	n.d.	36:31:33
Savannas on stony hillsides (n = 3)	4.6	4.0	14.41	3.2	0.21	8.40	2.60	0.74	60.45	7.22	1854	286	6.4	18.5	0.102	n.d.	29:31:40

F-test for main effects in the two-way analysis of variance (ANOVA) with interactions; the standard error is indicated in brackets; n.d. = not determined
* p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001 are significant differences for the vegetation type (no significant interactions between relief and vegetation, p ≥ 0.01)
Base saturation***, Mg***, Ca*** show also significant differences for the vegetation type but having significant interactions between relief and vegetation (p ≤ 0.01) and therefore require careful interpretation.

Table 3b. Chemical and physical properties of the subsoil at Kikulula and Lake Mburo National Park.

Vegetation type	pH (H₂O)	pH (CaCl₂)	CEC	Base saturation ***	Na	K ***	Mg	Ca**	Al*	H-ions*	C**	N**	C/N-ratio**	Fe	P***	Bulk density	Texture
			mmol/100g soil	(%)	mg/100g soil	mg/100g soil	mg/100g soil	mg/100g soil	mg/100g soil	mmol/100g soil	mg/100g soil l	mg/100g soil		mg/100g soil	mg/100g soil	g/dm³	clay: silt: sand (%)
Thicket clumps on plains (n = 6)	5.5	4.7	17.81	64.9	12.74	74.67	52.52	93.86	13.22	4.87	1403	254	5.4	18.2	0.200	1225	n.d.
	(019)	(0.26)	(0.90)	(3.50)	(1.26)	(20.49)	(5.67)	(8.81)	(3.45)	(0.51)	(224.1)	(11.9)	(0.63)	(4.61)	(0.059)	(66.3)	
Savannas on plains (n = 6)	5.0	3.8	19.68	38.7	39.91	11.67	33.29	60.43	38.21	7.93	1037	234	4.4	33.4	0.042	1353	51:31:18
	(0.17)	(0.08)	(1.09)	(3.55)	(8.15)	(1.34)	(3.47)	(10.79)	(5.90)	(0.57)	(67.9)	(8.6)	(0.26)	(3.26)	(0.005)	(36.2)	
Thicket clumps on gentle slopes (n = 6)	5.1	4.3	7.89	29.0	0.58	46.55	10.79	5.48	13.77	4.13	618	238	2.6	8.5	0.050	1258	19:7:74
	(0.16)	(0.19)	(0.61)	(5.48)	(0.33)	(4.71)	(2.45)	(3.34)	(2.91)	(0.42)	(27.8)	(4.0)	(0.12)	(0.83)	(0.009)	(17.4)	
Savannas on gentle slopes (n = 6)	4.8	4.1	9.00	6.0	0.01	4.78	5.05	0.54	28.77	5.24	436	221	2.0	7.3	0.041	1315	23:6:71
	(0.09)	(0.04)	(0.35)	(1.52)	(0.00)	(0.57)	(2.10)	(0.20)	(0.61)	(0.17)	(29.7)	(3.7)	(0.14)	(0.51)	(0.003)	(22.8)	
Thicket clumps on stony hillsides (n = 3)	4.8	3.9	13.33	15.1	0.50	17.12	6.58	20.05	45.50	6.28	2172	295	6.7	42.6	0.375	n.d.	35:32:33
Savannas on stony hillsides (n = 3)	4.8	4.1	10.34	1.6	0.42	4.52	0.22	0.07	42.72	5.44	567	210	2.5	2.2	0.020	n.d.	29:39:32

F-test for main effects in the two-way analysis of variance (ANOVA) with interactions; the standard error is indicated in brackets; n.d. = not determined
* p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001 are significant differences for the vegetation type (no significant interactions between relief and vegetation, p ≥ 0.01)
Mg*** show also significant differences for the vegetation type but having significant interactions between relief and vegetation (p ≤ 0.01) and therefore require careful interpretation.

corresponding value for the surrounding savanna, both in topsoil and subsoil, while the opposite is the case on stony hillsides. This may be due to the fact that thicket clumps on seasonally waterlogged plains and gentle slopes have higher termite activity than the surrounding savannas (see below), leading to more rapid decomposition of organic matter. Thicket clumps on all types of relief clearly show higher cation exchange capacity values in the topsoil than do savannas, though the differences are less pronounced in the subsoil. Base saturation values of thicket clumps are always considerably higher than those of the respective surrounding savannas, both in topsoil and subsoil. The values from seasonally waterlogged plains are always the highest and those from stony hillsides the lowest, with an exchange complex almost completely saturated with H⁺ and aluminium. Thicket clumps on seasonally

waterlogged plains and gentle slopes have lower Al and H⁺-values than savannas, both in topsoil and subsoil. On stony hillsides the Al and H⁺-values of thicket clumps and savannas are highest and very similar. The high Al-values on stony hillsides may be the result of the greater proximity to the regolith, which continuously supplies Al-ions.

Thicket clumps on all relief types show considerably higher values for K, Mg and Ca in topsoil and subsoil than savannas. This could be the result of (a) a greater rooting depth of woody plants in thicket clumps, increasing the content of available mineral nutrients in the system, and (b) a comparatively low leaching rate. Topsoil values for K, Mg and Ca tend to be higher than subsoil values with the main exception of the seasonally waterlogged Kikulula plains, which show systematically

Table 4. Dispersion pattern of *Macrotermes* and *Trinervitermes* mounds.

Termite species	Location	Size of site (ha)	N° of SU	Size SU (a)	n	mound dens. / ha	x	s^2/x	s^2	Green's index
Macrotermes	Kikulula plain	2.5	11	23.0	29	12	2.64	0.44	1.15	–0.019
Macrotermes	Lake Mburo plain	6.7	29	23.0	42	6	1.45	0.67	0.97	–0.008
Trinervitermes	Kikulula hillside	0.21	84	0.25	116	550	1.38	0.64	0.89	–0.003
Trinervitermes	Kikulula hillside	0.5	34	1.5	108	220	3.18	0.77	2.45	–0.002
Trinervitermes	Kikulula hillside	0.3	49	0.6	68	230	1.39	0.50	0.70	–0.007

s^2 = variance;
x = mean number of termite mounds per sampling unit (SU);
n = total number of termite mounds in sample.

higher values of K, Mg and Ca in the subsoil (due to the Bt-horizon of the Planosol). The Na-content of the seasonally waterlogged savannas on plains is high both in the topsoil and subsoil and may be explained by upward translocation of Na during the dry season. Thicket clumps on all types of relief give higher C and N-values in topsoil and subsoil than do the savannas. The highest values are found in thicket clumps on stony hillsides, reflecting their advanced forest character (Young 1976; Högberg 1989). Fe-values are consistently higher in the topsoil. The obviously high Fe-content of topsoil and subsoil in savannas on seasonally waterlogged plains is due to impeded drainage, which produces ferric iron mottles. The high Fe-content in thicket clumps on stony hillsides are probably a result of weathering processes in the regolith, which continuously supply Fe-ions. In savannas on stony hillsides the weathering products are more rapidly leached. Thicket clumps have a higher P-content in topsoil and subsoil than have the surrounding savannas. This is not unexpected given the positive correlation between organic matter and P-availability (Högberg 1992), possible dung accumulation from herbivores resting in thicket clumps, and slower leaching rates compared with those in savannas. Thicket clumps have a lower bulk density in both topsoil and subsoil than have savannas due to termite activities. The densest soils occur in savanna topsoils on gentle slopes and in savanna subsoils on seasonally waterlogged plains (a function of clay accumulation). The higher savanna topsoil values on gentle slopes are probably due to soil compaction by large mammals since the texture of topsoil and subsoil is similar. Thicket clumps and their surrounding savannas on both gentle slopes and stony hillsides show similar particle-size distribution for topsoil and subsoil. Only the topsoil of thicket clumps on stony hillsides has a higher clay and lower sand content than the surrounding savannas. This result is probably due to important surface flow over hillsides and leaching.

Termitaria

Mound-building termites of *Macrotermitinae* (*Macrotermes*, *Pseudacanthotermes* and to a lesser degree *Odontotermes*), *Nasutitermitinae* (*Trinervitermes*) and *Termitinae* (*Cubitermes*) occur in the Kagera savannas. *Cubitermes* mounds are always bare of vegetation (height and diameter of mound less than 0.5 m) and are therefore not further considered in this study. *Macrotermes* and *Pseudacanthotermes spiniger*, are almost exclusively located on valley bottoms and gentle slopes. Active and abandoned termite mounds may be vegetated and the largest *Macrotermes* mounds may grow up to a height of 4 m with a diameter of 15 m. *Pseudacanthotermes spiniger* are slightly of smaller size. Very few *Macrotermes* mounds occur on dry stony hillsides (they need a lot of water for mound building). On the other hand, *Trinervitermes* mounds are very frequent on stony hillsides having usually a size which does not exceed 1.2 m in height and 2 m in diameter. It was estimated that about 2/3 of all *Trinervitermes* mounds are partially vegetated. If the vegetation cover becomes too dense the mound gets abandoned, since it seems that these three types of termites do not like dense vegetation cover.

The dispersion pattern of *Macrotermes* and *Trinervitermes* mounds is shown in Table 4. The variances (s^2) of the studied termitaria sites are always smaller than the mean number of termite mounds per sampling unit. The dispersion pattern is therefore uniform. Green's Index supports for all studied areas a uniform dispersion pattern (see Bloesch 2002). The nearest distance between two *Macrotermes* mounds in Kikulula on seasonally waterlogged plain is on average 16.7 m (sd = 6.43) and is shorter than in the Lake Mburo seasonally waterlogged plain where the average is 27.6 m (sd = 4.90). *Trinervitermes* mounds in Kikulula stony hillsides show an average nearest distance between two mounds of 4.1 m (sd = 1.8).

Discussion

Vegetation dynamics

Bloesch (2002) confirmed and further defined the overwhelming role of few nucleus trees in the genesis of dry evergreen thicket clumps in East Africa as postulated by Lebrun (1947) and Germain (1952) for the eastern part of the Democratic Republic of the Congo, Liben (1961) for Rwanda and by Osmaston (1962) and Lock (1977) for Uganda. A similar pivotal role for the mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) in the genesis of thicket clumps in the subtropical Rio Grande Plains in Texas has been demonstrated by Archer et al. (1988) and Archer (1989).

The genesis of a thicket clump may start with a heliophilous tree or shrub, whose stem and crown offer support to progressively invading lianas playing an important role in development, along with termite activity. Increasing shade reduces grass growth, allowing germination of more sciaphilous plants inside the thicket clump, which then gradually replace the more heliophilous ones. The establishment of more heliophilous species (mainly lianas and scandent shrubs) at the periphery of the thicket clump favours the radial extension. With increasing size of the thicket clump, the life form spectrum changes greatly. Hemicryptophytes disappear almost completely and the proportion of lianas decreases. The reduced shading by the lianas in the centre of the thicket clump favours chamaephytes and geophytes, typical species of the understorey of forest formations. With increasing size the forest character becomes more apparent.

Soil variation

Since the parent material within each study area is identical for thicket clumps and surrounding savannas we postulate that thicket clumps and small patches of vegetation with forest character, together with termite activities (Williams 1968), must exert a strong influence on the soil leading to the distinct soil properties what is in line with Montgomery & Askew (1983) and Ross et al. (1992). The distinct soil properties of thicket clumps and savannas indicate that the genesis of the former started long ago.

On seasonally waterlogged plains, the growth of thicket clump beyond large termite mounds is prohibited (see below). The propensity of montmorillonitic clays to swell after rains and crack deeply upon drying out, imposes severe strains on plant roots (Cole 1986). Grasses are better adapted in general to such physical stress on these black cotton soils. Only *Acacia gerrardii*, *A. sieberiana* var. *kagerensis*, *A. zanzibarica*, *Balanites aegyptiaca*, *Phoenix reclinata* and occasionally some shrubs such

as *Carissa edulis* and *Gardenia ternifolia*, grow outside *Macrotermitinae* mounds in the Kagera Region. Only the gall-acacia *A. zanzibarica* forms open stands, while the other woody plants remain solitary in the seasonally waterlogged savanna but none of them initiate thicket clumps which are restricted to termitaria. Elsewhere in East Africa also *Acacia mellifera*, the gall-acacia *A. drepanolobium* and *A. seyal*, *A. xanthophloea*, *Borassus aethiopum* and *Hyphaene compressa* frequently occur on black cotton soils, especially where the conditions of impeded drainage are less severe (Bogdan 1958; Lind & Morrison 1974; Bloesch & Klötzli 2002). Seasonally waterlogged savannas (*mbuga* in Tanzania or *dambo* in Zambia according to Pratt et al. 1966, or hyperseasonal savannas in South America according to Sarmiento 1984) are widespread on flat areas in the Kagera Region (Touber & Kanani 1996). Under the present climatic regime these azonal formations on black cotton soils (Vertisol-Planosol complex) are relatively stable (Vesey-FitzGerald 1970) though, due to erratic rainfall, the flooding and drought vary greatly from year to year.

On stony hillsides, rock outcrops or sites with a high proportion of boulders may favour woody plants over grasses, firstly, because humus is scarce and mostly accumulates in cracks and fissures of the rocky subsoil or between the boulders, thus favouring woody plants with a more developed root system (in particular species with taproot systems) and secondly, because the scarcity of inflammable biomass at these sites protects forest regeneration from fire (Bloesch 2002). Therefore, sites having a very high proportion of boulders (soil cover > 80%), typically found along the crest and sometimes locally on slopes, are mostly afforested what is in line with Jackson & Gartlan (1965).

Role of termitaria

In Africa, mainly termites of the subfamily *Macrotermitinae* build large epigean structures, which form conspicuous features in the landscape (Darlington 1994). The association between termitaria and thicket clumps in seasonally waterlogged flat areas is well known and often called termite savanna (Pomeroy 1976, Walter 1973). Similar vegetation mosaics formed by earthmounds (*murundus*), are also found in Central Brazil (Diniz et al. 1986). Two forms of earthmound have been identified. According to Oliveira-Filho (1992a) earthmounds on seasonally waterlogged plains are of termite origin. The construction process begins with a small *Amitermes* (*Termitinae*) nest, leading to the production of a large termitarium by continued activity of *Cornitermes* species (*Nasutitermitinae*). On slopes however, earthmounds can develop as residual features formed by differential erosion (Diniz et al. 1986; Furley 1986). In contrast

to the Kagera Region most plant species occurring on the mounds are also present in the surrounding woody savanna (*cerrado*) flora (Oliveira-Filho 1992b). In the Kenya highlands earthmounds (*mima*) produced by rhizomyid mole rats are important determinants of vegetation patterns (Cox & Gakahu 1985). In the Kagera Region, all larger earthmounds are of termite origin built by a single *Macrotermitinae* species (*Macrotermes* spp. or *Pseudacanthotermes spiniger*).

Bakuneeta (1989) found that all new *Macrotermes herus* mounds were built in open habitats (and not in thicket clumps), after the nuptial flights (swarming) occurring at the beginning of the rainy season in September. Termites are able to build new mounds of about 60 cm within one month (Nye 1955) that enables them to stay above the flooded area in seasonally waterlogged savannas during the rainy season (October-November).

The uniform distribution pattern of *Macrotermes* mounds (and their dependent thicket clumps) on seasonally waterlogged plains and *Trinervitermes* mounds on stony hillsides in the Kagera savanna landscape is in line with the distribution pattern of *Macrotermitinae* mounds on the Loita plains of Kenya (Glover et al. 1964) and in northern Nigeria (Zonneveld et al. 1971), as well as with the distribution pattern of earthmounds occupied by *Cornitermes* spp. in Central Brazil (Diniz et al. 1986; Oliveira-Filho 1992a). The distance between termitaria depends most likely on the territory required by the termite colonies (competition) and site characteristics as shown by several studies from East Africa (Darlington 1982; Abe & Darlington 1985; Bakuneeta 1989).

On seasonally waterlogged plains and gentle slopes, I postulate that thicket clumps originate on at least partially abandoned (and un-maintained) *Macrotermitinae* mounds (see also Pearce 1997). I observed that on active mounds termites very rapidly repaired all damage caused, for example, by aardvarks (*Orycteropus afer,* Pallas 1766), or by animals sharpening their horns, rubbing their skin or licking salt. The surface pan of active mounds is too hard to be colonised by plants (Glover et al. 1964). On abandoned mound, however, damage is not repaired allowing erosion and the hard surface pan becomes at least partially weakened, thereby allowing plant growth. The subsequent establishment of woody plants on mounds is supported by frequent visits of a variety of granivores and frugivores. Termitaria are frequently abandoned mainly due to Doryline ants which can cause very high mortality in *Macrotermes* nests in Africa, often killing the whole population (Pearce 1997). Secondary colonisers, including termite colonies of different species, often resettle abandoned mounds (Pomeroy 1976; Darlington 1985).

Macrotermitinae mounds may initiate and support the growth of thicket clumps in three ways:

a. Fire protection as a result of the slight elevation above grass fires and the frequently bare soil at the foot-slope of mounds
b. Increased soil fertility (in many cases)
c. Good soil drainage in seasonally flooded, flat areas as a result of the higher elevation of mounds above the waterlogged level.
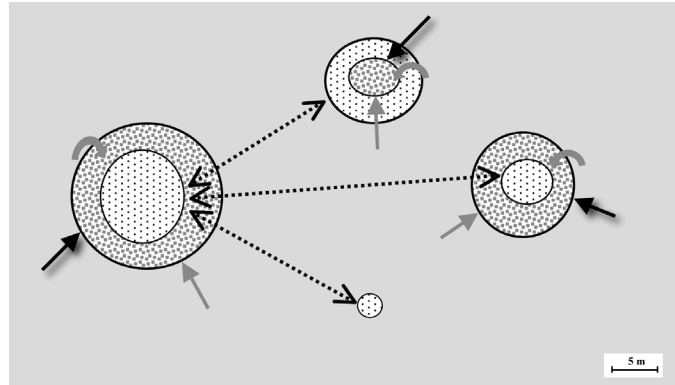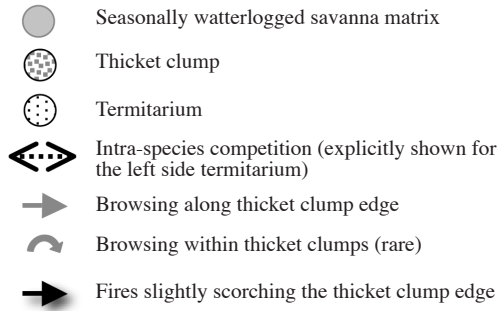
On stony hillsides, *Trinervitermes* mounds may help to initiate thicket clumps by providing a certain fire protection but they do not play the same decisive role as do *Macrotermitinae* mounds on seasonally waterlogged plains and gentle slopes.

Other determinants

Savanna fires usually only scorch the edge and do not penetrate intact thicket clumps or dry evergreen forest patches (Lock 1977). Bloesch (2002) postulated that during the last century, fire impact on the Kagera savanna landscape has changed considerably. The traditional pastoral late burning regime became, with time, more of an agricultural early burning regime. Over the past few decades, political insecurity has furthered an increasingly chaotic use of fire. Currently, frequent relatively cool early dry season fires may have favoured the expansion of thickets and forest patches on stony hillsides as shown by a simulation model (Bloesch 2002). Fire intensity is low in general since many areas are heavily grazed by cattle thereby reducing the fuel load (Skarpe 1992).

This afforestation trend is further accelerated by the presently low impact of herbivores on the dynamics of thicket clumps and forest patches. Only the remaining population of 150 - 200 elephants (*Loxodonta africana,* Blumenbach 1797) is likely to have a local impact on thicket clumps. Giraffe (*Giraffa camelopardalis,* Linné 1758), eland (*Taurotragus oryx*, Pallas 1766) and impala (*Aepyceros melampus*, Lichtenstein 1812) may greatly reduce the growth rates of savanna tree seedlings and saplings (Belsky 1984) but since they only occasionally browse along the edge of thicket clumps and forest patches (Bloesch 2002), their impact is low and mainly manifest on juvenile thicket clumps.

Contrariwise, hot, late dry season fires and high browsing impact (Smart et al. 1985; Van de Vijver et al. 1999) would favour the reduction of these formations. Late burning impact on the boundary is most pronounced at the downhill side of thicket clumps and forest patches with annual boundary shifts of up to 30 cm due to prevailing intense uphill burning (Bloesch 2002). Until recently, an important elephant and black rhinoceros (*Diceros bicornis*, Linné 1758) population lived in the Tanzanian part of the Kagera Region: In the Burigi Game Reserve only, the numbers were estimated to be

Seasonally watterlogged savanna matrix

Thicket clump

Termitarium

Intra-species competition (explicitly shown for the left side termitarium)

Browsing along thicket clump edge

Browsing within thicket clumps (rare)

Fires slightly scorching the thicket clump edge

Fig. 4. Diagram of thicket clump dynamics on seasonally waterlogged plains.

about 500 and 100 respectively, according to a 1974 aerial survey (Rodgers et al. 1977) but were decimated soon afterwards in the Kagera Region. Elephants, which may not only open the forest edges (Laws 1970) but may also break into thicket clumps and forest patches even on steep slopes like those of the Kagera Region as shown by Lock (1977) in the Ruwenzori National Park (formerly Queen Elizabeth National Park) in Uganda. As a result, light may increase sufficiently to permit the spread of grasses into the forest, thereby producing sufficient easily-flammable fuel to allow the penetration of savanna fires. This favours the spread of savannas, which are then maintained by regular burning.

Conclusions

According to topographic position we get the following dynamics of thicket clumps:

On seasonally waterlogged savannas on plains, the dynamics of thicket clumps are determined by termitaria and intra-species competition of their *Macrotermitinae* colonies. The latter dictate a minimal distance between two colonies (Fig. 4). The maximum size of a thicket clump is determined by the size of its termitarium, since woody plants cannot survive in the surrounding seasonally waterlogged savanna (on gentle slopes thicket clumps may expand beyond the termitaria). Fire and the current impact of herbivores have only a slight effect on the physiognomy and size of thicket clumps on flat areas. The longevity of the termite mounds (through recolonisation of abandoned mounds) and their mutualism with the vegetation allow a stable vegetation mosaic to develop over time what confirms the first hypothesis. Watson (1967) calculated by radio-carbon dating an age of at least 700 yr for a *Macrotermes goliath* mound of a height of 2.7 m (having *Odontotermes* as secondary colonisers) from an Iron Age burial ground in Rhodesia (Zimbabwe).

On stony hillsides, the dynamics of thicket clumps

are more complex and the study helped to elucidate the interactions of the factors (second hypothesis). In contrast to the situation on the plain, no single factor has a decisive role on stony hillsides. According to the site-specific situation a varying combination of factors determines the dynamics (Fig. 5). New thicket clumps arise not only on termite mounds but also on areas with rock outcrops or high proportions of boulders or on bare soil, providing a degree of fire protection. The size of thicket clumps is predominately determined by the fire regime and the browsing intensity. If fire intensity and frequency are low and the browsing impact modest, the thicket clumps extend by outward growth and adjacent clumps may coalescence under the current climatic conditions. Increased impact of fire and/or browsing may reverse the process, extending the savanna area at the expense of the thickets. The forest area is only increasing by the genesis of new thicket clumps and expanding forest boundary. The Kagera savannas may never convert directly into dry evergreen forest formations since low impact of fire and/or browsing only leads to an increased woody biomass of the savanna.

Currently, frequent cool, early dry season fires and the near absence of large browsers, have favoured the advance of thicket clumps and forests patches on stony hillsides in the Kagera savannas. The progressive expansion of the edge is demonstrated by (1) many typical savanna trees, like *Combretum molle*, which are completely enclosed by enlarging thicket clumps and forest patches; such trees could only have become established within savannas and, since they are not adapted to thicket clumps, will eventually decay; a parallel is reported in Brazil (Furley 1992; Ratter 1992); (2) pieces of charcoal that we found in the forest soil profiles since savanna fires only scorch the edge but do not enter this type of dry evergreen forest, and (3) the presence of abandoned large *Macrotermes* mounds within the forest about 50 to 150 m from the edge since these termites live in savannas and woodlands and are never found in closed-canopy forests (Harris 1971). It is argued therefore, that thicket
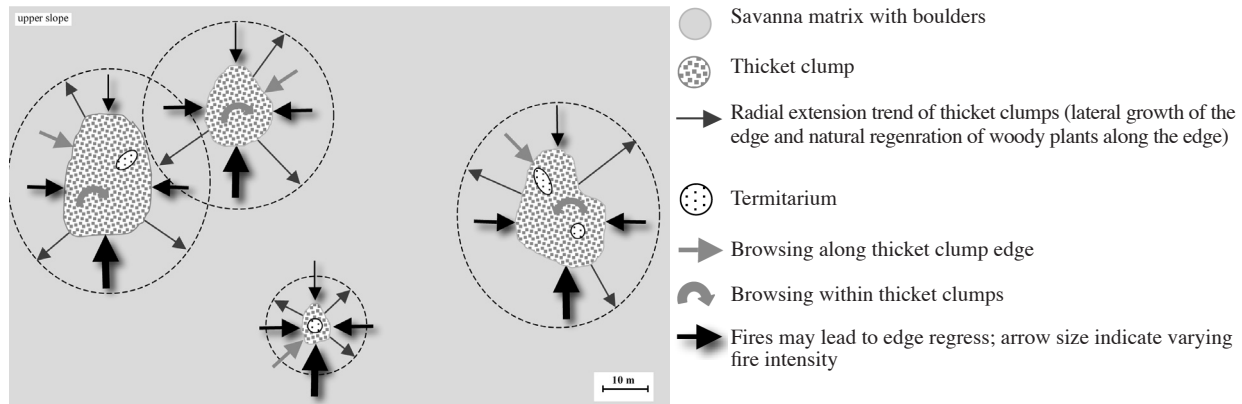
Fig. 5. Diagram of thicket clump dynamics on stony hillside sites (see model Bloesch 2002).

clumps and small forest patches on stony hillsides are not relics of previously large forests as stated formerly (Lebrun 1955; Troupin 1966; Rodgers et al. 1977) but they are dynamic parts of the contemporary Kagera savanna landscape.

In addition, on gentle slopes, frequent cool, early dry season fires, reduced browsing intensity and overgrazing by cattle have led also to a highly increased woody cover on many areas in the Kagera savannas, mostly revealed as bush or shrub encroachment (see Roques et al. 2001). These dense woody stands are composed exclusively of savanna woody plants. Many parts of the Kagera savannas are invaded by *Acacia hockii*, as in the Lake Mburo area, especially on toe slopes (similar to the Rwenzori National Park, Lock 1993) or at Karama on smooth rounded hilltops. In the Burigi Game Reserve in Tanzania many areas encroached with the thorny shrubs *Dichrostachys cinerea* and *Harrisonia abyssinica*.

Similar marked increases in woody biomass at a landscape scale have been reported for a wide variety of arid and semi-arid environments (Archer 1995; Bowman et al. 2001) and along the rain forest-savanna boundary (Ratter 1992; Schwartz et al. 1996). Forest expansion, however, is often masked by destruction caused by man's agricultural activities responsible for the ongoing rapid loss of tropical forest (Anon. 2007).

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