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Post-Disturbance Tree Species Regeneration and Successional Pathways in Mt Blakett and Kedowa Forest Blocks, Mau Ecosystem, Kenya

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Abstract: After decades of disturbance, the capacity of Mau ecosystem to regenerate and regain its pre-disturbance species composition is unclear. The focus of this paper is to determine whether tree species regeneration and successional pathways, are in the process of regaining ecosystem's pre-disturbance species composition. To achieve this, post-disturbance species regeneration and recruitment trends were evaluated and influences of forest disturbance on the distribution of colonizers, followers and climax species determined. Diameter at breast height (dbh) of mature trees was measured and disturbances recorded in plots, dbh of saplings measured in subplots and seedlings count in microplots. Densities and relative densities of seedlings, saplings and mature trees were examined across disturbance gradients, and regeneration and recruitment trends inferred. Frequencies, Duncan's Multiple Range Test (DMRT) and F-test were used to infer stability in the distribution of colonizers, followers and climax species across disturbance gradients. Regeneration in Kedowa was stable with a balanced recruitment into the sapling and mature stages while Mt Blakett had unstable regeneration and recruitment trends. Occurrence of colonizer, follower and climax species showed an unstable distribution in Mt Blakett and a stable and balanced distribution in Kedowa. This ensured inbuilt ecosystem resilience to disturbances and hence stable successional pathways in Kedowa. The unstable distribution in Mt Blakett is likely to result in changes in post-disturbance floristic composition, promoting an individualistic successional pathway. Generally, dominant colonizer species indicated loss of ecological resilience and therefore the sites may not regain their pre-disturbance stand composition in many years to come.

Key words: Mau ecosystem, post-disturbance, recruitment patterns, successional pathway, tree species regeneration

INTRODUCTION

Vegetation succession, traditionally referred to as the directional change in plant species composition over widely variable temporal and spatial scales (Taylor *et al*., 2009), is an important factor in forest ecosystem dynamics. Understanding it forms the basis for sound forest management (Augustin *et al*., 2001), since many forest management models are based on successional theories. For example, those used to project future forest composition assume that forest succession is a static process (Frelich and Reich, 1998, 1999; Augustin *et al*., 2001). This assumption is based on the notion of resilience to disturbances and oscillation or stable cycles. Nevertheless, changes do occur and that constantly change successional trajectory of stands over time. Similarly, other than facilitating succession or having little negative influence on it, colonizers of degraded lands may inhibit succession or even divert succession (Mesquita *et al*., 2001) for a certain period of time.

As stipulated by Mackey and Currie (2001) post-disturbance regeneration patterns give insights into the future stand composition and diversity. Dovciak *et al.* (2005) and Svensson *et al.* (2009) cite the case of competitive exclusion where recruitment of dominants decreased allowing emergence of new colonizing species. This can influence species composition and diversity. Post-disturbance species diversity is important in maintaining ecosystem redundancy. That is an ecosystem's insurance against major collapse of the system in case of perturbation. Having a number of species, all performing the same critical function in a similar way permits a shift from one species to another in case of emergency (Graaf *et al*., 1999). In stable cycles, succession assumes that species or a group of species follows another in the succession and the preceding species alters the environment to the advantage of the following species (Mc-queen, 1991) hence classical model.

The recovery process of an ecosystem such as Mau forest complex is mainly determined by post-disturbance regeneration and succession patterns. It takes 60 to 80 years and even longer for a tropical ecosystem to recover and regain its pre-disturbance structure (Plumptre, 1996).

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In Kakamega tropical rainforest, Fashing *et al*. (2004) observed that over 60 years after disturbances of 1940s, the forest was still recovering.

Depending on the severity of disturbance, the size of disturbances and rotation periods (Frelich and Reich, 1998; Svensson *et al*., 2009), the post-disturbance forest structure and species composition may change (Frelich and Reich, 1999) because they influence the successional trajectory. Again the severity of disturbance will dictate the recovery process. Besides, the size and degree of disturbance of deforested areas can determine the routes along which abandoned areas will become structured forests (Mesquita *et al*., 2001).

Frelich and Reich (1998), defined moderate severity disturbances as the ones that kill most of the overstory or most of the understory, leaving either a canopy layer or seedling/seedbank layer intact (e.g., logging, surface fire or patch crown fire). Where disturbance virtually removes all mother trees and part of the seedbank, recovery may take over hundred years (Graaf, 1986; Graaf *et al*., 1999) and over thousand years (Wardle *et al*., 1999) if the entire seedbank has been removed and soil structure destroyed. The intensity of soil disturbance profoundly influences the magnitude and direction of vegetation change (Halpern, 1988). Frelich and Reich (1998) caution that disturbances may lead to an individualistic successional pathway over time rather than any sort of stable cycle, in which case, Graaf (1986) calls for human intervention to aid in restoration.

Forest managers need to understand that some post-disturbance invasive species reshape the micro-environment making regeneration of other indigenous species impossible (Henderson, 2001). Forest managers therefore need to recognize the characteristics of potentially problematic invasive species at an early stage of their establishment in the forest. Post-disturbance species regeneration patterns should be monitored and actions taken against large scale shift in expected oscillation or stable cycles.

After decades of disturbance, the Mau ecosystem recovery process is not clear. The post-disturbance regeneration and succession pathways are unknown. Thus, the effect of disturbance on the forest regeneration, composition and succession pathways is unknown. There are fears that the ecosystem may be unable to regain its pre-disturbance stand composition and succession patterns. It is important to understand successional mechanisms that include those factors and causes such as time, disturbances and species' life history traits, that interact to drive successional pathways (Taylor *et al*., 2009). Projecting succession pathways has become an increasingly relevant component of ecosystem management, as forest compositional change is linked to timber supply, forest productivity, carbon sequestration, wildlife habitat suitability and social preference (Taylor *et al*., 2009).

A study on the post disturbance recovery process of the Mt. Blakett and Kedowa forest blocks in the Mau ecosystem was therefore, undertaken in order to determine whether the tree species regeneration and successional pathways, after decades of disturbance, are in the process of regaining the ecosystem's pre-disturbance species composition. Specifically, the study evaluated the post-disturbance species regeneration and recruitment trends and determined whether forest disturbance influenced the distribution patterns of the colonizers, followers and climax species. Understanding these gives insights on the capacity of the ecosystem to regenerate naturally and forms the basis upon which ecosystem restoration and human interventions can be undertaken.

METHODOLOGY

Description of the study site: The study was conducted in 2009, in Mt Blakett and Kedowa forest blocks, on the western dip slope of the Mau escapement, within the larger Western Mau block. The two study sites (Fig. 1) lie between 2000 and 2600 m above sea level (a.s.l). Soils are mainly mollic and andosols derived from tertiary volcanic parent materials (Jaetzold and Schmidt, 1983). Within the andosols, inclusions of cambisols occur on the steeper slopes and humic nitrosols. Soils are well drained, shallow to moderately deep clays and well drained, shallow to moderately deep friable clays. Rainfall is high and continuous with moderately high peaks in April. The mean annual rainfall is 2000 mm. Temperatures vary very little throughout the year, but are closely related to altitude, aspect and sunshine. Mean annual temperatures range from 11 to 16ºC, with greatest diurnal variation during the dry season.

Sampling design and data collection techniques: The two study sites (Mt Blakett and Kedowa) were selected subjectively to represent the disturbed and intact sites of the Western Mau. In Mt Blakett, four transects were established on the Eastern, Western, Northern and Southern parts of the hill while in Kedowa two transects were established in the western side of Kedowa forest block (Fig. 1). One transect ran eastwards and the other northwards.

Each transect, measuring 20 m × 250 m was subdivided into 10 m × 10 m plots. A GPS receiver was used to collect UTM coordinates of the corners of transects and the plot centres to aid future monitoring. The plots were further subdivided into 2 m × 5 m subplots and the subplots subdivided into 1 m × 2 m microplots.

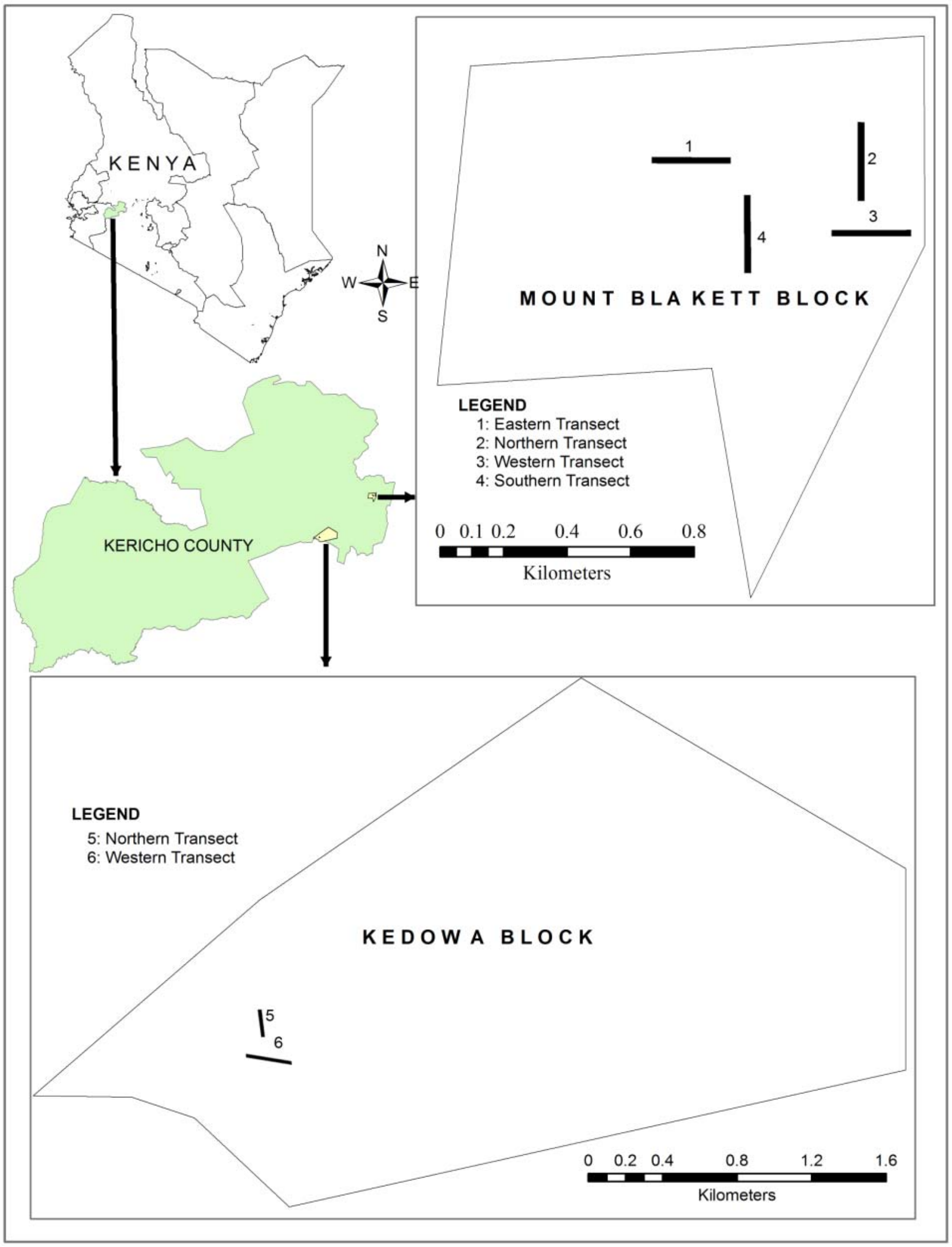

Fig. 1: A map showing the study sites

Complete enumeration was done on these data collection units.

In each plot, the slope and the dbh of all mature trees (dbh $\geq$5 cm) in the plot were measured. In addition anthropogenic disturbances such as charcoal making (No. of kiln), tree cutting (No. of stems), pit sawing (No. of saw pits), footpaths (No./plot), fire (presence/absence) grazing (presence/absence) and debarking (No. of stems) were recorded. In the subplots, dbh of all saplings (1 cm <dbh<5 cm) were measured while seedling count was done in the microplots. All the data collected were recorded in prescribed field data collection forms.

Methods of data analysis: The field data was summarised and organised in tabular form ready for further processing. The frequency, relative frequency, density (No. ha^{-1}) and relative density of all seedlings, saplings and mature stems in the two study sites were computed. In each site, the five densest species at the three stages were isolated and regeneration and recruitment trends examined.

In each transect, the disturbance measures were tabulated and differences in the magnitude of disturbances across transects and across disturbance gradients (sites) determined using the F-test. The effect of these disturbances on the regeneration and recruitment was inferred by examining the tree species densities at seedling sage and across the seedlings, saplings and mature stages.

All tree species were grouped into three categories: colonizers, followers and climax species. The Duncan Multiple Range Test (DMRT) was used to determine if there were significant statistical differences in the occurrence of the categories between the disturbed and undisturbed sites while the F-statistic was used to determine if there were significant differences within sites. Further, percentage frequencies were used to infer and compare stability in the distribution of serial stages (successional patterns) between the disturbed and undisturbed sites.

RESULTS AND DISCUSSION

Post disturbance species regeneration and recruitment trends: The computed frequencies, relative frequencies, densities (No. ha^{-1}) and relative densities of all seedlings, saplings and mature stems for each species in Mt Blakett and Kedowa forest blocks are shown in Table 1.

The densest species, *T. ellipticus*, seemed to have lost few individuals at sapling and mature stages (Table 1 and 2). However, the other five densest species seemed to drastically decrease at sapling and mature stages. It was also observed that *C. pannosa* and *D. augostifolia* in Mt Blakett, and *A. gummifera* and *S. zeyheri* in Kedowa, were not among the five densest species at sapling and mature stages. Fashing *et al.* (2004) and Mutiso (2009) made similar observations in Kakamega forest where most pioneers dropped from among the top densest species at seedlings stage and showed poor recruitment pattern to sapling and mature stages. Apart from *T. ellipticus* and *O. welwitchii*, none of the other five densest species at seedling, sapling and mature stages in Mt Blakett were captured in Kedowa. We attributed this to differences in disturbances in the two sites. Disturbances favour successful regeneration and recruitment of colonizer species. Low disturbances in Kedowa (Table 3) could have drastically reduced the competitive ability of the colonizers observed at seedling stage to undergo successful recruitment to the upper age cohorts. However, newcomers to the five densest species were recorded at the sapling and mature stages. The newcomers in Kedowa are climax species (Table 2). The low disturbances in Kedowa (Table 3) implies that the climax species remained relatively intact even as the greater part of Mau ecosystem was undertaking major disturbance-related species successional pathways. As long as the climax species are intact, the colonizer species can only show their prominence at seedling stage and remain suppressed under the canopy or face catastrophic mortality. In such an event, none or few are recruited to the successive age cohorts such as saplings and mature stage.

In Mt. Blakett, most of the five densest species are colonizers while in Kedowa they are the climax species. However regeneration (seedlings) in both sites is dominated by colonizers. Out of the five densest species, *T. ellipticus* had a very strong recruitment pattern as evidenced by high density of seedlings and saplings (Table 2). *T. ellipticus* is a colonizer species that effectively invades disturbed forest ecosystems (Henderson, 2001). It has a strong proliferation capacity, effectively regenerating through root suckerings. This strategy gives it a competitive ability over other indigenous species by ensuring enough regeneration propagules. Availability of propagules of potential colonists may influence successional trajectory, leading to competitive displacement of indigenous species by superior competitors (Dovciak *et al*., 2005). As was observed in the study sites (Fig. 2 and 3), *T. ellipticus* has a tendency of forming a heavy thicket with its seedlings and saplings regenerating successfully under the canopy (Verdcourt, 2002). This can lead to out-competing of other indigenous plants by invasive species.

The magnitude of forest disturbance as recorded in the 0.01 ha plots are shown in Table 3. There was no significance difference in disturbances within sites and between sites ($p>0.542$). However, both the standard errors of those in Mt Blakett (37.8%) and Kedowa (55.3%) were very high, explaining why the test of significance did not capture the obvious differences in the two means. The graphical representation in Fig. 3 shows that the disturbances were more in Mt. Blaket than in Kedowa. The reason could be that Mt Blakett is adjacent to the highly human disturbed Mau summit as compared to the more interior Kedowa.

Differences in tree species recruitment among the five densest species was attributed to observed forest disturbance. For example in Mt Blakett, the first three densest species at seedling and sapling stages were colonizer species, because it was more disturbed than Kedowa (Table 3). As a result of the disturbances, some species completely disappeared at sapling stage (Table 1 and 2). Most of the disturbances led to large gaps that favoured easy colonization by invasives such as *T. ellipticus*. This explains why there was a strong correlation between some tree species and charcoal making sites. For example *S. Mauritianum* had a Pearson

Table 1: Tree species regeneration patterns in the study area

	Mt. Blakett Block						Kedowa Block						
	Density(No.ha^{-1})			Relative density			Density (No ha^{-1})			Relative density			
	SE	SA	MS	SE	SA	MS	SE	SA	MS	SE	SA	MS	Remarks
Albizia gummifera	0.5	-	-	0	-	-	456	11	8	15	1.3	1.7	Tree species found in
Bersama abyssinica	0.5	-	3	0	-	0.2	15	8	-	0.6	0.9	-	both Mt. Blakett and
Cassipourea malosana	1	-	1.5	0.1	-	0.1	-	-	26	-	-	3.2	Kedowa forest blocks
Celtis africanaafricana	18	-	7	0.8	-	0.5	50	6.5	72	1.6	0.9	9.1	
Chionanthus battiscombei	3.5	-	2	0.2	-	0.2	36	10	4	2.1	1.2	0.5	
Claredendron capensis	-	-	2	-	-	0.2	67	30	-	4.1	3.6	-	
Clausena anisata	12	-	-	0.5	-	-	-	6	1.5	-	0.7	0.2	
Croton macrostychus	-	-	0.5	-	-	0	78	78	3	3.4	3.4	0.4	
Cussonia spicata	0.5	1	-	0	0.1	-	-	-	4.5	-	-	0.6	
Cussonia holstii	1.5	0.5	0.5	0.1	0	0	-	-	2.5	-	-	0.4	
Diospyros abyssinica	1	-	4.5	0.1	-	2.5	-	-	7.5	-	-	1	
Dolyalis macrocalyx	-	-	2	-	-	0.4	49	17	3	2.1	2	0.4	
Dovyalis abyssinica	5.5	1.5	2.5	0.2	0.1	0.2	13	-	5	0.4	-	0.7	
Drypettes gerrardii	6	0.5	0	0.3	0	0	270	118	110	15	15	14	
Ekerbegia capensis	3	2	0	0.2	0.2	0	-	-	4	-	-	0.5	
Euclea divinorum	11.5	15	84	0.5	1	5.3	-	-	13	-	-	1.7	
Ochna ovata	4.5	1	2	0.1	0.1	0.1	81	13	18	3	1.6	2.2	
Olea welwitchii	81	9.5	67	3.4	0.8	4.2	3	19	69	0.2	2.3	8.6	
Podocarpus falcatus	1	-	-	0.1	-	-	60	1.5	10	2.8	0.2	1.4	
Prunus africana	4	0	0	0.2	0	0	6	-	1	0.4	-	0.2	
Scolopia zeyheri	72	13.5	41	2.8	1.3	2.4	327	8	12	9.4	1	1.4	
Solanum mauritianum	-	2.5	1	-	0.2	0.1	57	17	9.5	1.8	2.3	1.2	
Tarconanthus camphoratus	39	97.5	116	1.6	9	7.2	1.5	-	1	0	-	0.2	
Teclea nobilis	40.5	10	29	1.8	0.8	1.9	60	29	41	2.4	3.6	5.1	
Trichocladus ellipticus	1302	1045	828	50	77	51	521	366	313	20	48	38	
Trimelia grandifolia	71	4	2.5	2.8	0.3	0.2	29	15	1	1.8	1.8	0.2	
Vangueria madagascarensis	14.5	3	0.5	0.6	0.2	0.1	331	59	4.5	11	7.4	0.6	
Vernonia auriculifera	1	-	-	0	-	-	-	1	-	-	0.1	-	
Tree species found only in Mt Blakett													
Cartha edulis	1	0.5	0.5	0	0.1	-							
Cathium keniensis	-	-	0.5	-	-	0							
Cotoneaster pannosa	324	-	2	8.6	-	0.1							
Dodonaea augustifolia	202	9.5	4.5	4.9	0.9	0.3							
Erica arborea	11	2.5	14	0.5	0.2	0.8							
Ficus natalensis	25	2	5	0.6	0.2	0.4							
Ficus indica	-	-	17	-	-	0.9							
Flacortia indica	-	0.5	-	-	0	-							
Juniperus procera	23	11.5	67	0.9	1.1	3.8							
Maytenus senegalensis	1	-	3	0	0.1	0.5							
Nuxia cogesta	8	0.5	2.5	0.4	0.1	0.2							
Ochna hostii	3	-	-	0.1	-	-							
Olea hochesterri	0.5	1.5	8	0	0.1	0.5							
Olea africana	219	13	112	9.2	1.1	6.7							
Osyris lanceolata	0.4	4.5	6	0.1	0.4	0.4							
Polyscias fulva	1	-	-	0.1	-	-							
Rhus natalensis	9.5	52.5	23	0.4	4.1	0.6							
Rhus vulgaris	2.5	4.5	0.5	0.1	0.4	0							
Teclea simplifolia	8.5	1	3	0.4	0.1	0.2							
Toddalia asiatica	20.5	-	-	0.8	-	-							
Trichilia emetica	-	1	-	-	0.1	-							
Unidentified	3.5	2	1	0.2	0.2	0.1							
Warbugia ugandensis	2	0.7	0.5	0.1	0	0							
Tree species found only in Kedowa													
Bischovia japonica	1	-	1	0.1	-	0.1							
Dombeya goetzenii	31	21	8	1.9	2.5	1.1							
Ehretia cynamosa	8.5	5	13	0.2	0.6	1.7							
Fagaropsis angolensis	20	8.5	9	1.1	1.2	1.2							
Manilkara discolour	-	-	2	-	-	0.3							
Meyna tetraphylla	-	-	1	-	-	0.2							
Polyscias kikuyuensis	12	-	4	0.8	-	0.6							
Scherebia alata	-	-	3.5	-	-	0.4							
Strychnos usambarensis	-	8	3.5	-	0.9	0.4							
Syzygium afromontanum	6	-	9.5	0.2	-	1.2							

correlation coefficient (r) of 0.89, *T. ellipticus* 0.93 and *V. auricufera* 0.87. Mutiso (2009) also recorded a strong positive correlation (r: 0.90) between charcoal making and invader species; *S. mauritianum* in Mt Elgon and Kakamega forests. Thus the observed disturbances (Charcoal making, grazing, tree cutting, footpaths etc.) in most cases favoured successful regeneration and recruitment of colonizers while hindering indigenous species of economic importance (Henderson, 2001).

It has emerged that the invasive species have been successfully out-competing regeneration of climax species, hence the reason why some of the late seral

Table 2: Density of the five densest species in Mt Blakett and Kedowa forest blocks

Seedlings		Saplings		Mature	
Species	Density (ha^{-1})	Species	Density (ha^{-1})	Species	Density (ha^{-1})
Density of the five densest species in Mt Blakett forest blocks					
T. ellipticus (colonizer)	2458	*T. ellipticus* (colonizer)	2089	*T. ellipticus* (colonizer)	828
C. Pannosa (colonizer)	647	*T. camphorates* (colonizer)	195	*T. Camphoratus* (colonizer)	116
T. Camphoratus (colonizer)	477	*R. natalensis* (colonizer)	105	*O. Africana* (climax)	112
O. Africana (climax)	438	*O. Africana* (climax)	26	*E. divinorum* (colonizer)	83.5
D. augostifolia (colonizer)	403	*O. welwitchii* (climax)	20	*O. welwitchii* (climax)	67
Density of the five densest species in Kedowa forest blocks					
T. ellipticus (colonizer)	521	*T. ellipticus* (colonizer)	366	*T. ellipticus* (colonizer)	312.5
A. gummifera (colonizer)	456	*D. gerrardii* (climax)	118	*D. gerrardii* (climax)	110
V. madagascarensis (follower)	331	*V. madagascarensis* (Follower)	59	*C. Africana* (climax)	71.5
S. zeyheri (colonizer)	327	*T. nobilis* (climax)	29	*O. welwitchii* (climax)	68.5
D. gerrardii (climax)	270	*O. capensi s*(climax)	19	*T. nobilis* (climax)	41

Table 3: Anthropogenic disturbance in sampled sections of Mau ecosystem

	Transects						Transect means	
Disturbance type	MB. East	B. West	MB. South	MB. North	W. Ked.	N. Ked.	Mt. Blakett	Kedowa
Charcoal making (No. of kiln)	17	7	5	10	5	13	9.75	9
Tree cutting (No. of stems)	174	109	142	121	59	88	136.5	73.5
Pit sawing (No. of saw pits)	0	0	0	0	0	0	0	0
Foot paths (No./plot/Ha)	22	19	33	27	18	14	25.25	16
Fire (Presence/Absence)	0	2	21	2	0	0	6.25	0
Grazing (Presence/Absence)	21	22	27	24	12	17	23.5	14.5
Debarking (No. of stems)	10	9	13	10	10	8	10.5	9
Mean							30.25	17.43
SE %							37.80	55.32

*: MB- Mt Blakett, N. Ked. - North Kedowa, W. Ked. - West Kedowa

Table 4: Occurrence and distribution of colonizers, followers and climax species in study sites

	Mount Blakett			Kedowa		
	Colonizers	Followers	Climax	Colonizers	Followers	Climax
Seedlings (No/ha)	89.3	4.0	33.7	151.2	78.6	69.7
Saplings (No/ha)	69.7	1.7	4.80	60.5	19.0	35.0
Mature stems (No/ha)	48.3	1.4	27.9	32.1	8.4	35.3
	Mount Blakett			**Kedowa**		
	MB. East	MB. West	MB. South	MB. North	N. Ked.	W. Ked.
Colonizers %	73.1	50	55.6	64.3	48.6	44.8
Follower %	7.7	18.8	19.4	17.9	31.4	34.5
Climax %	20.8	13.3	25	17.9	20	20.7

*: MB: Mt Blakett; N. Ked.: North Kedowa; W. Ked.: West Kedowa

T. ellipticus

Fig. 2: Regeneration of saplings of *T. ellipticus* in Mt Blakett

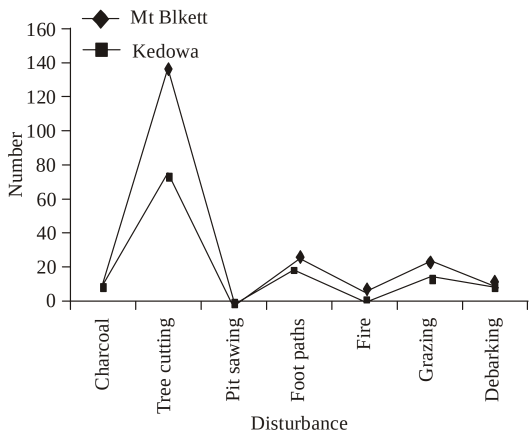

Fig. 3: Graphical representation of disturbances between Mt. Blakett and Kedowa forest blocks

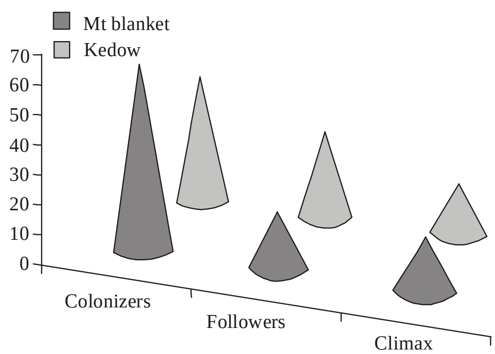

Fig. 4: Frequencies (%) of trees in succession stages in studied sites of Mau ecosystem

stages species such as *O. welwitchii*, *D. gerrardii*, *C. africana* and *T. nobilis* are lacking at seedling stage but are prevalent at the mature stage (Table 1 and 2). Hitimana *et al.* (2004) have shown that, due to disturbances, some species maybe at low densities or disappear at sapling stage while others show their prominence at sapling stage. Mutiso (2009) suggests that such species that disappear at sapling stage could be some of those fugitive booms and burst species that show catastrophic mortalities at seedling stage.

Forest disturbance and occurrence and distribution patterns of colonizers, followers and climax species: The Occurrence and distribution of colonizers, followers and climax species, summarised in mean number per hectare for the study sites are shown in Table 4. Duncan Multiple Range Test (DMRT) revealed significant differences ($p<0.02$) in the occurrence of colonizers, followers and climax species between the two study sites. In Mt Blakett, the One Way F statistic (F_{st} 16.125, $F_{0.05}$ 5.143) revealed significant differences in the occurrence of colonizers, followers and climax species while there was no significance difference (F_{st} 0.905, $F_{0.05}$ 5.143) in Kedowa. Thus, in Mt Blakett, the distribution in numbers per hectare between colonizers, followers and climax species was significantly different, a pointer to unstable successional patterns. On the other hand, the distribution in Kedowa was not significantly different, implying stable successional patterns.

Table 4 shows the percentage of colonizers, followers and climax species in the study transects. All transects in Mt Blakett had at least 50% of species under the category of colonizers unlike Kedowa block which had less than 50%. The Eastern block had the highest colonizer species (73.1) compared to all the other studied sites. Kedowa block had a more stable distribution of the species with the percentage of species decreasing from colonizers to followers then climax. However, a rather skewed distribution of the same was observed in all the transects in Mt Blakett (Table 4). Observed differences in the occurrence of colonizers, followers and climax species are an indicator of existence of gradients in disturbances severity (Fangliang and Pierre 2002; Rydren *et al*., 2004). Such differences are likely to result to changes in post–disturbance floristic composition and different successional trajectory for individual stands (Frelich and Reich, 1998). Catastrophic, or large-scale, disturbances profoundly alter the composition and structure of plant communities (Halpern, 1988). Based on the occurrence of the three successional stages, it is clear that though the two sites received moderate severity disturbance (Table 3). Mt Blakett was more disturbed than Kedowa

Figure 4 reveals an unstable distribution of colonizer, follower and climax species in Mt Blakett, while that in Kedowa is stable. In Mt Blakett, colonizer, follower and climax species had 62.7, 19.6 and 17.6 occurrence, respectively, while in Kedowa, the occurrence was 48.6, 32.4 and 18.9%, respectively. Mt Blakett had very high number of colonizer species while Kedowa showed a fairly balanced diversity of the colonizers, followers and climax species. A post–disturbance stable diversity of colonizers, followers and climax species cushions an ecosystem against species extinction and leads to quick recovery (Imbert and Portecop, 2008). Therefore, the stable distribution of colonizers, followers and climax species observed in Kedowa will ensure inbuilt ecosystem resilience to disturbances.

The observed unstable distribution in Mt Blakett maybe due to persistence disturbances that might have interfered with the parallel and cyclic (nutrients) ecosystem processes. Such interference adversely affects the reorganization of functional species (Drever *et al*., 2006). As suggested by Wardle *et al*. (1999) parallel configuration allows essential processes to be taken over by one population of organism from another while cyclic configuration is expected in nutrient cycling and/or decomposition of complex substrate. Thus, post-disturbance balance of early and late successional communities as was in Kedowa ensures both parallel and cyclic configurations are not interfered with.

It has emerged that the stable successional stages in Kedowa confer the ecosystem the much needed redundancy necessary for post–disturbance restoration of ecological integrity. The low redundancy in Mt Blakett is an indicator of detrimental disturbance. The reduced diversity drastically reduces ecosystem stability and sustainability. Kuffer (2006) observed similar scenario whereby reduced diversity in island floras led to higher vulnerability of the oceanic islands with some niches becoming vacant. Given that the Mau ecosystem is still dominated by colonizer species such as *T. ellipticus* three decades after disturbance is a clear indication of an ecosystem on the verge of losing its ecological resilience and consequently stable cycle. Dovciak *et al.* (2005) caution that if restricted opportunity windows occur frequently enough over broad spatial and temporal scales, they may eventually come to represent the dominant successional pathway in a given region. For quick recovery, it is important for an ecosystem to absorb disturbances without undergoing fundamental change (Drever *et al*., 2006). Again, Frelich and Reich (1998) cautions that changes in severity of disturbance may lead to an individualistic successional pathway over time. The fact that the main canopy species in Mt Blakett is a colonizer (*T. ellipticus*) projects a poor future stand composition. When disturbance is beyond a certain critical limit, the ecosystem can 'flip off' to an alternative state to the detriment of all the biota inhabitation (Kumar, 2001).

The low redundancy in Mt Blakett is an indicator of a poor future ecosystem stability and sustainability. Managers need to understand that in highly disturbed ecosystems, restoration of pre-disturbance stand floristic structure and composition require human intervention. Finegan and Camacho (1999) recommend silvicultural treatments to aid in restoration of degraded tropical ecosystems. However, Frelich and Reich (1998) caution that any treatment should mimic the natural disturbance regimes.

CONCLUSION

In Mt. Blakett, most of the densest species are colonizers while in Kedowa they are climax species. Regeneration in both sites is dominated by colonizers. Colonizers are successfully recruited to mature trees in Mt. Blakett. Though colonizers dominate seedling stage in Kedowa, they are not recruited to sapling and mature stages which are dominated by climax species. It has emerged that colonizers and especially the invasive species such as *T. ellipticus* are successfully out-competing climax species in regeneration and recruitment. In the long run this may probably lead to individualistic successional pathways and affect the post-disturbance forest composition. Forest disturbances are more prevalent in Mt Blakett than in Kedowa leading to an aggressive regeneration of colonizer species.

Mt. Blakett has a very high density of colonizers species and an unstable distribution of colonizer, follower, and climax species as compared with Kedowa which has a balanced diversity and stable distribution of colonizers, followers and climax species. The stable post disturbance diversity and distribution of colonizers, followers and climax species in Kedowa will ensure inbuilt ecosystem resilience with well balanced successional pathways, leading to quick recovery of the pre-disturbance species composition. However, in Mt. Blakett the reduced diversity and unstable distribution reduces ecosystem stability, sustainability and ability to recover its pre-disturbance species composition. In general the domination by colonizer species in both sites is an indicator of an ecosystem on the verge of losing its ecological resilience and consequently stable cycle.

RECOMMENDATIONS

- Disturbances in Mt Blakett and Kedowa forests should be controlled. This will promote successful recruitment of seedlings to sapling stage and reduce browsing and exposure of juvenile seedlings to scorching sunlight.
- It is recommended that any efforts applied in the rehabilitation of degraded sites such as Mt Blakett should mimic natural regeneration processes and that the notion that succession is a static process and that forests repeat the same regeneration and successional stages after each disturbance should be carefully reviewed.
- Further, extensive studies on regeneration patterns and the emerging invasive species such as *T. ellipticus* are required. Such studies would give insights on the extend of the weed invasiveness, its ecological impact and how the invasion may be reshaping the microenvironment of the sites to an extend of affecting post-disturbance stand species composition.
- It is advisable that managers undertake succession modelling (empirical, mechanistic or hybrid mechanistic) to understand the successional pathways for appropriate ecosystem planning and management.

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