Afr. J. Ecol. 1990, Volume 28, pages 174–188

Forest composition and its regeneration dynamics; a case study of semi-deciduous tropical forests in Kenya

B. N. KIGOMO[1], P. S. SAVILL[2] and S. R. WOODELL[2]

[1]*Kenya Forestry Research Institute, PO Box 20412, Nairobi, Kenya;* [2]*Department of Plant Sciences, South Parks Road, Oxford University*

Summary

Distribution of the forest blocks carrying *Brachylaena huillensis* as a component species are shown and details of species composition, structural and size distribution of three of these; Karura, Muguga and Ngong in the central highlands were investigated. The procedures for the various investigations are given.

Much of the remaining semi-deciduous forest patches in Kenya are characterized by open canopies mainly as a result of selective cutting of the commercial emergent trees in the past. The stands are comprised of many families but of comparatively few species. Species composition and structure indicates poor correlation with other regional forests, suggesting the importance of conserving these forest patches.

Size-structure analysis revealed that the forests are dynamic and component species including *B. huillensis* are significantly ($P < 0{\cdot}01$) represented from seedling to large diameter stems. There were, however, fewer stems between 50 and 80 cm dbh than those above the 80 cm dbh. This is a reflection of past selective cutting of better formed stems within this range. Stems above 80 cm dbh are mainly poorly formed.

B. huillensis is the most important, social and commercial species in these forests. To be able to direct its management in order to meet a balance between its exploitation and conservation, further studies on its reproductive and actual growth dynamics are recommended.

Key words: forest, Kenya, *Brachylaena*, composition, structure, regeneration.

Résumé

L'on montre la distribution de blocs forestiers dont *Brachylaena huillensis* est un composant et l'on recherche des détails sur la composition des espèces, la distribution de structure et de taille de 3 d'entres eux: Karura, Muguga et Ngong dans les hauts plateaux centraux. On donne les procédures pour les différentes investigations.

Une grande part des îlots de forêts semi-décidues restants se caractérisent par des canopées ouvertes, dues principalement à un abattage sélectif des grands arbres à valeur commerciale dans le passé. On note la présence de nombreuses familles mais, comparativement, de peu d'espèces. La composition et la structure des espèces montrent peu de corrélation avec les autres forêts régionales et donc l'importance de sauvegarder ces îlots forestiers. Leur analyse taille-structure montre que les forêts sont dynamiques et les espèces composantes, y compris *B. huillensis*, sont significativement ($P < 0{\cdot}01$) des semis aux troncs de grand diamètre. Il y avait toutefois moins de troncs compris entre 50 et 80 cm de diamètre qu'au-dessus de 80 cm de diamètre. C'est le reflet d'un abattage antérieur sélectif de troncs mieux formés de cette taille. Les troncs au-delà de 80 cm sont pour la plupart mal conformés. *B. huillensis* est l'espèce la plus importante, au point de vue social et commercial, de ces forêts. Pour être à même de mener correctement sa gestion pour trouver l'équilibre entre exploitation et conservation, on recommande d'effectuer des recherches supplémentaires sur la dynamique de reproduction et de croissance actuelle.

Introduction

Although most indigenous trees and shrubs of the semi-deciduous forest formation type are known taxonomically, very little is specifically known of their ecology, regeneration potential, conservation and responses to management. Yet the number of most tree species is continuously being reduced and the ecosystems in which they occur are being disturbed on a massive scale. The underlying dangers of continuing exploitation have been realized and the need for better management of the remaining woods is called for. This requirement calls for urgent information necessary for developing appropriate management systems that could take advantage of natural dynamic processes which must first be understood.

The continued existence of most of these species is dependent on the safeguarding of the ecosystems in which they occur. Studies such as Connel & Slatyer's (1977) are based on community properties but they implicitly acknowledge the importance of the life history of individual species in determining the trend of succession. Results of studies by Drury & Nisbet (1973) led them to conclude that most of the phenomenon of succession of regeneration paths could be understood as consequences of differential colonizing ability, growth and survival of species adapted to grow in different environments.

Apart from an attempt to understand the dynamics of forest formation, the emphasis of the second part of the present exercise was to attempt to evaluate the ability of one forest species *B. huillensis* at establishing and growing to maturity in the semi-deciduous forests as developing communities. This is a vital first step (Noble & Slatyer, 1980) leading to the successful establishment and stability of a species in an ecosystem.

Materials and methods

Study areas

For the purpose of the present study only those forests of the semi-deciduous formation type carrying *B. huillensis* as a component species are considered. The distribution of these is shown in Fig. 1a.

B. huillensis is a tree belonging to the family Asteraceae (=Compositae). It is the only woody species in the East African Compositae to develop to timber size (Lind & Morrison, 1974). The tree is also dioecious.

Most of the coastal residual stands have been exploited and over-cut to the extent that *B. huillensis*, among other major species, is no longer considered to be of an exploitable size. Investigations in this study were therefore mainly carried out in Karura and Ngong forests and in Muguga and Dagoretti nature reserves (Fig. 1b).

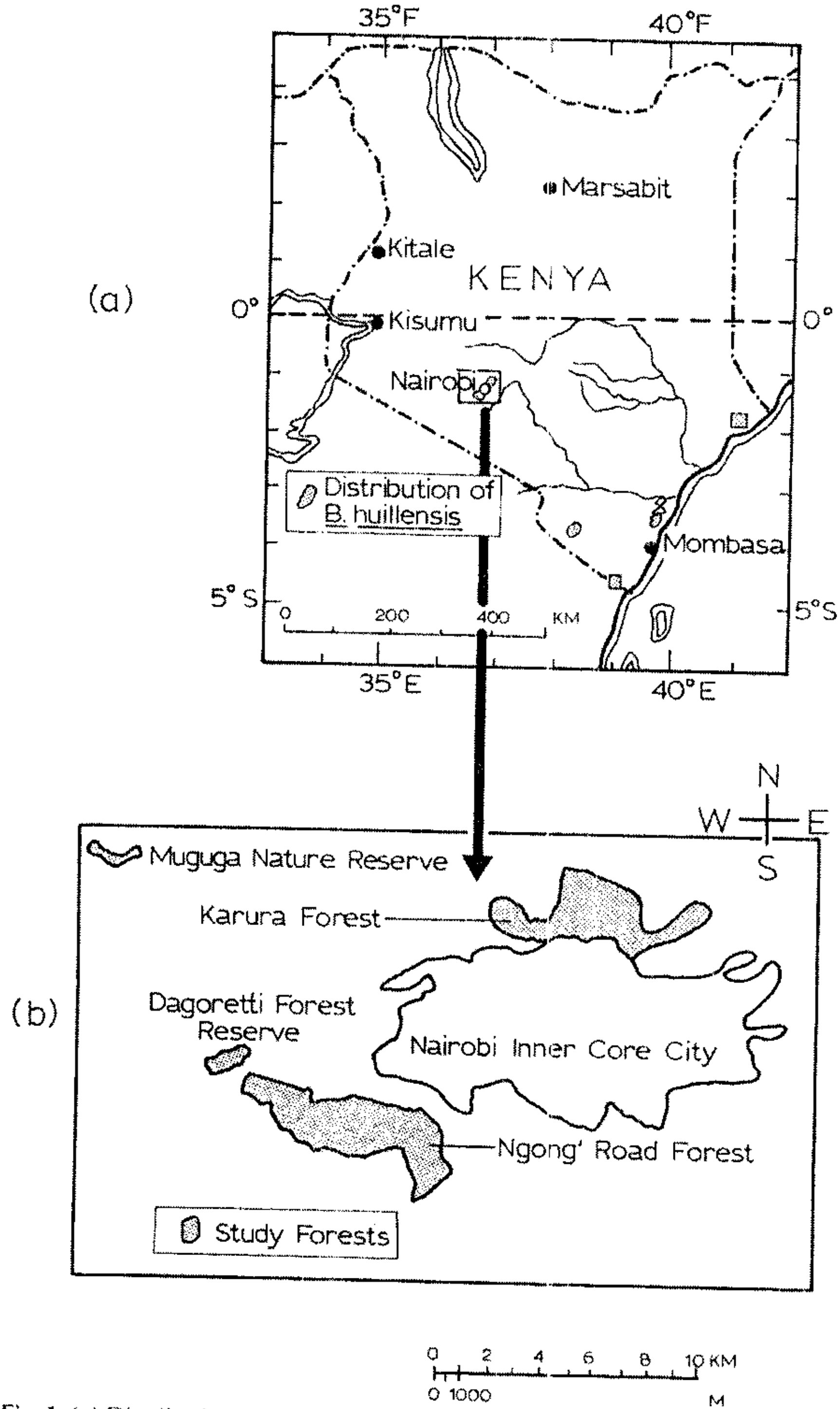

Fig. 1. (a) Distribution of forest patches with *Brachylaena huillensis*. (b) Location of the ma n study forest areas.

Sampling for species composition and recruitment

Vegetation sampling was carried out at three levels as shown in Fig. 2. Twenty-four, 30 × 50 m randomly located rectangular plots were used for measurement of various tree and site parameters. All trees of 3 cm diameter at breast height (dbh) and above were recorded by dbh, species and life-form status (E for emergent, M

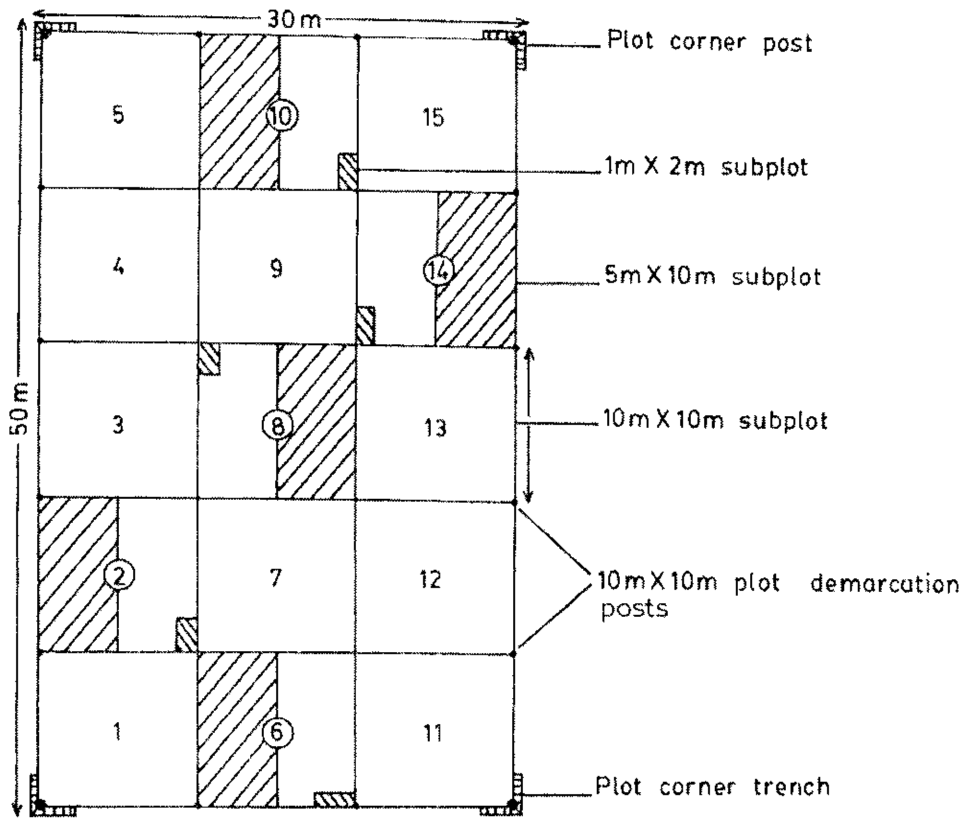

Fig. 2. Sample plot layout. *Note:* The posts at 10 m intervals along the perimeter of the main plot were used to establish the 10 × 10 m sub-plots using string. A tape measure and a 2-metre calibrated rod were used in the establishment of the 5 × 10 m and 1 × 2 m small sub-plots.

for main canopy, U, understorey and S for shrub or suppressed) in each of the 15 plots of 10 × 10 m. Saplings of 1 m and above in height but less than 3 cm dbh were tabulated by species and number (for *B. huillensis*) in the 5 × 10 m plots. Seedlings below 1 m in height were recorded by species and number (for *B. huillensis*), otherwise by numbers only for other species from the 1 × 2 m plots.

Data organization and analysis

Species composition and stand comparisons. Species enumerations were summarized by density and mean tree diameter per plot, and mean basal area per tree for each species. All the values per plot were converted to values per hectare. Basal area per tree was determined by dividing total basal area by the number of trees and basal area for a species by dividing total basal area of the species with the number of trees of the species. Relative density, dominance (basal area) and frequency of each species were obtained from the following equations;

$$\text{Relative density} = \frac{\text{number of individuals of the species}}{\text{number of individuals of all species}} \times 100$$

$$\text{Relative dominance} = \frac{\text{total basal area of single species}}{\text{total basal area of all species}} \times 100$$

$$\text{Relative frequency} = \frac{\text{number of sample units in which the species occurred}}{\text{total sample units}} \times 100$$

$$\text{Importance value} = \text{sum of relative density, relative dominance, and relative frequency}$$

'Importance value' was used in characterizing the stand composition status by species. Sorensen's index of similarity (Mueller-Dombois & Allenberg, 1974), $IS = (2c/A+B) \times 100$, was used for comparing species similarity in the sample blocks and the study forests, where c = sum of importance values of species common to both stands and samples, and $A+B$ = total importance values of species in first sample and in the second sample or stand, respectively.

Size-distribution profiles. All saplings and tree measurements were sorted out by diameter classes, number and by forest blocks and physical sites. Measurements and counts of *B. huillensis* were also sorted out separately by diameter class of 5 cm dbh and numbers against each size class in each sample unit. To allow comparisons between stands, the number of stems or saplings in each diameter class were converted to stems per 0·45 ha for all the species or 1 ha for *B. huillensis* alone. These data were then tabulated for use in all subsequent analyses.

Age-structure and recruitment model. To examine the nature of development or recruitment trend using the constructed diameter-class profiles, a mathematical relationship (the power function model), $Y = Y_0 X^{-b}$, described by Hett & Loucks (1976), was used in its linear transformed form,

$$\ln Y = \ln Y_0 - b \ln x,$$

where Y is the number of stems or saplings in any diameter class x, Y_0 the initial input into the populations at time zero and b the mortality rate with time. Least-squares fit of this model was performed for the age-structure diagrams of all species and those of *B. huillensis* alone.

Results

Species composition and status

The most common tree species in Karura are listed in Table 1. The list gives, in decreasing order, the status of each species in terms of spatial dominance, distribution, frequency and its ecological or importance value in the forest. Tree species composition in Ngong and Muguga forests are similarly listed in Tables 2 and 3 (respectively). A full list of the importance value rating of families in the three forests is presented in Appendix I. Table 4 presents a list of the common shrubs and herbs in the three forests.

The dominant genus is *Teclea* (Rutaceae) with a preponderance of *T. simplicifolia* and *T. trichocarpa* (Tables 1, 2, 3). *Teclea* spp. were also abundant in the shrub, sapling and seedling classes and its full importance is further displayed in Table 4. It is notable from the lists, especially Table 3, that for a general ecological analysis of vegetation, quantitative composition based on one relative value may be misleading insofar as the importance of each species is concerned.

Table 1. Overall relative importance of the common tree species in Karura forest

Species	Mean stem dbh (±SD)	Relative dominance (%)	Relative density (%)	Relative frequency (%)	Importance value (CV)
Teclea trichocarpa	9·1 ± 4·17	12·6	24·2	89	125·8 (27·9)
Teclea simplicifolia	9·3 ± 1·79	7·8	14·6	81	103·4 (25·7)
Drypetes gerrardii	11·5 ± 2·61	10·7	11·2	76	97·9 (25·6)
Strychnos henningsii	8·4 ± 5·37	6·7	12·9	77	96·6 (32·4)
Brachylaena huillensis	27·5 ± 15·58	15·5	5·8	61	92·3 (54·4)
Lawsonia lucida	12·0 ± 7·22	5·8	5·8	60	71·6 (41·1)
Croton megalocarpus	17·0 ± 7·92	6·9	3·7	44	54·7 (47·2)
Strychnos usambarensis	8·5 ± 5·78	2·7	6·6	35	44·3 (46·5)
Craibia brownii	10·6 ± 6·13	3·0	3·4	31	37·4 (83·4)
Diospyros abyssinica	24·7 ± 11·3	5·1	1·4	24	30·5 (71·4)
Elaeodendron buchananii	16·6 ± 9·72	2·4	1·3	19	22·7 (70·0)
Manilkara discolor	12·4 ± 8·16	0·8	0·7	12	13·5 (114·5)
Ochna ovata	6·3 ± 3·06	0·1	0·5	8	8·6 (114·1)
Ficus thonningii	19·2 ± 6·32	1·9	0·5	5	7·4 (129·7)
Canthium keniense	7·4 ± 0·82	0·1	0·6	5	5·7 (108·8)
Allophylus stachyanthus	6·7 ± 4·30	0·1	0·4	5	5·5 (232·7)
Olea spp.	10·7 ± 2·22	0·4	0·5	4	4·9 (108·2)
Grewia similis	7·4 ± 0·9	0·05	0·2	4	4·3 (90·7)
Maytenus spp.	6·2 ± 3·21	0·05	0·3	2	2·4 (145·8)
'Others'	—	3·3	2·4	39	44·7 (41·4)

SD—Standard deviation of mean tree dbh within forest block.
CV—Coefficient of variation (%) within forest block.
'Others'—minor species which include; *Albizzia gummifera*, *Cassipourea malosana*, *Clausena anisata*, *Croton alianus*, *Ekebergia rueppeliana*, *Erythrococca bongensii*, *Makhamia hildebrandtii*, *Scutia myrtina* and *Suregada procera*.

The underwood is overwhelmingly dominated by *Teclea* spp. in the three forests followed by *Ochna ovata* and *Vangueria linearisepala* and other minor species. The main canopy trees, *B. huillensis*, and *C. megalocarpus* in Ngong and Karura, and *O. africana*, *C. capense*, and *C. megalocarpus* in Muguga, are scattered widely, indicating open upper strata up to an average height of 27 m. The dominating *Teclea* layer averages 20 m and does not show a clearly defined stratum. The shrubs of the *Teclea* spp., *Clausena anisata* and *Crotalaria mauensis* among others in Muguga and also the noxious *Lantana camara* in the open areas of Ngong and Karura merges with the understorey layer.

The few lianes were mainly *Trimeria bakeri*, *Scutia myrtina* and *Pterolobium stellatum*. Parasitic plants included *Ficus thonningii* which seems to be a major problem on *B. huillensis*. *Loranthus woodfordiodes*, *L. usuiensis* and *Viscum nervosum* were also common but less damaging. Only sedges and grasses grow in the few open grades with a few scattered shrubs of *Rhus natalensis* and *Acokanthera schimperi* on raised patches.

Relationships between the semi deciduous study forests and other regional forests

Several moist tropical forest tree species of Kenya are represented in the study forest. More notable species include *Croton megalocarpus*, *Diospyros abyssinica*,

Table 2. Overall relative importance of the common tree species in Ngong Forest

Species	Mean stem dbh (±SD)	Relative dominance (%)	Relative density (%)	Relative frequency (%)	Importance value (CV)
Teclea simplicifolia	10·2±4·85	16·1	30·2	97·7	144·7 (6·3)
Brachylaena huillensis	13·9±11·1	20·2	14·9	74·1	109·2 (42·5)
Teclea trichocarpa	12·1±4·93	6·8	10·0	68	84·8 (30·7)
Drypetes gerrardii	12·6±6·50	7·0	8·7	67	82·7 (33·5)
Elaeodendron buchananii	14·24±7·24	7·2	7·0	52	66·2 (57·7)
Diospyros abyssinica	20·3±7·62	9·3	5·0	47	61·3 (59·4)
Calodendrum capense	16·6±9·1	5·5	4·4	48	57·9 (54·4)
Croton megalocarpus	21·8±8·14	8·4	4·0	45	57·4 (46·7)
Ochna ovata	10·4±5·45	2·0	4·2	41	47·2 (45·5)
Olea spp.	22·1±7·60	2·1	0·9	16·7	19·7 (73·1)
Maytenus spp.	11·7±7·65	1·6	1·4	16·4	19·4 (135·0)
Canthium keniense	6·9±3·51	0·3	1·2	15·6	17·1 (73·7)
Schrebera alata	31·3±16·62	3·5	0·9	11·2	15·6 (132·1)
Lawsonia lucida	16·1±5·65	0·8	0·8	12·6	14·2 (36·6)
Grewia similis	6·0±4·23	0·2	0·9	11·1	12·2 (58·2)
Ekebergia rueppeliana	12·2±5·08	0·5	0·5	7·6	8·6 (139·5)
Ficus thonningii	47·6±19·9	1·7	0·2	3·0	4·9 (155·1)
Strychnos usambarensis	13·9±0·42	0·2	0·2	3·8	4·2 (126·2)
Craibia brownii	8·5±4·8	0·1	0·2	3·0	3·3 (303·1)
'Others'	—	4·1	3·0	34·0	41·1 (40·9)

SD—Standard deviation of mean tree dbh within forest block.
CV—Coefficient of variation (%) within forest block.
'Others'—minor species which include; *Acokanthera longiflora, Clausena anisata, Cussonia spicata, Ehretia cymosa, Euclea divinorum, Dombeya burgessiae, Manilkara discolor, Margaritaria discoidea, Scutia myrtina* and *Warburgia ugandensis*.

Drypetes gerrardii and *Ochna holstii*. The occurrence of these species in semi-deciduous forest type is accompanied by an associated reduction in their size. There are fewer tree species but a higher density per unit area in these forests than in the tropical high forests (Richards, 1952). A high proportion of species comprise shrubs, herbs and a few non-timber species. The incidence of deciduous and narrow-leaved species is higher, possibly as an adaptation to the low moisture conditions.

Nearer to the study forests (about 200 km away) but at a higher elevation, there exists a patch of a dry montane forest on the leeward side of the Mau ranges, described by Kerfoot (1963). Although rainfall does not differ much, temperatures are lower and the vegetation carries a proportion of tropical high forest secondary species like *Polyscias ferrugenera, Fagara macrophylla, Macaranga kilimandischarica* among (few) others. A rough comparison with the study forests indicated affinities of only 25% for dominant, sub-dominant and understorey species, 30% for smaller trees, 27% for genera of shrubs, 22% for lianes and about 55% for epiphytic plants. The epiphytic species seem to display a wider ecological amplitude. The two forest types also differed in the number of tree species and maximum dimensions of dominants.

Table 3. Overall relative importance of the common tree species in Muguga Forest

Species	Relative dominance (%)	Relative density (%)	Relative frequency (%)	Importance value
Teclea simplicifolia	11·7	27·0	40·7	79·4
Calodendrum capense	21·8	5·1	10·9	37·8
Olea africana	25·1	3·9	8·3	37·3
Warburgia ugandensis	8·7	6·9	14·7	30·3
Teclea spp.	3·9	9·0	13·6	26·5
Ehretia cymosa	2·7	7·4	15·5	25·6
Croton megalocarpus	6·0	5·4	9·6	21·0
Vangueria linearisepala	1·4	6·6	12·4	20·4
Fagaropsis angolensis	3·9	3·7	9·2	16·8
Vepris glandulosa	2·0	4·2	9·9	16·1
Ekebergia rueppeliana	4·0	1·2	3·1	8·3
Ritchiea albersii	1·0	2·0	4·9	7·9
Trimeria bakeri	0·8	2·0	4·9	7·7
Turraea holstii	1·5	2·7	3·3	7·5
Cassipourea malosana	3·0	2·0	4·9	7·2
Canthium schimperiana	2·8	1·2	3·1	7·1
Erythrococca bongensis	1·2	2·0	3·4	6·6
Olinia usambarensis	1·2	1·0	2·4	4·6
Cassine buchananii	1·1	1·2	2·1	4·4
Albizia gummifera	1·2	1·0	1·9	4·1
Clausana anisata	1·1	1·0	1·4	3·5
Grewia similis	0·1	0·7	1·8	2·6
Dovyalia abyssinica	0·5	0·5	1·2	2·2
Acokanthera schimperi	0·5	0·3	1·2	2·0
Maytenus undatus	0·4	0·5	1·2	2·1
Maytenus senegalensis	0·1	0·5	1·2	1·8
Euclea divinorum	0·5	0·7	1·0	2·2
Ficus thonningii	0·3	0·2	0·6	1·1
Schrebera alata	0·1	0·2	0·6	0·9
Juniperus procera	0·1	0·1	0·6	0·8
Rhus natalensis	0·02	0·2	0·6	0·8
Oxyris campressa	0·1	0·1	0·6	0·8

Other tree and shrub species occurring with lower frequency include, *Fagara usambarensis*, *Croton macrostachys*, *Diospyros abyssinica*, *Drypetes gerrardii*, *Ochna holstii*, *Dodonaea viscosa*, *Neobotonia macrocalyx*.

In tropical high forests, the family Rutaceae is less important (see for example vegetation studies in Ghana by Hall & Swaine, 1976), but species of this family become more important in their population and distribution under drier conditions (Lieberman, 1982). Tree species composition of the study forests correlated only broadly with other regional forests. It is particularly noted that the preponderant presence of Rutaceae is a characteristic indicator of dry climatic conditions. Concomitantly *Teclea* spp. and *B. huillensis* are important indicators of the dry semi-deciduous forest formation. These forests occur within the climatic limit of the closed forest formation types and merge with the woodland savanna vegetation.

Table 4. Overall frequency for the most common shrubs and ground flora in Karura, Ngong and Muguga Forests

Species	Frequency (%)		
	Karura	Ngong	Muguga
Teclea spp.	84·6	88·4	72·8
Phaulopsis imbricata	57·8	60·5	70·5
Pupalia lappacea	38·8	41·2	42·6
Setaria megaphylla	43·6	48·2	40·4
Clausena anisata	28·9	31·4	27·6
Pavonia urens	25·3	29·4	21·2
Vernonia lasiopus	17·6	18·7	13·7
Crotalaria uauensis	19·3	12·9	15·4
Lantana camara	31·6	8·8	18·2
Senesio petitiana	6·2	9·8	11·6
Abutilon longicuspe	4·3	6·9	8·9
Euclea divinorum	8·2	6·9	6·2
Scutia myrtina	9·0	7·2	6·9
Erythrococca bongensis	8·1	8·9	9·8
Solanum indicum	7·9	8·9	10·6
Cyphostemma maranguense	3·2	6·9	3·2
Dombeya mastersii	1·6	3·7	1·2
Asparagus africanus	3·2	3·8	1·2
Aspilia latifolia	3·1	3·9	4·6
Hypoestes aristata	1·6	3·6	1·8
Pterolobium stellatum	0·8	2·8	2·6
Cyanthula cylindrica	0·8	1·8	2·2

(Other shrubs and ground flora occurring with lower frequency included, *Cucumis ficifolius*, *Indigofera swanziensis*, *Opuntia vulgaris*, *Toddalia asiatica*, and *Carissa edulis*.)

Table 5. Sorensen's Index of similarity for the floristic composition of the sampled stands in Karura, Ngong and Muguga Forests

Forest blocks and stands	Index of similarity (%)
Ngong V–B and ridge stands	100·00
Karura V–B and ridge stands	97·4
Karura and Ngong forests	76·9
Ngong and Muguga forests	62·7
Karura and Muguga forests	53·8

V–B—Valley-Bottom stands.

Species composition and structural affinities of the study forests

A more detailed comparative analysis among the study forests and stands indicated that they were fairly similar in species composition (Table 5). The closer the distance between two forests or stands, the higher the similarity between them, indicating the degree to which closely associated species will interact thus sharing ecological niches in space. The observation may also suggest the possibility of a previously continuous forest.

Table 6 shows the distribution of canopy trees, understorey trees and shrubs in the three forests. While Karura and Ngong forests have a low percentage of canopy trees, Muguga nature reserve has a higher representation of emergents. The difference may be attributed to historical exploitation of the forests. The emergent trees

Table 6. Life form spectrum* in the Karura, Ngong and Muguga Forests

Forest block	Life-form categories: Canopy trees	Understorey trees	Shrubs
Karura	13·3	28·8	57·9
Ngong	17·0	30·9	52·1
Muguga	25·6	56·7	17·7

*All calculations based on rooted frequency. Each life-form category given as percentage of all recorded tree individuals.

in Karura and Ngong have been under heavy exploitation for a long time while the nature reserve at Muguga, though disturbed earlier, has been protected by the Research Station Director at Muguga since 1951 (Kigomo, 1985).

B. huillensis was frequent in both Karura and Ngong (Tables 1 and 2) but was absent from a small natural forest of about 60 ha less than 3 km north-west of Ngong forest and in Muguga Nature Reserve, some 15 km in the same direction. While the small altitude and therefore possibly temperature differences at Muguga may explain this, the reasons for its absence in Dagoretti (Fig. 1b) so close to forests carrying the species is unclear. Its responses to past disturbances and any management interventions are not also clear.

Age (size) structure and recruitment trends

Figure 3(a) and (b) show diameter distribution profiles of all tree species in valley-bottom and upper-ridge stands in Ngong and Karura forests, respectively. Both profiles show a decrease in population per unit area as diameter class increases. There are many small diameter trees and very few individuals are above 55 cm dbh. In the upper diameter-classes there are more larger diameter trees in the upper ridge stands than in the valley stands, particularly in Ngong. In Ngong also, the valley-bottom stands carried higher populations of saplings and young pole (sizes to 18 cm dbh) than the upper ridge stands. Saplings and lower stem diameter-classes in Karura were consistently more numerous in upper ridge stands. This minor difference in recruitment potential may be attributed to the physical differences between the valley-bottom sites in both forests.

Both Fig. 3(a) and (b) also show results of least-squares fit of the power function model on the tree population/diameter-distribution curves to test the population dynamics and rate of depletion over a period of time. The population/diameter distribution in both forests is well described by the power function analysis ($r^2 = 0{\cdot}95$ and $0{\cdot}89$, $P < 0{\cdot}01$, for Karura and Ngong, respectively). This result indicates that the stands have been in general undergoing continuous regeneration. The slope of the equation has been used to interpret and to estimate depletion or mortality rate within a stand over time (Hett & Loucks, 1976; Veblem *et al.*, 1980). Both forests indicated a similar population depletion or mortality rates, with Karura showing an average mortality rate in log stems/log diameter-class of $-2{\cdot}45$ and Ngong of $-2{\cdot}25$.

Figure 4(a) and (b) shows the diameter distribution of *B. huillensis* in the two site types in Ngong and Karura forests respectively. As in the general tree species

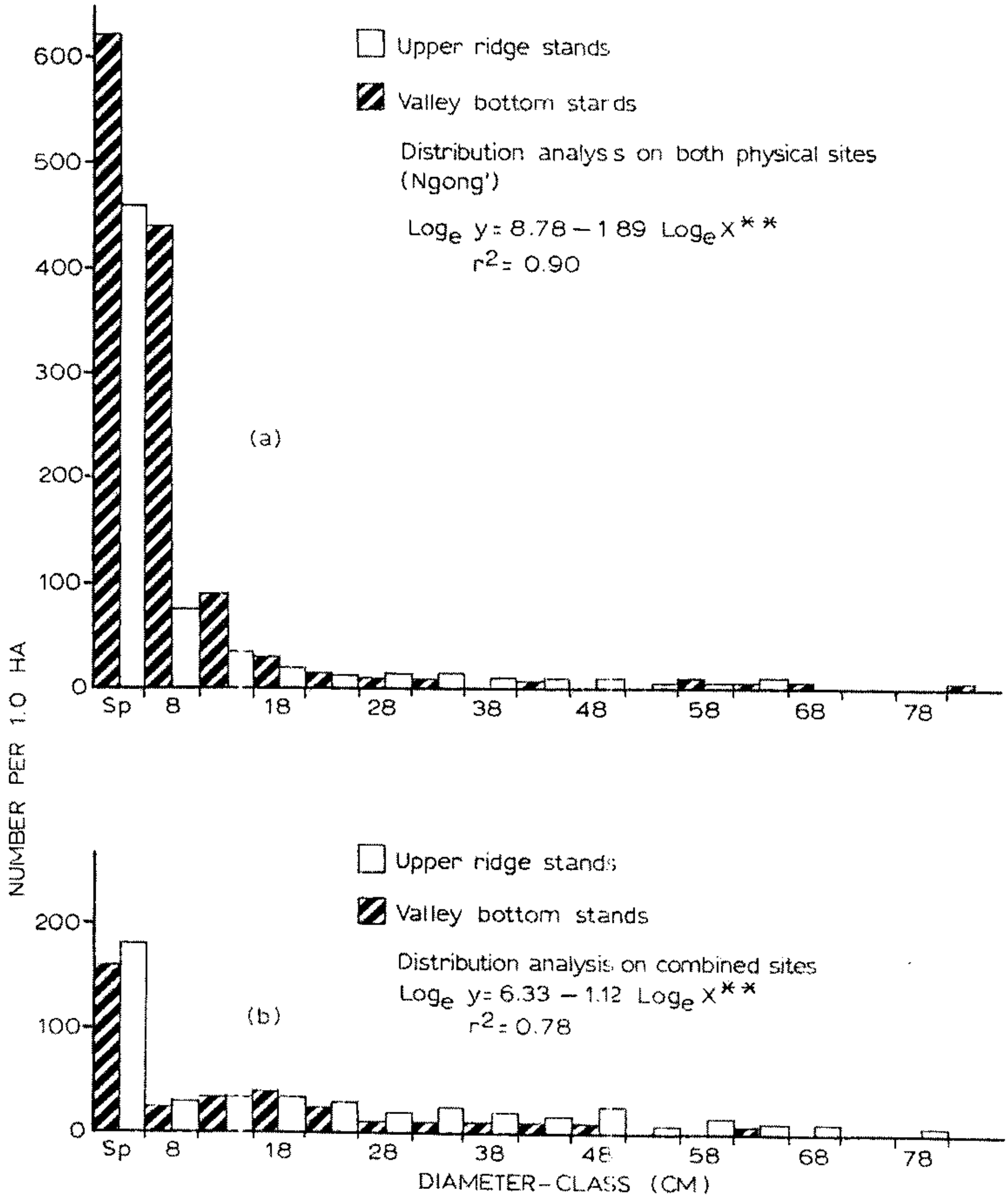

Fig. 3. Size-structure diagram and application of power function model for stand development in Ngong (a) and Karura (b) forests. Diameter class used is 5 cm dbh class beginning at 3 cm. ** = Significant at 0·1% probability level.

analysis in Ngong, recruitment in valley bottom stands tended to be better represented in the smaller tree size classes up to stems of 23 cm dbh. In older individuals upper ridge stands were better represented. This may support the suggestion that well drained soils could be an asset to better growth of the tree. Very few individuals were above 55 cm dbh on either site.

Larger trees were marginally better represented in Karura than in Ngong especially on upper ridge stands. On an overall basis, Karura stands were more dense (1892 stems/ha) than Ngong stands (1576 stems/ha).

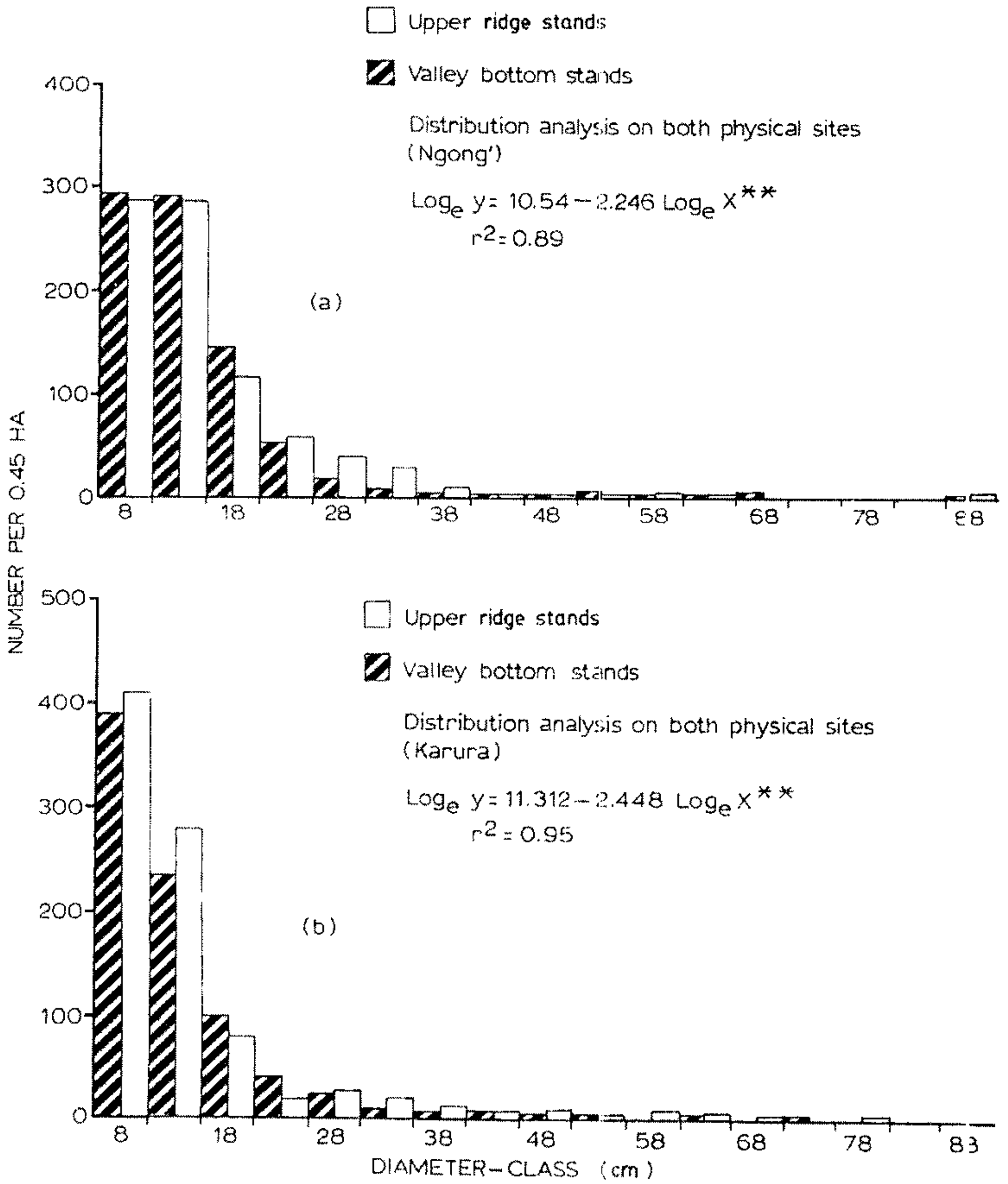

Fig. 4. Size-structure diagram and application of power function model for the recruitment trend of *Brachylaena huillensis* in Ngong (a) and Karura (b) forests. Size classes used are sp (saplings <3 cm dbh but >1 m height), and as in Fig. 3.

Application of the power function model to the diameter distribution of *B. huillensis* in Ngong indicated a good fit for valley-bottom stands ($r^2 = 0{\cdot}87$) and the upper ridge stands ($r^2 = 0{\cdot}92$, $P < 0{\cdot}01$, Fig. 5a). The fit to the diameter distribut on of the species in Karura was also significant ($P < 0{\cdot}01$) for valley-bottom stands ($r^2 = 0{\cdot}84$) and for upper ridge-stands ($r^2 = 0{\cdot}86$, Fig. 4b). Variation of populat on per unit area is better explained by size class in Ngong (87% and 92%). But the long-term mortality rate was higher in both sites in Ngong (−1·706 and −0·914) than in Karura (−1·941 and −1·288). However, in both forests tree population mortality has been higher in valley-bottom stands (−1·941 and −1·288 for Ngong and Karura respectively) than in upper ridge stands (−1·706 and −0·914, for Ngong and Karura respectively).

Discussion and conclusions

The forests under study comprise many families each represented by only a few tree species. The dominant family (Rutaceae) is predominantly represented by *Teclea* spp. which form the main canopy species of about 20 m in height. There are only few emergent canopy species which include, *Croton megalocarpus* in Karura, Ngong and Muguga forests, *Brachylaena huillensis* in Karura and Ngong, *Calodendrum capense* in Muguga, and *Olea africana*, mainly in Muguga but also in Ngong and Karura.

These patches show poor tree species composition and size distribution affinities with other remaining forest vegetation in Kenya; an observation that calls for more serious and urgent attention to be given to the conservation of forest patches. Bray (1956) defines a stable plant community as one having individuals of the dominant species present in all diameter classes. Investigation of the forest structure allows an examination of the dynamics and therefore the possible stresses imposed mainly by the overstorey species (Meyer, 1952). Two of the major forests studied were analysed for their stability by tree diameter distributions. The forests are poorly represented in large diameter class individuals except those poor and fluted trees left during past selective cutting. Over most of the sample stands there is little doubt that recruitment of one or other of the species occurs at various stem sizes (and therefore possibly ages) as reflected by strong coefficients of determination (r^2) ranging from 0·87 to 0·95 derived from diameter class distribution analysis.

Forest structures characterized by an emergent canopy of widely spaced individuals of great size standing in an uneven-aged matrix of other species as noted with the study forests suggest that succession is in progress (Jones 1945; Whittaker, 1974). The structure therefore of the study forests is consistent with the hypothesis that in the absence of catastrophic disturbance the emergent *B. huillensis* will regenerate through the main canopy species of *Teclea* spp. (and others) and will replace, in great part, the secondary gap-filling species like *C. megalocarpus*, *C. capense* and *D. abyssinica*, as the latter come to maturity and start losing their canopy dominance. This observation is corroborated by the high coefficients of determination (r^2), ranging from 0·84 to 0·92, thus indicating the potential of *B. huillensis* to maintain itself within a developing stand despite some past disturbances in the form of selective cutting of the species.

Vegetation change has been interpreted simply as the differential growth and survival of species available in spatially and temporarily varying environments (Egler, 1954; Drury & Nisbet, 1971, 1973). While part of environmental variation may be a consequence of the action of the plants on the environment, frequently, it is the result of repeated major disturbances by factors largely external to the vegetation (see studies by Veblem *et al.*, 1980, and Whitmore, 1974). In the light of possibilities of effecting controlled interventions in the semi-deciduous forests under study, the major requirement is to relate observable processes to the observed forms analysed in the present study. This, in essence, means relating parameters like size and spatial distribution to modes of reproduction of the more dominant, commercial species. *B. huillensis* is the most commercially important species in the forests under study, and there is an urgent need therefore to understand its reproductive and growth dynamics under various environmental conditions within the forests. Such understanding would assist in its management.

Acknowledgments

This paper presents results of part of a longer study programme funded jointly by the Government of Kenya and the Overseas Development Administration (ODA), whose support is acknowledged.

The assistance of Messrs L. Kihura, N. Gachathi, S. Wakaba and E. Achola in the field assessments is also greatly appreciated.

References

BRAY, J. (1956) Gap phase replacement in maple-basswood forests. *Ecology* **37**, 598–600.

CONNEL, J.H. & SLATYER, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Nature* **111**, 1119–1144.

DRURY, W.H. & NISBET, I.C.T. (1971) Inter-relations between developmental models in geomorphology, plant ecology and animal ecology. *General Systems* **16**, 57–68.

DRURY, W.H. & NISBET, I.C.T. (1973) Succession. *J. Arnold Arbor.* **54**, 331–368.

EGLER, F.E. (1954) Vegetation science concepts. I. Initial floristic composition, a factor in old field vegetation development. *Vegetation* **4**, 412–417.

HALL, J.B. & SWAINE, M.D. (1976) Classification and ecology of closed canopy forest in Ghana. *J. Ecol.* **64**, 913–951.

HETT, J.M. & LOUCKS, D.L. (1976) Age-structure models of balsam fir and eastern hemlock. *J. Ecol.* **64**, 1029–1044.

JONES, E.W. (1945) The structure and reproduction of the virgin forest of north temperate zone. *New Phytol.* **44**, 130–148.

KERFOOT, O. (1963) The vegetation of S.W. Mau Forest. *E. Afr. agr. For. J.* **29**, 295–318.

KIGOMO, B.N. (1985) A note on the phytosociological status of *Vepris glandulosa*; an endangered tree species. *Promotion of Science and Technology* **10**(2), 23–26. Kenya National Academy, Nairobi.

LIEBERMAN, D. (1982) Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.* **70**, 791–806.

LIND, E.M. & MORRISON, M.E.S. (1974) *East African Vegetation*. Longman Group Ltd., London.

MEYER, H.A. (1952) Structure, growth and drain in balanced uneven-aged forests. *J. Forest.* **50**, 85–92.

MUELLER-DOMBOIS, D. & ALLENBERG, H. (1974) *Aims and Methods of Vegetation Ecology*. John Wiley & Sons Inc., New York.

NOBEL, I.R. & SLATYER, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5–21.

RICHARDS, P.W. (1952) *The Tropical Rain Forest*. Cambridge University Press, Cambridge.

VEBLEM, T.T., SCHLEGEL, F.M. & ESCOBARR, B. (1980) Structure and dynamics of old-growth *Nothofagus* forests in the Valdivian Andes. *J. Ecol.* **68**, 1–31.

WHITMORE, T.C. (1974) Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands. *Common Forestry Institute Paper* No. 46, Oxford University.

WHITTAKER, R.H. (1974) Climax concepts and recognition. In: *Vegetation Dynamics* (Ed. R. Knapp). W.R. Junk, The Hague.

(*Manuscript accepted 25 April 1990*)

Appendix I

Family (tree and shrubs) status in Karura, Ngong and Muguga natural forests (Dominance values weighted by representative species' 'Importance Value')

Family	Dominance value		
	Karura	Ngong	Muguga
Rutaceae	263·8	258·2	280·1
Euphobiaceae	146·3	132·8	127·6
Oleaceae	20·1	28·6	38·2
Cannellaceae	8·4	12·8	30·8
Compositae	89·8	100·7	20·2
Loganiaceae	72·6	60·2	30·9
Celastraceae	55·4	42·3	27·9
Ebenaceae	45·4	49·4	27·5
Flacourtiaceae	42·9	16·0	0·5
Ochnaceae	27·9	29·2	18·6
Rubiaceae	11·4	14·6	27·4
Boraginaceae	14·6	13·4	25·6
Meliaceae	4·9	8·3	15·6
Papilionaceae	20·4	16·4	14·8
Tiliaceae	8·3	11·6	9·8
Rhizophoraceae	8·9	4·6	7·2
Sapotaceae	6·7	12·6	1·0
Moraceae	6·2	4·2	7·2
Oliniaceae	4·6	5·4	0·8
Mimosaceae	8·7	6·2	8·1

(Other minor families include; Apocynaceae, Araliaceae, Caesalpinaceae, Cucurbitaceae, Malvaceae, Rhamnaceae, Liliaceae, Sapidaceae, Solanaceae, Sterculiaceae and Tilliaceae.)