

Chapter

Regeneration Dynamics of an African Tropical Forest Canopy Dominant Tree Species

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Abstract

The population structure and regeneration of *Olea welwitschii* in Kakamega differs in different forest blocks. There are differences in abundance between the forest blocks, that can be explained by past human-forest interactions – harvesting by mechanized loggers who clear-felled stands of desired merchantable species and the skilled pitsawyers who selectively harvested desired tree species. There is a clear absence of seedlings/saplings pointing to a lack of regeneration inside the forest over the last 40 years. Intense seed predation by rodents and attack by fungal pathogens account for up to 99% mortality of fruits and seeds under the parent crowns. *Olea welwitschii* seedlings/saplings are evident in forest glades. These glades have been maintained by grazing and burning. Fires discourage the growth of trees, while grazing encourages the establishment of mound-building termite species upon which, grassland species such as *Combretum molle* colonize. Grazing appears to inhibit rodent predators while *Combretum molle* serves as perch and nesting sites for avian frugivores. Avian frugivores drop *Olea* seeds under *Combretum*'s crowns, which germinate and establish under reduced predation and fungal attacks germinate and establish. Patches inside the glades in which *Olea* regenerates become centres from which the forest continues to invade the glades.

Keywords: *Olea welwitschii*, Kakamega forest, seed predation, seed dispersal, regeneration, canopy dominants, glades

1. Introduction

The Elgon teak, *Olea welwitschii* (Knohl) Gilg. & Schelleneb is a canopy emergent tree in the family Oleacea [1]. This tree species is indigenous to sub-Saharan Africa ranging from Cameroon in the west to Ethiopia and Kenya in the east, and south to Angola, Zambia, and Mozambique [2]. It is typically a forest tree species, that grows from lowland tropical rainforests to evergreen montane forests [3]. The tree can grow to a height of 25 m with a straight bole and a small crown. It has a pale gray to white bark, that is grooved vertically. The flowers are small and white, in sprays to 8 cm long. The fruits are narrow, oval, and have small drupes. Its wood is extremely good, and stable with esthetic timber used in shipbuilding. It is also used to make fine

furniture, door and window frames, and any other applications that require strong, durable, and stable wood. It is termite resistant and its branches are also used for firewood while its bark is medicinal. This species dominates the western Kenya forests, especially the Kakamega and Mt. Elgon forests. In these forests, *Olea welwitschii* does not show notable evidence of natural regeneration under the parent crowns [4]. This paper examines the factors that may be responsible for the lack of apparent natural regeneration in the Kakamega forest, Kenya.

The family Oleacea has been prized since the dawn of civilization. For instance, its most famous member, the olive (*Olea Europa* L.) was cultivated 3000 years B.C [5]. Today, in a large part of the world, the olive still represents life and plenty in the minds of men. The European ash (*Fraxinus excelsior*), another member of the Oleacea, was used by Greeks to make cupid bows. The most familiar members of the family are the jasmine species (*Jasminum* spp.) which have been favorites in home gardens for centuries [2].

Three Oleacea genera -*Schrebera*, *Olea*, and *Linociera*, occur in Africa [6]. Of these, *Olea* is by far the most common and widespread. In Kenya, it is represented by five species -*Olea africana* Milla, *Olea hochstetteri* Baker, the East African olive, *Olea kilimandscharica* Knobl, *Olea mildbraedii* (Gill & Schelleneb) and *Olea welwitschii*.

Olea welwitschii is typically a rainforest tree species endemic to Mt. Elgon [7, 8]. It also occurs in Kakamega, North, and South Nandi forests which appear to be its easternmost limit. Information on the pollination ecology of this species is scant. In Kakamega and the neighboring Kisere forests, *Olea welwitschii* is canopy dominant comprising some 7.5 and 49 percent respectively of the total volume of merchantable species [9]. Prior to 1966, this species comprised 69% of the total utilizable timber in the Kakamega forest and by 1980, this percentage had dropped to a mere 7.5% due to uncontrolled harvesting by commercial loggers.

In the Kakamega forest, it grows in localized patches of very few senescing adults -except for those in enrichment plantations. Kisere forest dominates the canopy but shows a skewed population distribution in the 500-ha forest [10]. For instance, it occurs in an almost pure stand in the south, east and north-eastern parts of this forest, and in neither forest does *Olea welwitschii* exhibit any apparent natural regeneration.

2. Study sites and methods

2.1 Study sites

Three study sites were selected from different parts of the forest. Two sites were selected in the southern part of the forest while another site was in the northern part of the forest (**Figure 1**). Each of the three sites was contiguous with forest glades (grassy areas that are surrounded by forest). The northern study site was located in the Kisere forest which is part of the National Reserve and a long-time nature reserve. The southern study sites were located in the newly established Kakamega Forest National Reserve and at the Kakamega Forest Station. All three study sites had large mature *O. capensis* adults. The southern study sites have been logged selectively in the 1970s and early 1980s. During logging, many large *O. capensis* adults were selectively harvested [9].

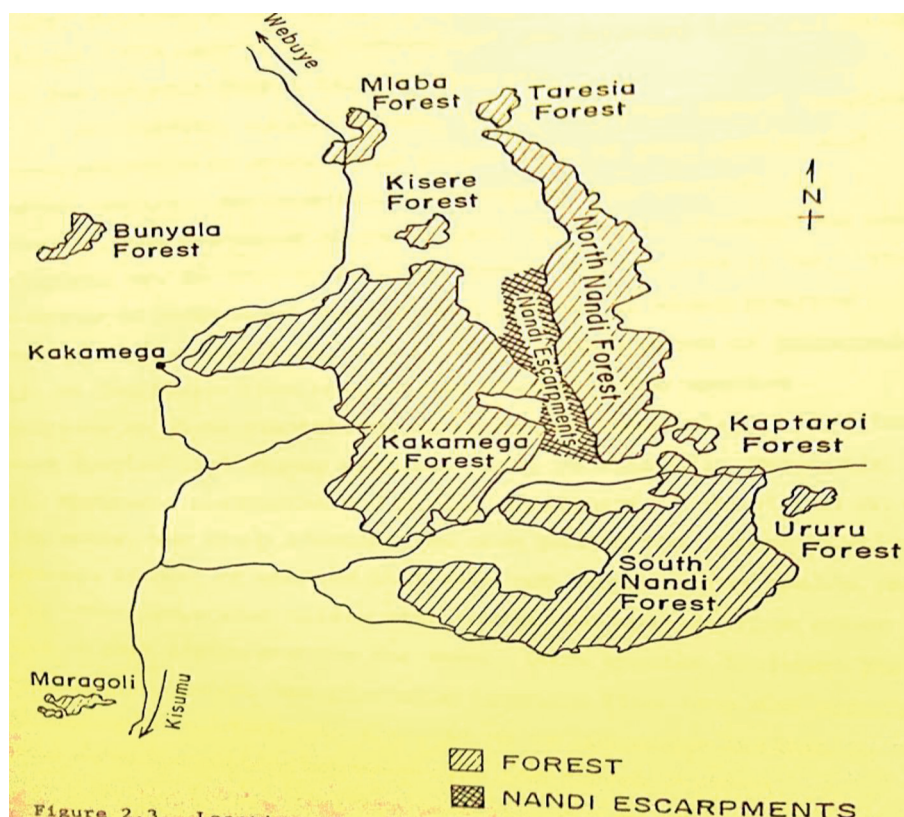


Figure 1.
 Map of the Kakamega forest complex. Source: [9].

2.2 Study methods

Plotless methods were used throughout the sampling regime [10–14]. Density and size-class distribution were measured using a wedge prism B.A.F. 4.6 m² which allowed the discrimination between trees of different size classes. Distances between sampling points were established using a tape measure. Distances from this tree to the nearest closest first, second, and third nearest neighbors were measured [10, 11, 15]. A wedge prism was used to establish of variable plots that were evenly and randomly distributed within the study sites along established transects.

Spacing was determined by comparing the mean distances to the nearest neighbors with the distance from random points to the nearest tree [14, 15]. The mean observed distance was calculated using the formula,

$$rA = \bar{E}r / N \quad (1)$$

where N is the number of measurements of distance in the observed population or sample and r is the distance in any specified units from a given individual to its nearest neighbor.

Because seedlings and saplings could not be sampled using the wedge prism method, 25×25 m quadrats located randomly within the study sites were employed. These quadrats were inventoried for seedlings and saplings. All young plants not exceeding 0.5 m in height with a measurable diameter at the base were classified as saplings. Their heights were also measured using a clinometer. Adults of all tree species present were identified and their Dbh was measured using a 2.5 m Dbh tape measure.

3. Results

3.1 Population structure of *Olea welwitschii*

Olea welwitschii in Kakamega and Kisere forests exhibit a multimodal population structure that is unique for a tropical forest tree. Most studies of the population structure of tree species in tropical forests have revealed that most of these species will tend to show an inverse J-shaped curve [16, 17]. The inverse J-shape population structure has been shown to vary depending on the species in question. For instance, [18, 19] found variations in the J-shape curve depending on whether the species in question was a climax tree that was permanently established or seral species of type I or II of either invading or unstable types in a mixed forest. These variations in the J-shape have also been demonstrated in forest trees in Ghana, west Africa [20, 21].

There are two explanations for the multimodal population distribution in *Olea welwitschii*. The first explanation invokes past human disturbances mainly, extractive harvesting. Kakamega forest has been logged in the past (for 50 years) [22]. In principle, this logging was supposed to be selective but there appears to be no evidence of this practice. If implemented, selective logging would have minimized overexploitation of certain preferred species of trees more so in size class distribution. But selective logging is difficult to implement because it requires strict supervision and manpower.

To date, there are no reported cases in tropical forests where supervised selective logging has been achieved. Besides, selective logging would be easier if trees in tropical forests were uniformly distributed or were in monospecific stands, but the spacing of trees in tropical forests is not uniform [23, 24]. It is therefore clear that logging cannot explain the multimodal population structure of *Olea* given the similarity of the population structure in logged and unlogged sites in the forest. Thus, careful logging can only explain differences in abundance.

The second explanation of the multimodal population structure is based on regeneration dynamics. *Olea welwitschii* regenerates in waves such that groups of trees are clustered in various age groups that correspond to periods of population recruitment. These age groups appear to be a function of the existence of conditions that favor germination and establishment. But for such a pattern to occur, requires that conditions for regeneration occur in waves or bursts. The differences in age groupings when calculated in years, would provide information on time periods between different regeneration events and whether these events are cyclical or random in nature. Such an explanation would imply that the largest individuals of *Olea* in the forest are not relics of a colonizing species, rather, they represent a different older age group.

The population structure of regeneration that *Olea welwitschii* in Kakamega forest is typically a northern temperate that has been observed among maple-basswood

forests [19], oak-hickory forests [20], the new forests in Pennsylvania [21] and the hardwoods in New England (USA) [23]. These forests share one common phenomenon, disturbance, which has been shown to be a major cause of wave patterns of regeneration. A high correlation was reported between disturbance and population recruitment in their study of age-class distributions among various tree species in the New Forest of Great Britain [24]. The regeneration pattern in the species was not continuous and the successful establishment of seedlings was dependent on disturbance by fire and hurricanes.

3.2 Size-class, density, and density distribution

The density and spatial distribution of *Olea welwitschii* vary in Kakamega and Kisere forests (**Figure 2**). The overall size-class structure is significantly different in both forests. In addition, the mean Dbh in the Kakamega forest varies between 56.1 ± 49.6 cm – 97.3 ± 65.4 cm while in the Kisere forest, it is 107.7 ± 58.2 cm. In essence, the population structure of *Olea welwitschii* shows a multimodal distribution (**Figure 2**) instead of the inverse J-shaped population structure typical of most tropical tree species [25, 26].

The density of *Olea welwitschii* varies depending on the forest site in question. **Table 1** summarizes the density in different blocks of forest. In all three sites, the values of R indicate that *Olea welwitschii* has a varied degree of clumped distribution.

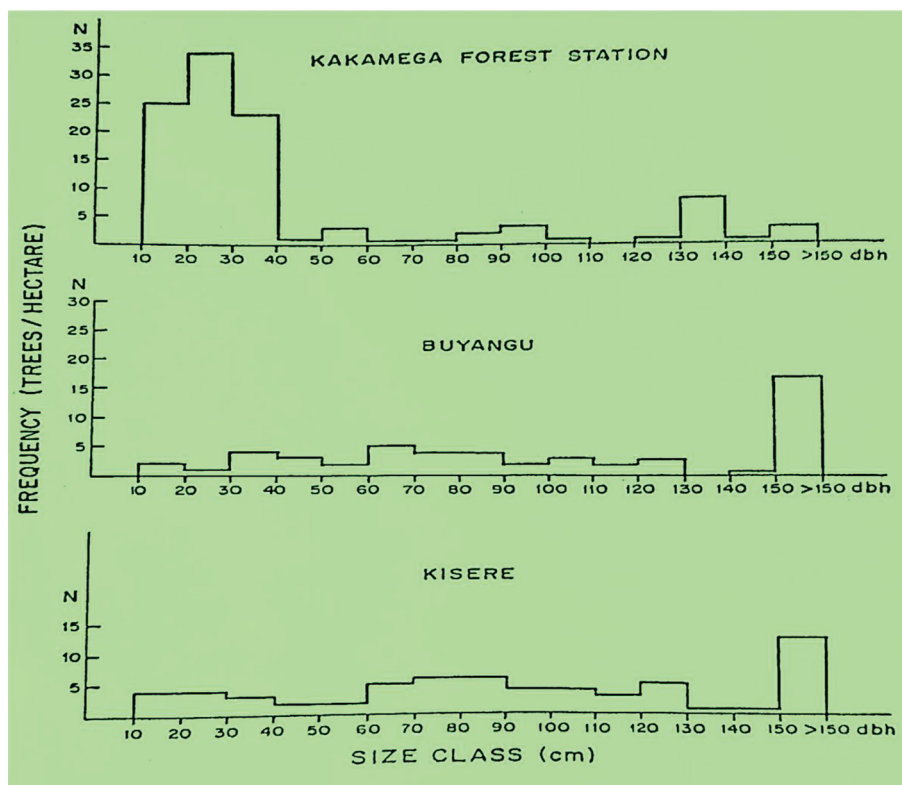


Figure 2.
 Population structure of *Olea welwitschii* in different sites in Kakamega forest.

Forest Sites	Density/ha	Spatial contagion (R)	Z value
Kakamega Station	8.4	94.6	0.012
Buyangu	6.3	143.6	0.014
Kisere	425.2	368.0	0.002

Table 1.

Density of *Olea welwitschii* in three different forest sites together with values of the spatial contagion and the significance level.

The species is highly clumped in the Kisere forest. Variation in clumping appears to correspond to the degree of exploitation in the past [9].

The presence of the multimodal distribution pattern suggests periods of regeneration that are interspersed with periods of no regeneration [27, 28]. In fact, it has now been established that very small intensities of disturbances will produce a non-J-shaped population structure. According to [29, 30], non-J-shaped size-class distribution structures are relatively common and may represent stable population structures. The modal size-class distribution at the Kakamega forest station is probably due to enrichment planting rather than natural regeneration.

3.3 Natural enemies of natural regeneration

Perhaps the question to ask at this point is “why does *Olea welwitschii* not regenerate inside the forest and does *Olea welwitschii* regenerate at all? One fact that is clear is that *Olea welwitschii* fruits every other year with flowering commencing in November of the fruiting year with small fruits appearing in early February. These fruits are drupes with a thin layer of edible pericarp while the endocarp is stony. The stony endocarp houses the seed. Fruits of *Olea welwitschii* attract mammal visitors such as the black and white colobus (*Colobus guereza*), Sykes monkeys (*Cercopithecus mitis stuhlmani*) redbtail monkeys (*Cercopithecus Ascanius*) and the giant tree squirrels (*Protoxerus stangeri*). There are also avian visitors that include black and white-casqued hornbills (*Bycannistes subcylindricus*) and barbets (Fam. Capitonidae and greenbulbs (Fam. Pycnonotidae). These frugivores eat the pericarp and drop the stony endocarp.

3.4 Seed predation, fungal pathogens, and chemical interactions

Seed predation has been demonstrated to influence spatial patterns of regeneration of many plant populations [31, 32]. Seed predation may take place before seed dispersal (pre-dispersal) or after dispersal (post-dispersal). It is clear that plants and their seed predators from ecological systems have high atemporal and spatial variability with regard to seed and predator abundance. For instance, seed predation may be intense in years when other resources are scarce and low when other resources are abundant. Besides, seeds that fall under the parent tree may suffer disproportionately high levels of predation from density-dependent obligate seed predators that are resident at the parent tree [33–35]. The impacts of fungal pathogens are likely to increase with the ongoing climate change with a tendency for increased precipitation [36]. Seeds that are dispersed some distance away from such parent trees may experience low levels of seed predation [36]. In *Olea welwitschii*, smaller fruits (70%) suffer high predation rates than the larger ones (30%). In addition, more small fruits fall below the parent plant (89%)

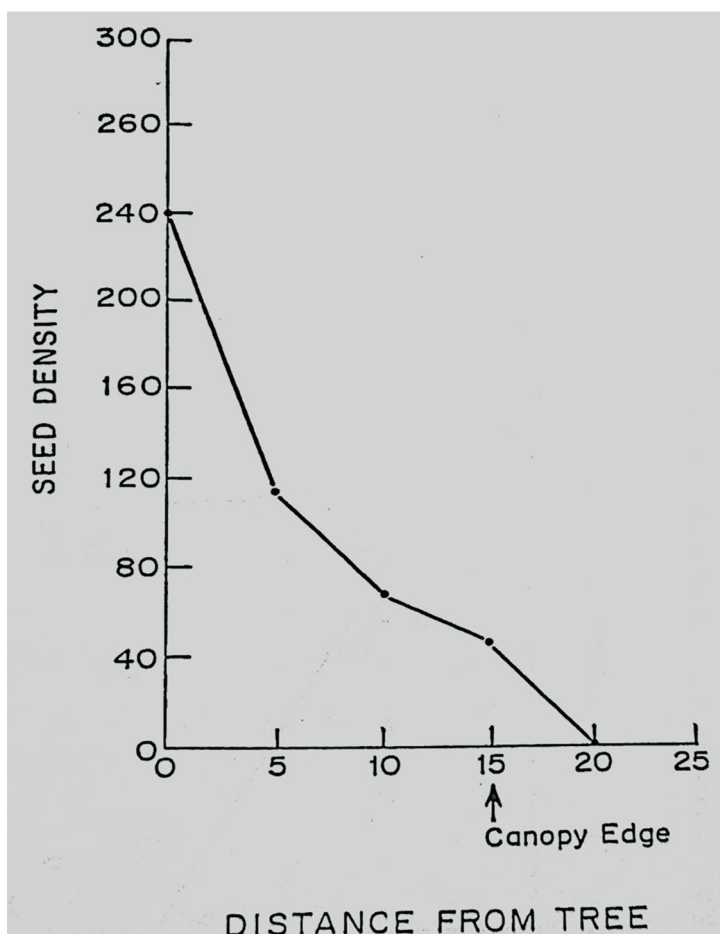


Figure 3.
 Seed density as an inverse function of the distance from the parent crown.

than large ones (11%). Fruit and seed density is a decreasing function of distance from the parent trees and tends to be highly leptokurtic (**Figure 3**). Data on predation rates on fruits and seeds placed along transects away from the parent trees reveal that density has no influence.

Distance from the parent tree appears to have a significant effect on the rates of seed and fruit predation. Regardless of density, seeds tend to be eaten within hours of falling on the ground below the parent tree while fruits tend to be ignored. In fact, predation rates can be ranked with seeds within 10 m of the parent crown inside the forest (away 95%), fruits in the forest (>10 m) from the parent crown (68%), seeds in the forest away (>10 m) from the parent crown (48%) and fruits under the parent crown (7%). Clearly, while seed predation is distance-dependent, fruit predation is distance independent. The major seed predators are rodent species *Praomys jacksoni* whose population increases significantly under the *Olea welwitschii* crowns during fruiting. In addition, *Olea welwitschii* seeds under the parent tree suffer a high proportion of fungal attacks. Interestingly, mold infection tends to be influenced by seed density majority suffering an infection in the first 24 hours after falling from

the parent tree. Two mutually exclusive mold species have been identified that are responsible for seed attack -*Cercospora* sp. and *Gloesporium* sp. These two fungal species are obligate parasites of *Olea* that live on the leaves of the parent tree whose spores mature just before the onset of rains and are dispersed by raindrops [37, 38].

There is also evidence of chemical interactions in the germination of *Olea welwitschii* seeds. Studies by [9] have demonstrated that phytotoxin leachates from shoots of the parent tree inhibited the germination of *Olea* seeds. This apparent allelopathy and has been reported in many plant species [39–41]. This finding confirms the observation by the forest nursery workers that *Olea* seeds take longer to germinate (30 days on average) while the majority of the seeds do not germinate at all. In fact, shoot leachates additionally retard the growth of seedlings making seedling establishment difficult.

3.5 Factors that enhance natural regeneration

The absence of *Olea* seedlings inside the forest would appear to suggest that this canopy dominant does not regenerate at all. However, a survey of the nearby forest grasslands (glades) reveals the presence of seedlings and saplings of *Olea welwitschii*. These glades are characterized by abundant termite mounds and unique tree species (*Combretum molle*) that grow on them. The common termite species were *Cubitermes montanus* and *Macrotermes* sp. Interestingly, in glades without *Combretum molle*, there were fewer termite mounds and the species of termite present was different (*Odontotermes* sp. And *Sphaerotermes* sp. (Tables 2 and 3). The glade with *Combretum molle* and *Cubitermes montanus* and *Olea* seedlings/saplings are referred to as the *Olea* Regeneration Sites (ORS). The ORS tend to be heavily grazed with little evidence of burning while non-ORS glades tend to have long grass and are subjected to regular burning, sometimes annually.

In ORS, *Olea* seedlings/saplings tend to be found on *Cubitermes montanus* mounds.

3.6 *Olea* regeneration sites

Studies by [9] have demonstrated a strong association between termites and *Combretum*. For instance, of the 582 sampled in one of the glades, 422 (75.5%) had *Combretum molle* growing on them while 160 (27.5%) did not have *Combretum* on them. In addition, mounds in ORS tend to be highly aggregated. Clumping appears to be strong in areas where *Combretum molle* is permanently established but less clumping in areas with establishing *Combretum* trees. Mounds in non-ORS tend

Glade	Type	Mounds per Ha
Kisere	ORS	627.2
Kalunya	Non-ORS	206.4
Khavega	Non-ORS	123.2
Khasali	Non-ORS	131.2
Miyao	Non-ORS	112.0

Table 2.
Cubitermes distribution in ORS and Non-ORS glades in Kakamega forest.

Glade	<i>C. montanus</i>	<i>Odontotermes</i> sp.	<i>Sphaerotermes</i> sp.	<i>Macrotermes</i>	Total
Kisere	627.2	0	0	1.6	628.8
Kalunya	206.4	32	4	0	242.4
Khavega	123.2	40	0	0	163.2
Khasali	131.2	8	0	0	139.2
Miyao	112.0	2.8	0	0	114.8

Table 3.
Termite's species found in different glades in Kakamega forest.

to be regularly or randomly spaced pointing to the strong influence of *Combretum* on mound distribution. It appears like *Combretum* cannot establish strongly in areas without termite mounds. The mechanism by which *Combretum* establishes on mounds remains unclear and needs further investigations. What is clear is that establishment of *Combretum molle* on mounds appears to be a necessary first step in *Olea* regeneration. And the establishment of *Combretum* on mounds appears to inhibit the growth of the mounds forcing termites to construct yet another mound a short distance from the dying mound; with the process repeating itself.

3.7 Agents of seed dispersal

Olea seeds weigh a little over 1gm making it hard for them to be dispersed by wind. In addition, most *Olea* seedlings tend to occur at a distance from the parent trees inside the forest. This points to the animal dispersal of *Olea* seeds. *Olea* has two potential fruit predators -forest mammals and birds. For mammals, the home ranges would limit them from long-distance dispersal leaving birds as the best candidates for dispersal. Such avian *Olea* seed dispersers tend to be non-forest and reside in ORS and are capable of flying up the canopy, are highly frugivorous and non-territorial. Observational determination of *Olea* seed dispersers revealed that the yellow-whiskered greenbul (*Andropadus importunis*), the joyful greenbul (*Chlorocichla laetissima*), and the common yellow-vented bulbul (*Pycnonotus goiavier*) as the most efficient dispersers of *Olea* seeds from the forest into the ORS. **Table 4** clearly shows that *P. goiavier* makes far more visits to fruiting *Olea* than the other two, making it the most probable transporter of *Olea* seeds into the ORS. But these dispersers also facilitate germination. Seeds collected from their droppings germinated earlier and faster than those that had not been eaten.

Figure 4 shows the flight paths of the three dispersers. It is clear that the common yellow-vented bulbul is the only one that flies directly from the ORS into the fruiting *Olea* in the forest and back.

Disperser	Before Fruiting	During Fruiting	After Fruiting
Common yellow-vented bulbul	156	2344	115
Yellow-whiskered Greenbul	0	85	1
Joyful Greenbul	0	3	0

Table 4.
Number of visits to fruiting Olea by three possible dispersers.

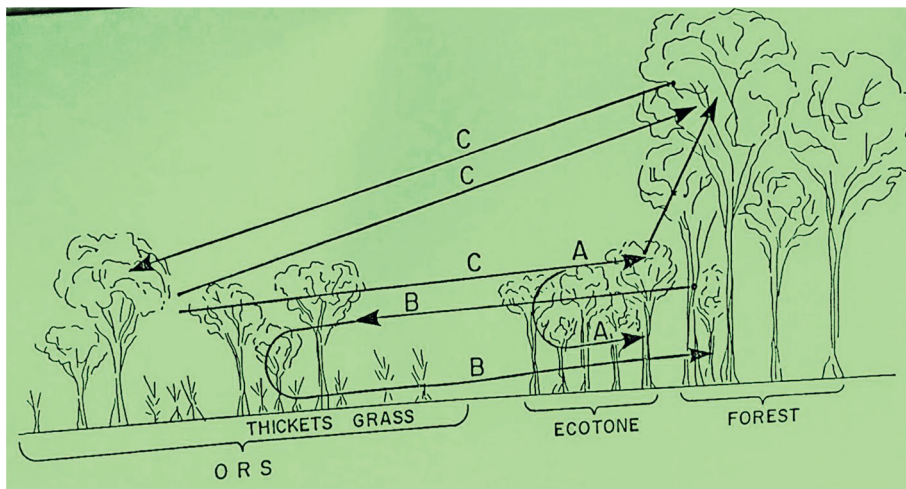


Figure 4. Flight path of dispersers from the forest to the ORS. A is the flight path for the joyful greenbul, B for the yellow-whiskered greenbul and C for the common bulbul.

4. Conclusion

Does *Olea welwitschii* in Kakamega forest regenerate in response to disturbances that can explain its population structure? One common disturbance in tropical forests is the canopy openings resulting from tree falls [42]. And the *Olea* response to such a disturbance would be demonstrated by the presence of a large pool of seedlings/saplings inside the forest. Unfortunately, such pools do not exist [43]. What kind of disturbance could *Olea* regeneration be responding to? Regeneration of *Olea* appears to respond to disturbances that are unique in nature [44]. The formation of glades (open grassy areas in the forest) is one such unique disturbance that allows the regeneration of this species. Glades are by definition, disturbed sites that differ from openings in the canopy that last longer before they are transformed into a forest. Faunal and floral communities in these glades differ from those in the forest. The closest resemblance of glades to the forest lies in the species composition of canopy forest trees that are in their early and intermediate stages of succession.

Glades have two attributes that are seen to determine whether *Olea* will regenerate or not, low rates of seed predation, given their distance from the fruiting trees, and low incidences of attack by fungal pathogens, given their low humidity. Low seed predation rates are a function of the reduced population of rodents that destroy seeds and reduced numbers of rodents in these sites result from intense grazing which reduces ground cover that would otherwise provide habitats for the seed-eating rodents and fires that are used to stimulate the growth of new grass. Fire and grazing combined reduce ground cover. But fires affect the second component of *Olea* regeneration in the *Olea* Regeneration Sites (ORS) -termites. These glades are dominated by mound-building *Cubitermes montanus* which are absent in non-ORS. Studies by [45] revealed that fire reduces the density of mound-building termites.

The presence of mounds seems to encourage the establishment of a tree species, *Combretum molle* under whose crown, *Olea* seedlings can be found. The interplay between termites and *Combretum* on one hand and the common bulbul (*Pycnonotus barbatus*) appear to drive the regeneration of *Olea* in the Kakamega forest (**Figure 5**).

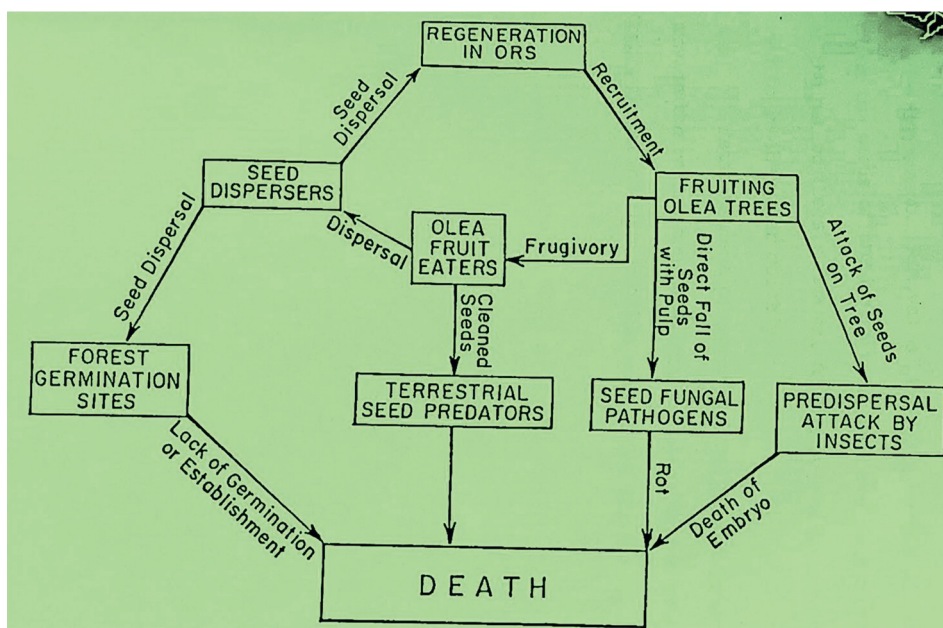


Figure 5.
 Summary of destination and fate of *Olea* seeds in Kakamega forest. Successful seeds are those that are dispersed to the ORS.

A similar observation has been reported in Budongo forest, Uganda by [46] where it was observed that in sample plots where *Olea welwitschii* was regenerating, there were many grassland-type termites' mounds of *Bellicosus aurivilli* Sjost.

The absence of grass on the termite mounds keeps away grazing herds enabling *Combretum* to establish itself. Established *Combretum* ultimately shades the mounds preventing grass from growing. But *Combretum* is an important perch tree for the common bulbuls (and other bird species) during swarming of termites which tend to congregate above these tree species. The common bulbuls are strictly frugivorous and feed on *Olea* fruits during the fruiting season, even though they are open-country species. During fruiting, seeds are then dropped by the bulbuls under the crowns of *Combretum* and the microclimates under the crowns facilitate the germination of *Olea* seeds [44, 47]. Contrary to reports by [48, 49], *Olea* is not a colonizing species in view of its regeneration dynamics.

Survival of *Olea* seedlings in these ORS is good despite attacks by grazing domestic herds of the forest-adjacent communities. Survival of the saplings is also subject to harvesting by forest-adjacent communities. *Olea* poles tend to be harvested for use in the construction of grain storage units [50]. The diagram below summarizes the important processes in the regeneration dynamics of *Olea* in the ORS in the Kakamega forest. Disturbances that cause glades are the most important processes in the chain of events that will ultimately facilitate regeneration not only of *Olea* but also of other small-fruited canopy tree species inside the forest.

Regeneration of *Olea welwitschii* outside the forest is unique for a tropical forest tree species that is not a colonizer. Such a strategy of regeneration has not been reported for any other forest canopy dominant in the tropics. A number of studies have reported species with regeneration characteristics similar to those of *Olea*. Studies by [51] found that *Pithecellobium saman* and *Enterolobium cycloparm* were incapable of regenerating under their own crowns even though there were sufficient

viable seeds to colonize gaps in their vicinity. Successful seeds were those that were dispersed to germination sites outside the forest in pasture fields where cattle were the possible dispersal agents [46].

Small-fruited canopy trees species like *Olea welwitschii*, *Prunus Africana*, and *Sapium ellipticum* tend to be the first forest tree species to establish in the ORS, representing a new category of forest tree species regenerating outside the forest. They, however, lack the characteristics of colonizing species such as rapid growth, short generation time, and a short lifespan that is typical of early colonizers like *Trema guinensis*, *Polyscias kikuyensis*, *Croton megalocarpus* and *Macaranga kilimanjaris* in Kakamega forest. Neither are they large gap colonizers given that they are absent in large gaps inside the forest [52]. Once established, the composition of the canopy remains the same contrary to the predictions of the Mosaic Theory [53]. What does change is the composition of the under-canopy species brought about by the different sets of dispersers that inhabit the under-canopy in the forest [54].

The canopy structure in the ORS derives from the origin of patches in different parts of the regeneration sites. Each small patch represents a refuge or safe site in which seeds of these canopy trees germinate and establish [55–57]. The patchy nature

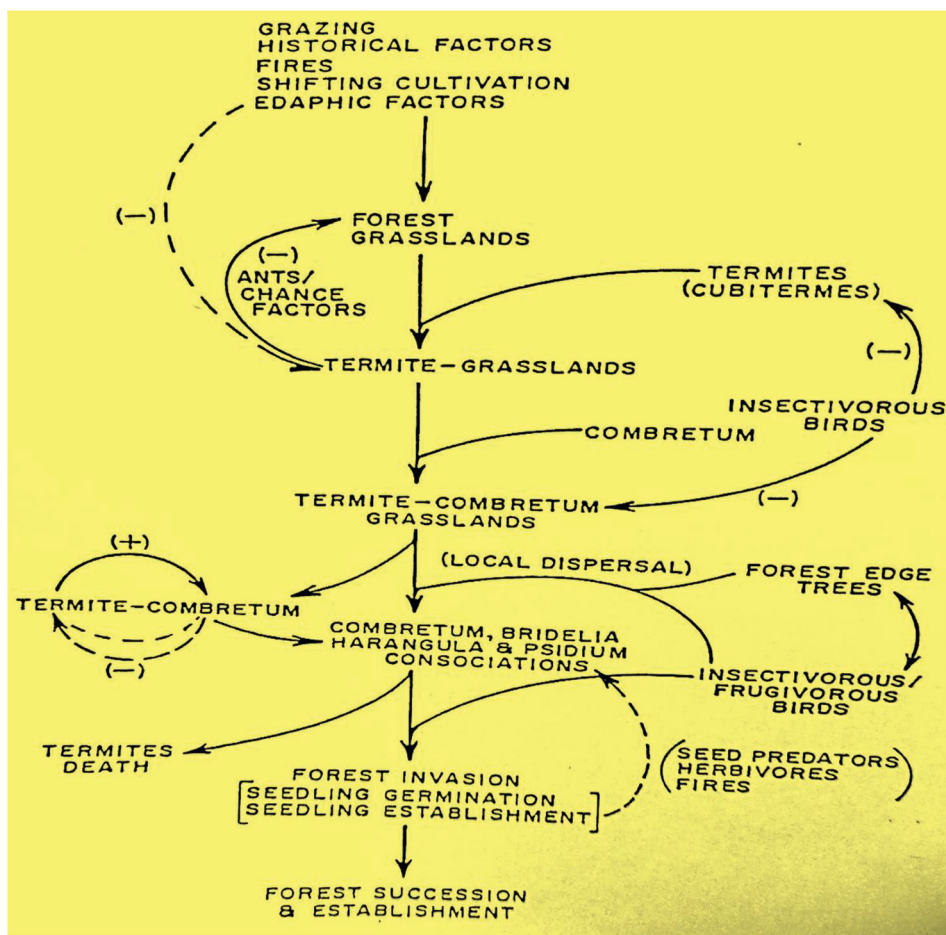


Figure 6.
Summary of olea regeneration cycle in Kakamega forest.

of these safe sites means that patches of forest develop independently and in parallel to each other. Expansions of these patches over time lead to coalescence which ultimately joins the larger forest block through the forest edge to form a continuous forest [58, 59]. In essence, the forest regenerates by shifting (a moving forest) the spatial distribution of the canopy dominants. Conditions necessary for the regeneration of the canopy dominants are rather specific requiring mound-building termites, a tree species that specialize in growing on these mounds, a transport agent, and later, a pool of the small-fruited forest canopy dominants (**Figure 6**). It is clear that canopy trees in the Kakamega forest initiate regeneration outside the forest.

Studies by [60, 61] have shown that the regeneration of a few canopy tree species such as *Prunus africana* can take place inside the forest successfully if the process is managed [62, 63]. In the Kakamega forest, past disturbances have resulted in the domination by the understory shrub, *Brillantaisia* sp., a light-demanding perennial herb [60, 63].

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