Impediments to regeneration of *olea capensis* in the kakamega tropical forest

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ABSTRACT

Olea capensis is one of the canopy dominants in the Kakamega forest that shows no regeneration inside the forest. Like canopy dominants in other tropical forests, adults are widely spaced and, seedlings and saplings where present are usually hundreds of metres away from the parent plants. This study examined strategies of regeneration of this important species to determine its recruitment patterns. Most seedlings/saplings occurred considerable distances from the parent trees. Experimental manipulations of seeds revealed that forest rodents and fungi accounted for over 90 per cent of seed mortality around the parent trees. Observation on dispersers revealed that ecotone birds were responsible for seed dispersal into new areas that provided a safe haven for the seeds to germinate and establish. Further examination of seed predation in these areas showed insignificant levels of predation. There was also a relationship between location of seed deposit and presence of termite mound growing trees, suggesting a coincidental interplay between feeding behaviour of the dispersers and dispersal of Olea capensis seeds. Findings of this study point to importance of understanding the biology tree species of concern for successful regeneration efforts. In particular, knowledge of seed dispersers and predators is crucial.

Introduction

It has clearly been demonstrated that the Elgon teak (*Olea capensis capensis*) does not regenerate inside the Kakamega forest (Tsingalia 1988, 2009). Analysis of the population structure has clearly shown that there has been no regeneration inside the forest within the last 50 years. Further evidence to support this scenario has been derived from careful scrutiny of data collected during the forest inventories of the 1960s and 1970s when the composition of the undergrowth was well-documented (Oruko 1979). None of the documented seedlings belonged to Olea capensis. Despite this apparent lack of evidence of regeneration, adult Olea capensis fruits every year (pers. observ.) between November and April. *Olea capensis* fruits are drupes with a thin edible pericarp but a tony endocarp. The endocarp is so hard that it takes a pair of pliers to crack it. The seed is housed inside the stony endocarp. *Olea capensis* fruits attract an array of frugivores including the black and white collobus monkeys (*Collobus guereza stangeri*). Avian frugivores include the black and white casqued hornbills (*Bycannistes subcylindricus*), barbets (Fam: Capitonidae) and the greenbulls (Fam. Pycnonotidae). All these frugivores remove the pericarp and drop the stony endocarp on the forest floor below the parent tree.

Dominant canopy tree species in tropical forests have been shown to exhibit poor recruitment (Connell 1975; Hubbell 1979; Caper *et al.,* 2005). Given this observed, surprisingly few studies have investigated mechanisms that may be responsible for the lack of regeneration in these canopy dominants. Poor or total lack of regeneration among canopy dominants species in tropical forests appears to be a pan-tropical problem (Sarukhan 1979; Whitmore 1975).

Several theories have been formulated to account for the lack of or poor regeneration. They include the mosaic theory of regeneration (Aubreville 1938; Connell *et al* 1984; Smith 1984), the restriction site factor theory (Janos 1980, 1983; Mabberly 1983; Denslow et al., 1987; Turnbull *et al*., 2000; Verheyan and Hermy 2001), seed dispersal limitations (Janzen 1970, 1971; Augspurger 1984 and anthropogenic factors (Bawa *et al.,* 1985; Vickers 1988; Bawa 1990; Chapman and Chapman 1997).

Seed predation, including fungal pathogens have been shown to influence spatial patterns of regeneration in many plant populations (Cavers 1983; Wilson 1983, 1985; Condit *et al*., 1995; Lord *et al*., 1995; Silva Matos 1999; Ehrlen and Eriksson 2000; Wright 2002; Pena-Claros De Boo 2002). Seed predation occurs at two levels: before seeds are dispersed (pre-dispersal seed predation) and after seeds are dispersed (post-dispersal predation). Plants and their seed predators form ecological systems with high temporal and spatial variability, both with regards to seed and predator abundance (Janzen 1971; Reisman-Berman 2006).

Predation on seeds for instance may be very high in years when other resources are scarce but very low in succeeding years when resources are abundant. Seeds that fall under the parent tree may suffer disproportionately high levels of seed predation from density-dependent obligate seed predators (Janzen 1970; Ehrlen and Eriksson 2000). Seeds dispersed some distance away from such parent trees may experience low levels of predation (Gilbert et al., 1994; Whitmore and Brown 1996; Connell and Green 2000).

This study sought to investigate reasons that hinder Olea capensis from regenerating inside the Kakamega forest and whether this tree species regenerates at all. To answer these questions, seed and fruit predation and the effects of fungal pathogens were examined to determine their relative roles in inhibiting regeneration of *Olea capensis* and strategies employed by this tree to mitigate the effects of these predators.

Methods

Seed Predation

Studies on seed predation were conducted between November 2010 and April 2011. Seed predation experiments were carried out at two levels. First, I examined pre-dispersal fruit predation levels. The objective was to determine whether

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fruit destruction before dispersal was a significant cause of seed mortality. Rectangular fruit traps made out of mosquito netting material that had a collecting surface area of $0.25m^2$ were randomly place to cover all the four quadrants under the canopy of five randomly chosen fruiting adult Elgon teak trees (Howe and DeSteven 1979; Howe 1980). The netting material was placed on stands constructed of bamboo sticks that were 1m high from the ground. Traps were watched over all day to ensure their safety. Fallen fruits were collected every 24 hours. Fruit traps were set out in March 2010 when the first mature fruits first appeared and were maintained throughout the fruiting period. They were discontinued at the end of August 2011. All collected fruits were inspected for signs of arthropod attacks and other forms of animal damage and were then counted. Fruit trapping was spread to cover early (March-May) and late (July-August) fruiting periods. Fruit damage during early fruiting was considered as pre-dispersal predation. To study post-dispersal seed predation, the area under the crown of each of the randomly selected fruiting trees, were divided into four quadrants. Within each quadrant, a number of $1m^2$ quadrats were established randomly on the ground to cover at least ten percent of the total canopy area (Howe 1980). Twenty to forty one square metre quadrats were set up under each of the five randomly selected trees. Howe (1980) showed that 10-30 percent sampling of the total canopy area on the ground was a good representative sample. All the fruits were collected by hand from the ground in each quadrat. They were then inspected for damage, insect holes and fungal pathogen attacks. Collections were repeated at biweekly intervals.

Frequency- and distance-dependent seed predation was also examined using two methods. The first methods involved the use of $1m^2$ as described above. Additional $1m^2$ controlled quadrats were established in which equal numbers of seeds and fruits were placed. A total of 30 such quadrats were established and were inspected every 12 hours for one month to determine the differences in seed and fruits predation rates. In quadrats where all fruits and seeds were consumed, they were quickly replenished.

The second method tested the effects of density and distance on predation using 50m long transects with the trunk of the fruiting tree as the start point. Five trees were randomly selected and under each tree, two transects north-south and east –west were established. Additional two transects were set up in areas where there were no fruiting Olea capensis tress. These areas were at least 100m from the nearest fruiting *Olea capensis* tree. The objective was to compare seed predation rates on experimental clumps of fruits and seeds near and far away from fruiting *Olea capensis*. Eleven sampling points were set up at a five a metre interval along the 50m transects. Each sampling point was identified by driving a very thin bamboo stick into the ground about 200cms from the experimental seeds and fruits without causing any apparent disturbance in the study area.

Three sets of seed density experiments were placed along each transect. In all the experiments, both seeds and fruits were used simultaneously. In the first experiment, seeds and fruits were placed in a pile at each sampling point along the line transect. The number of seeds per pile was 1, 5, 20, 50 or 100 per $1m^2$ per sampling point. On transects established further away from the fruiting Olea capensis adult trees, these densities were varied sequentially (low to high) starting from one end of the transect line. On transects established under fruiting *Olea capensis* trees, the trunk of the tree was used as the starting point with density increasing outwards. In the second experiment, the same density of treatments were assigned randomly to the

eleven sampling points along the transect line rather than sequentially. In the final experiment, a density of 5 seeds was placed at each station on all the transect lines.

Seed Predators of Olea capensis

A trapping grid was established under the crowns of *Olea capensis* to determine seed and fruit predators inside the forest. The objective was to determine if there were any differences in predator density both around the fruiting *Olea capensis* trees and away from fruiting trees inside the forest. Such differences would explain the distance-dependent seed predation rates observed in the previous observational and experimental studies.

In October, 2010, a trapping grid system 50mx50m using 15 Sherman traps, day and night throughout the fruiting period (Delany 1972; Martin and Dickinson 1985) were set up. Trapping was carried out every day for two months during the fruiting period in the forest.

A further trapping grid of 50mx50m was established in randomly selected locations that had no fruiting Olea capensis trees. Because traps were limiting, trapping was carried out sequentially in the two locations. Because of the smaller number of traps, trapping was carried out in a 0.05ha area at 10m interval (Cheeseman and Delany 1979; Svenning 2001; Muller-Lindau *et al.,* in press). The traps were baited with ripe bananas and were inspected twice a day (morning and evening). Towards the end of December, 2007, traps were stolen but were replaced in early March 2011. Attempts to capture-mark and release the animals using toe clipping technique (Martin and Dickinson 1985) or earmark technique (Southwood 1978) was unsuccessful for lack of proper toe-clipping and earmarking equipment. Specimens were instead identified by examination inside the trap and then released later.

Fungal Pathogens

During sampling of Olea capensis fruits on the forest floor, large numbers of moldy Olea capensis fruits were observed. Careful examination revealed that attack by fungal pathogens seemed to start with the pericarp and later spread into the endocarp to attack the seed through the micropyle. Seeds in advanced stages of fungal infection had lost an estimated 50-75 percent of the viable seed tissue inside the endocarp.

Rates of fungal pathogen attack were estimated by examining seeds from an earlier cohort of seeds collected from the forest floor and inspected for attack by rodents and pathogens in 2008. These seeds were easily distinguished from the 2010 cohort in being black or brown and without a pericarp. Seeds from the 2010 crop were neither black nor brown; rather they appeared like freshly scrapped drupes. A total of 18000 seeds were inspected.

The influence of fruit density on fungal infection rates were examined using piles of 1, 5, 20, 50 or 100 fruits per station. Fruits were paced at these relative densities in a random fashion under the parent crown and were inspected every 24 hours for infection.

Seed Removal Rates from Under the Crown of other Tree Species

Janzen (1970) and Connell (1971) argued that seed removal rates of a given species should be higher under the parent crowns than under crowns of other species. To test this hypothesis, *Olea capensis* seeds and fruits removal rates under crowns of five commonly occurring canopy dominants in the study area as a function of distance were examined. *Croton megalocarpus, Funtumia latifolia, Trelipsium madascariensis, Ficus exasperate* and *Prunus africana* species were selected for this experiment. Two 50m transect lines were established under each of the five individuals of each species. At every 5m

interval, along the transect line, 5 Olea capensis seeds and fruits were placed in a pile and inspected every 24 hours.

Results

Pre-dispersal Seed Predation

A total of 1386 fruits were collected from traps under the five fruiting trees. Of these, only 3 percent had insect holes the rest were undamaged. A closer comparison of the size and weight of fruits that were attacked showed that smaller fruits were attacked more than the larger ones. Seventy (70) percent of fruits with insect holes were small while 30 percent were large. There were more small fruits in the traps (89 percent) than large ones (11percent). Interestingly, all fruits that were attacked had holes the posterior end where the fruit is attached to the peduncle.

Density of Seeds

Fruit and seed density was a decreasing function of distance from the parent trees and was highly leptokurtic (figure 1). Most seeds and fruits were found under the parent crowns that averaged $450m^2$ (n=10) in area. Predation rates on fruits and seeds placed along transect lines were not influenced by density regardless of the position with respect to the canopy. The probability of seed and fruit removal was independent of density within the range of densities examined (Kruskal-Wallis X^2=9.08, p>0.05)
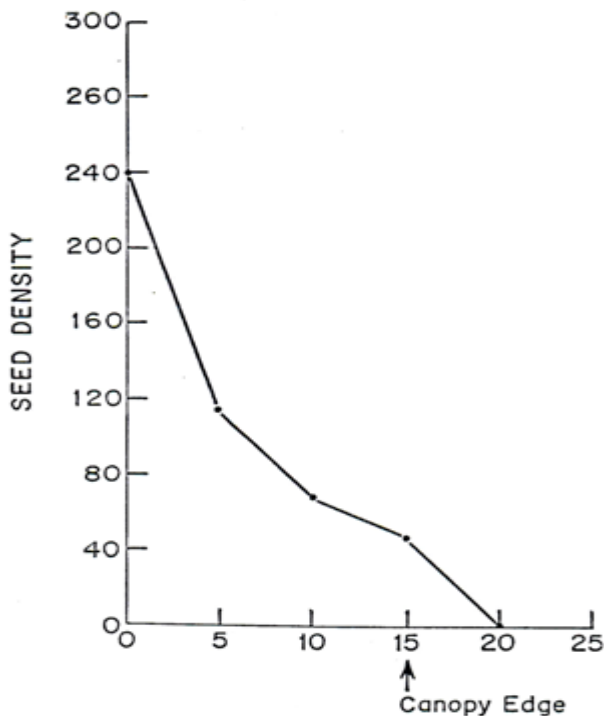

Figure 1: Olea seed and fruit fall as a decreasing function of distance from fruiting trees.

Over 90 per cent of seeds and fruits fell under the canopy of the parent trees.

Effects of Distance

Distance from the parent tree had a significant effect on the rates of seed and fruit predation. Regardless of density, seeds were removed within six hours of falling on the ground below the parent crown, while fruits were ignored by predators. In once incidence, only 3 of the experimental 400 fruits were eaten. Predation on seeds was independent of the time of theduty. Seeds closer to the parent were preyed upon more than fruits within the same range of distance from the parent crown (z=8.839, p=0.0122). This distance effect was more pronounced within 10 metres of the parent trees. Beyond 15 metres of the

parent crown, seed and fruit predation rates did not differ significantly (H=50.42, p>0.1).

Effects of Habitat

Habitat here refers to the area under the crown of the fruiting Olea capensis or away from these fruiting trees. A comparison of seed and fruit removal rates near and far away from the fruiting trees revealed significant differences between seed and fruit predation rates. Seed predation rates decreased significantly with distance from the parent tree (figure 2, r=0.817, p<0.01). Fruit predation rate was independent of the distance from the parent crown (figure 3, r=0.2037, 2-tail, p>0.01).
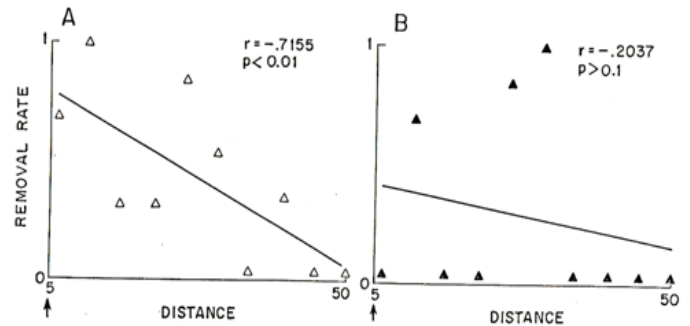

Figure 2: Effects of distance on removal of seeds and fruits from the parent crowns of Olea capensis. A is the effects of distance on seed predation rates, while B if the effects of distance on fruit predation rates.

Predators of *Olea capensis*

One species rodent, *Praomys jacksoni* was trapped. The capture rate of this species inside the forest was 4.32 animals per trapping night. The majority of the captures were near and around Olea capensis adults (3.71 animals per trapping night) rather than farther away (0.61 animals per trapping night; z=8.74, p<0.01). Five individuals of *Praomys jacksoni* were caged and presented with Olea seeds and fruits. Each animal was presented with 20 seeds (pits) and fruits. All the seeds were eaten over a 12 hour period by each of the caged individuals. None of the fruits were eaten. Further evidence of predation on *Olea capensis* seeds by *Praomys jacksoni* was obtained from direct observation inside the forest under fruiting Olea trees, by sitting quietly for at least two hours under a fruiting individual. It was possible to observe *Praomys jacksoni* individuals come out their nests to feed on seeds on the forest floor.

Fungal Pathogens

Table 1 shows the results of the influence of fruit density fungal pathogen infection rates.

Table 1: Effects of density on fungal pathogen infection on fruits and seeds of Olea capensis in Kakamega forest

Density/m^2	Percentage Infection Rates after:	
	24 Hours	48 Hours
1	0	0
5	20	40
20	25	60
50	40	75
100	40	85
X^2 Value	29.562	39.696
p-value	<0.001	P<0.001

Mold infection was greatly influenced by density (x^2=55.867, p<0.001). Overall, about 30 percent of the fruits were infected within the first 24 hours after falling on the ground, rising to 65 percent 48 hours later. Identification of the mold revealed that two mutually exclusive fungal species were responsible for the attack. They were *Cercosporella* sp. and *Gloesporium* sp. These fungal pathogens are obligate parasites

of *Olea capensis* that live on the leaves (Prof. Mibey pers. comm.), and their spores mature just before the onset of rains and disperse in rain drops. Experimental fruits far away from *Olea capensis* adults using the same relative densities (1, 5,10,20,50, and 100) showed no signs of mold infection even after two weeks of close examination.

Results of experiments with seeds also showed that seeds not eaten by rodent predators under the parent crowns were infected with the same fungal species. Infection rates of seeds was, however, much slower than fruits. The mean percent infection rate for seeds was 2 after 24 hours and 4 after 48 hours based on the relative density of 100 seeds. In some experimental seeds, infection did not commence until after four days and in some cases, up to one week.

Seed Removal Rates under Crowns of Other Species

Table 2 shows the mean seed and fruit predation rates under the crowns of five conspecific canopy dominants in the Kakamega forest. Mean seed and fruit predation rates were higher under crowns of all trees examined except *Croton megalocarpus* and *Funtumia latifolia* than under the crowns of the remaining trees (t test, p<0.001). There was no difference between mean fruit predation rates at the two tree species (t=0.879, p=0.202). Mean seed predation rates at the two tree species, however, differed significantly (t=4.869, p<0.001).

Table 2: Mean fruit and seed predation rates of Olea capensis at the five commonest canopy dominants in Kakamega forest.

Canopy Tree Species	Mean Seed Predation rate	Mean Fruit Predation Rate	t-value	p-value
Croton megalocarpus	0.609	0.795	1.465	0.087
Funtumia latifolia	0.777	0.732	-0.506	0.312
Trelipsium madascariensis	0.875	0.105	-10.423	0.001
Prunus africana	0.896	0.105	10.995	0.001
Ficus exasperata	0.836	0.155	-11.656	0.001

Mean seed predation rates under the crowns of *Trelipsium madascariensis*, *Prunus africana* and *Ficus exasperata* differed significantly from the mean fruit predation rates.

There were significant differences in the predation rates of seeds at different tree species (F=33.497, p<0.001), being highest at *Prunus africana* (0.896) and *Ficus exasperata* (0.875). Removal rates of fruits did not differ under crowns of all tree species tested (F=1.439, p=0.2668). Overall, removal rates of seeds were higher than that of fruits for all crowns examined (F=54.866, p<0.001).

Table 3: Correlation coefficients between Olea fruit and seed predation rates and distance from the trunks of the five commonest canopy dominant in the Kakamega forest (ns=not significant).

Tree Species	Seed s	p-value	Fruits	p-value
Croton megalocarpus	-0.520	ns	0.442	ns
Funtumia latifolia	0.516	ns	-0.269	ns
Trelipsium madascariensis	-0.371	ns	0.406	ns
Prunus africana	-0.228	ns	0.228	ns
Ficus exasperata	0.602	<0.05	-0.537	<0.05

Distance did not affect the mean seed predation rates at all the tree species except *Ficus exasperata* (Spearman, 2-tail, p<0.05; table 3). This effect was positive for seeds and negative for fruits.

Discussion

Results clearly show that density is not important in seed and fruit predation of Olea capensis seeds. The failure to find greater predation rates for seeds in large clumps suggests two things: (i) for predators involved, large clumps are no easier to find than small clumps, and (ii) these predators remove all the seeds they find regardless of clump size. A range of densities perhaps greater than those used in this study might reveal the upper limit beyond which seed density might determine the fate of individual seeds.

Density-dependent seed predation has been observed in a variety of ecosystems (Wilson and Janzen 1972; Platt 1976; Sork and Boucher 1977; Stapanian and Smith 1978; Willson and Mellampy 1983; Connell et al 1984; Willson and Hoppes 1986; Wright 2002). In all these studies, weeds were placed in clumps as was done in this study. In some studies, density had little or no influence on seed predation rates (Sork 1983; Mittlebach and Gross 1985; Pouli *et al.*, 1999; Reisman-Berman *et al.,* 2006) as was found true for Olea capensis. It appear like the importance of seed density is perhaps determined largely by the foraging behaviour of particular seed predators (Reichman and Oberstein 1977; Ehrlen and Eriksson 2000; Connell and Green 2000).

The decrease in seed predation under the crown of *Olea capensis* with distance from the parent plant coincided with a decrease in the capture rate of Praomys jacksoni. Such distance-responsive patterns of seed predation have previously been reported by a number of researchers (Janzen 1970, 1971a, 1972, 1972b; Howe and Primack 1975; O'Dowd and Hay 1980; Nathan and Muller-Lindau 2000; Wright 2002). Erratic fruit predation rates under and beyond the crowns of Olea capensis adults examined in this study may suggest the existence of a second rodent fruit predator which was not identified. This is supported by results of feeding experiments and direct observation of *Praomys jacksoni* in the field which showed that it feeds preferentially on seeds. Low predation rates of fruits under the parent crowns suggest competitive exclusion of this second rodent fruit predator by Praomys jacksoni under the Olea crowns.

Predation risk varied markedly both within and between experimental arrays, indicating spatial patchiness in the activity patters of seed predators. These large differences in predation risk between localities perhaps reflect variation in seed predator populations. Differences in predation rates were also pronounced over small distance, as also reported by Mittlebach and Gross (1985). Adjacent seed piles often differed in fate though separated by very small distances. In some case, there were marked consistency in predation between adjacent seed and fruit piles. These patterns probably reflect home range and activity patterns of small mammalian seed predators. In interpreting these findings, is has been assumed that predation rates are proportional to seed removal rates. This is because rodents do cache seeds, some of which might escape predation and germinate (Howard and Evans 1961; Abbot and Quink 1970; Whitmore and Brown 1996; Wills *et al.*, 1997). Some of my experimental seeds might have been cached. Husks of seeds preyed upon were left behind in about 60 percent of the seeds but only about 15 percent of the fruits.

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