Influence of light intensity on the population structure and distribution of *Commiphora guillauminii*

Michael P. Curran, University College Dublin, Ireland

Ernest Nti Acheampong, Kwame Nkrumah University of Science and Technology, Ghana

Abstract

In this study, we investigate the influence of light intensity on the population age structure and recruitment of *Commiphora guillauminii* in an un-logged region of Kirindy forest. A total of 368 individual trees with different diameter sizes were recorded in the study area comprising of 152 grids (25 m x 25 m). The results of the study suggest that light intensity plays a major role in the recruitment of young saplings of *C. guillauminii*. Furthermore, the clumped nature of these saplings in areas that are devoid of older trees suggests that long-distance primary seed dispersal by birds heavily outweighs short-range secondary dispersal in recruitment success.

INTRODUCTION

Commiphora guillauminii is an endemic species to Madagascar. It is distributed throughout dry to sub-arid deciduous forests and is a very important timber species, holding both ecological and economic value. As such, regeneration is very important in the maintenance of a viable, harvestable population.

In the Reserve Forêt de Kirindy (Kirindy forest) *C. guillauminii* is the dominant canopy species, representing up to 42% of the tree species of diameter greater than 40 cm at breast height (dbh) (Hunziker 1981). In 1984, it was recorded that *C. guillauminii* made up 80-90% of the wood logged in the forest (Schwitter 1984).

Observations made seem to indicate that there was lack of regeneration of young seedlings and saplings of *C. guillauminii* in dense, high canopied forests. Further east in the same forest it was observed that there was an abundance of young species and recruitment appeared to be high. Here, the canopy cover is lower; the soil top-layer thinner and there appeared to be more ambient light striking the forest floor. This led us to believe that there was some factor(s) influencing the recruitment of *C. guillauminii* present in the eastern region but absent in the western region.

There are numerous possibilities that could explain the apparent discrepancy in age distribution of *C. guillauminii.* One such factor that stood out was the difference in light intensity between the two regions. This led us to believe that *C. guillauminii* is a light demanding sapling that can only grow in very bright environments. To test this hypothesis, we examined the change in light intensity across a transect running roughly east to west and correlate this with population age structure and distribution. According to our predictions, there should be abundance of young trees at the sapling stage in areas of high light intensity and less abundant in areas of low light intensity.

If reproducing trees are located in very high canopied areas where very little light reaches ground level, short distance seed dispersal should be expected to be less effective than long range dispersal where there is a greater chance of the seed reaching a light-rich environment that is further away. *Commiphora* seeds are known to be primarily distributed by birds and secondarily distributed by a single ant species, *Aphaenogaster swammerdami* (Böhning-Gaese *et al.*, 1996). Colonies of *A. swammerdami* have been shown to be associated with *C. guillauminii* trees, whose diaspores are an important food source for the ants.

Therefore, in this specific example, we hypothesise that ant dispersal is having little or no effect in the recruitment of *C. guillauminii* from those adult trees located in the light poor forest. Consequently, the only method of seed dispersal that is effective is dispersal over long distance by birds. According to our predictions, one should find an abundance of young trees in the light rich eastern region of the forest with very few reproducing adults present.

MATERIALS AND METHODS

Study site

The study was carried out in the Reserve Forêt de Kirindy/Centre de Formation Professionelle Forestière (CFPF) (20º03'S, 44º39’E) over a 10 day period in November 2005 (dry season). Kirindy forest is a 10,000 ha dry deciduous forest in Western Madagascar located 60 km north east of Morondava. Average annual temperature and precipitation is 24ºC and 799 mm respectively. The survey site had not previously been logged commercially for wood.

The study was carried out over a well-established grid system with grid lines ranging letters A to G and numbers 1 to 26. These grids were established and are maintained by the Deutsches Primatenzentrum (DPZ).

Study species

Commiphora guillauminii grows up to 20 m in height with a trunk diameter of up to 80 cm dbh (Perrier de la Bathie, 1946, as cited in Sorg & Röhner, 1986). It is easily recognisable by its yellow/orange bark that peels in coarse pieces to reveal a photosynthetic green under-bark. It is the most abundant species of the five species of *Commiphora* (Burseraceae), which are known to occur in the forestry concession (Rakotonirina, 1996). Adult trees have long branchless trunks with crown starting at 6-12 m height. The species is dioecious, flowering from September to December (Perrier de la Bathie, 1946 as cited in Sorg & Röhner, 1986).

A total of 152 grids (25m x 25m) were surveyed. For each *Commiphora* tree found, the position within the grid (relative to the nearest grid lines) and diameter at breast height (dbh) was recorded. Standing dead and fallen trees were not recorded.

Light intensity readings

Light readings were taken before sunrise between 5:00-5:45 am at ground level at the intersection of each gridline. This period ensured that there was no direct light entering the forest and readings would not be influenced by shadow etc. As a control, light readings were also taken in an open area. To obtain a standard value for comparison (the ‘diffuse site factor’) that was independent of the time of the readings, the open area and forest readings were used to get a percentage of the light incident on the canopy that was reaching the forest floor at each location.

RESULTS

Light intensity across the transect area

From the light measurements taken across 23 transect lines (2 to 26) it was found that light levels remained relatively constant from transect 2 to 20 (Fig. 1). From 21 to 26, light levels show a marked increase in mean of up to 30 percent. The range and variance in light intensity increases gradually across the entire transect space (variance data not shown).

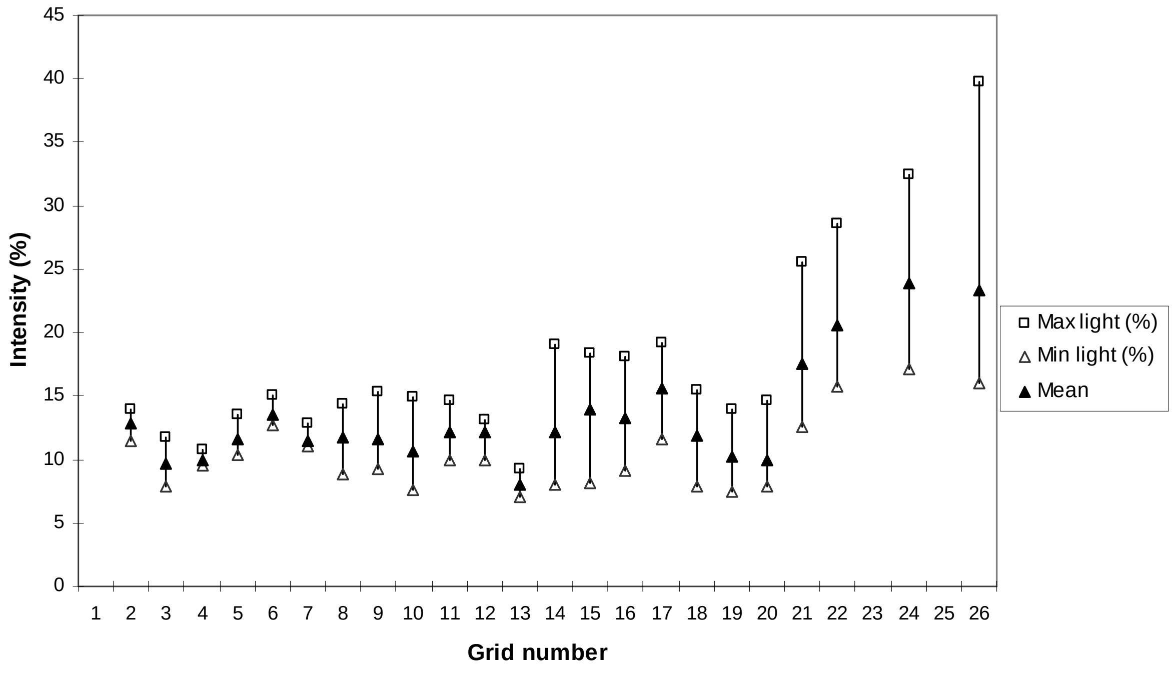

Fig. 1 Mean light intensity remains relatively constant from gridlines 1 to 20 followed by a sharp increase. The range increases gradually across the transect area. Intensity is represented on the Y-axis with grid numbers on the X-axis. Five measurements were taken from each grid line, the mean of which is shown on the graph along with minimum and maximum values.

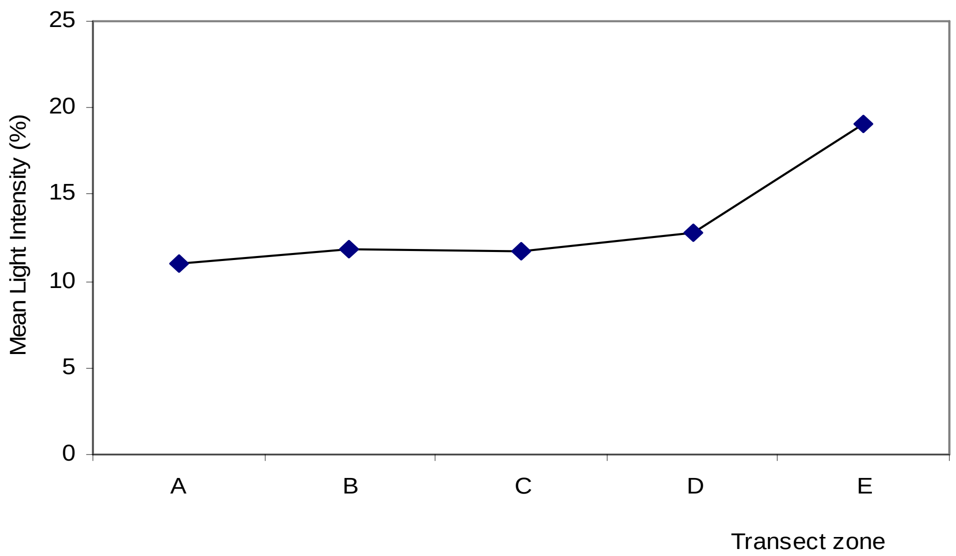

Fig. 2 The study area was divided into 5 equal size zones, roughly based on forest structure, forest geography, mean light intensity and range of intensity. The zone means show a marginal increase up to zone D followed by a sharp increase at zone E. Mean light intensity is shown on the Y-axis with transect zones A to E on the X-axis.

The transect area was split into 5 zones that attempt to homogenise data on light intensity mean, range, forest geography and structure. Zone A (2-5) consists of a dark, open under-story, high canopy and relatively constant light intensity mean and range. Zone B (6-10) is similar to zone A in forest structure and light mean but differs in range. Zone C (11-15) and D (16-20) show an increase in range as the geography of the land becomes more complicated, including a riverbed that bisects the transect area from northeast to southwest with numerous side channels and varying canopy and understory densities creating a range of light conditions. Zone E (21-26) has a generally low, open canopy with changing land topography, high light levels and very wide light ranges.

C. guillauminii age distribution within the zones

A total of 368 individual trees of *Commiphora guillauminii* was recorded within the transect area. Tree density, age composition and distribution differed between the five forest zones. The greatest number of young trees (diameter between 0-10 cm) occurred at Zone E whilst the least number of young trees were recorded at Zone A. This trend was less apparent in the middle aged species which approached a more even distribution. The trend appeared to be reversed in the oldest age class (dbh 51-60 cm).

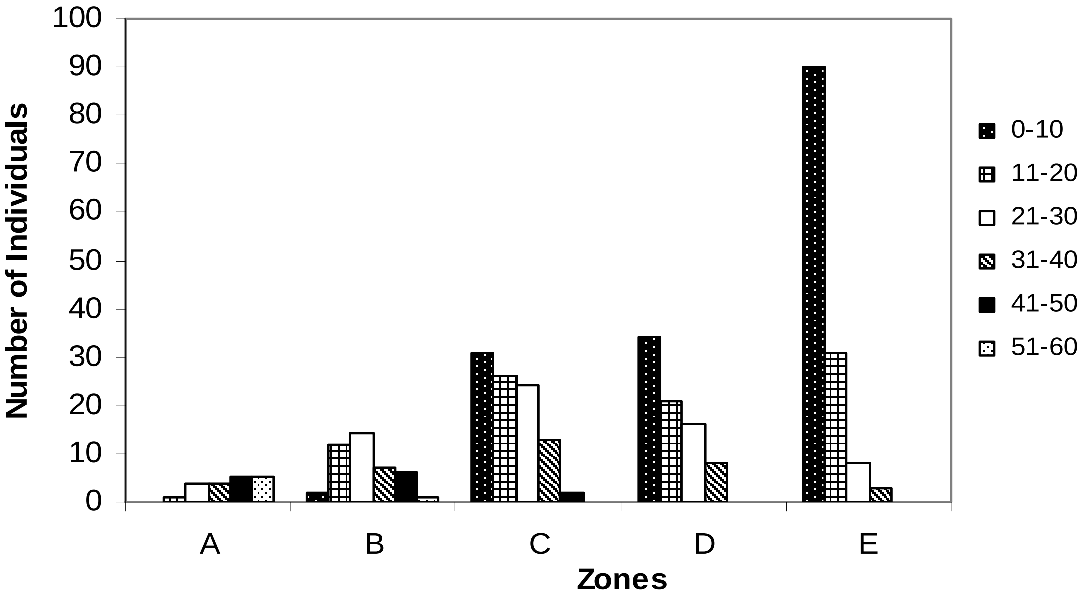

Fig. 3 Population age structure in the various forest zones. The Y-axis represents the number of individual trees at each zone, whilst the X-axis shows the zones as they are found roughly from east to west.

Distribution of *C. guillauminii* trees across the transect area

Fig. 4 shows the distribution in space of all the *C. guillauminii* trees in the study area. For each tree, the distance to its nearest neighbour was calculated (NN-distance) and these distances were plotted on a histogram in 2 m intervals up to 20 metres, then 5 metre intervals up to 30 m, and finally a 10 metre interval from 50 to 60 m (Fig. 5).

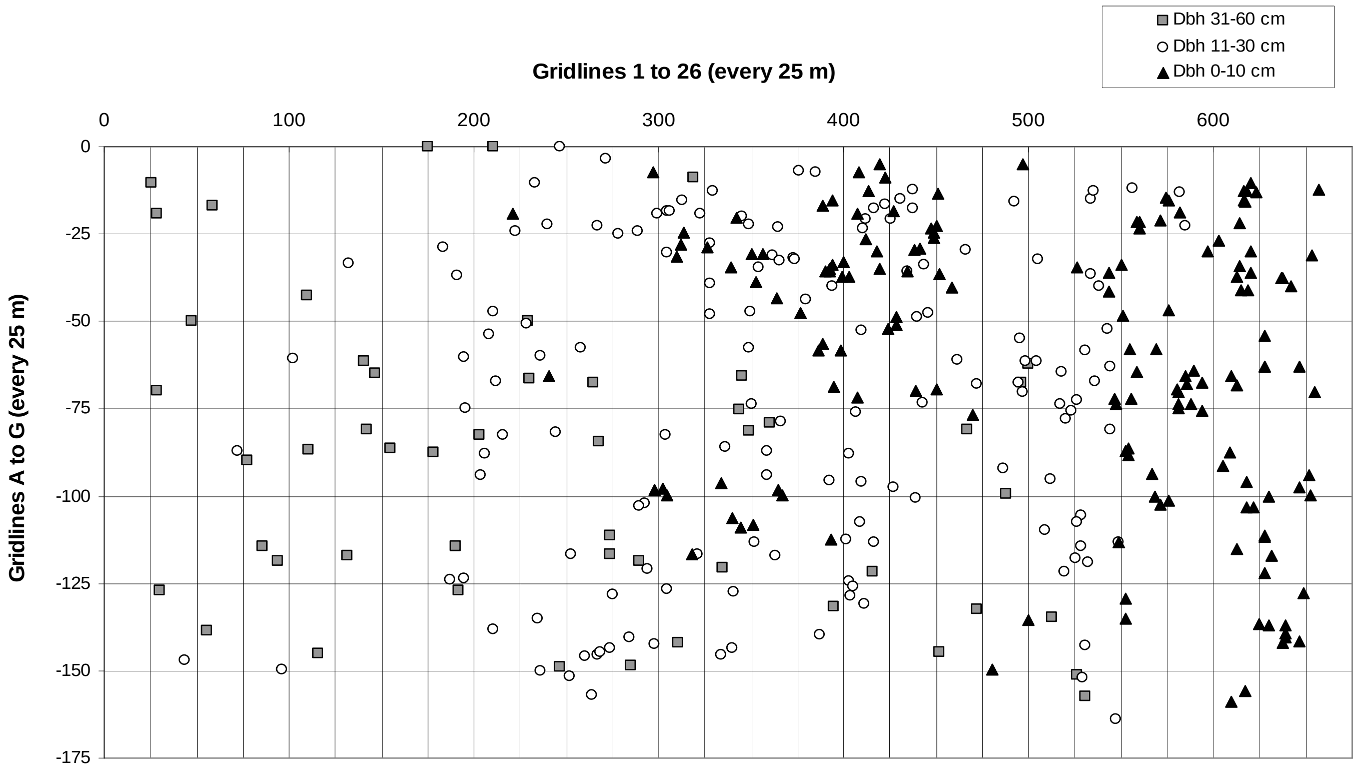

Fig. 4 Distribution of all *Commiphora guillauminii* trees across the study area. Gridlines 1 to 26 are represented on the X-axis with lines A to G on the Y-axis. The grids on the map are uniformly 25 m squares and do not reflect the actual size and shape of the real grids which vary across the transect line. This is merely to give some indication of scale.

A Kolmogorov-Smirnov (K-S) normality test was performed on each of the three size classes' NN-distributions. The small trees (0-10 cm dbh) showed a skewed distribution to the left of the histogram (K-S D: 209, $P<0.01$). The intermediate size class (11-30 cm dbh) showed a less pronounced skewed distribution to the left than the small class (K-S D: 171, $P<0.01$). The largest size class (31-60 cm dbh) showed a near normal distribution under a 1% significance level (K-S D: 130, $P>0.01$).

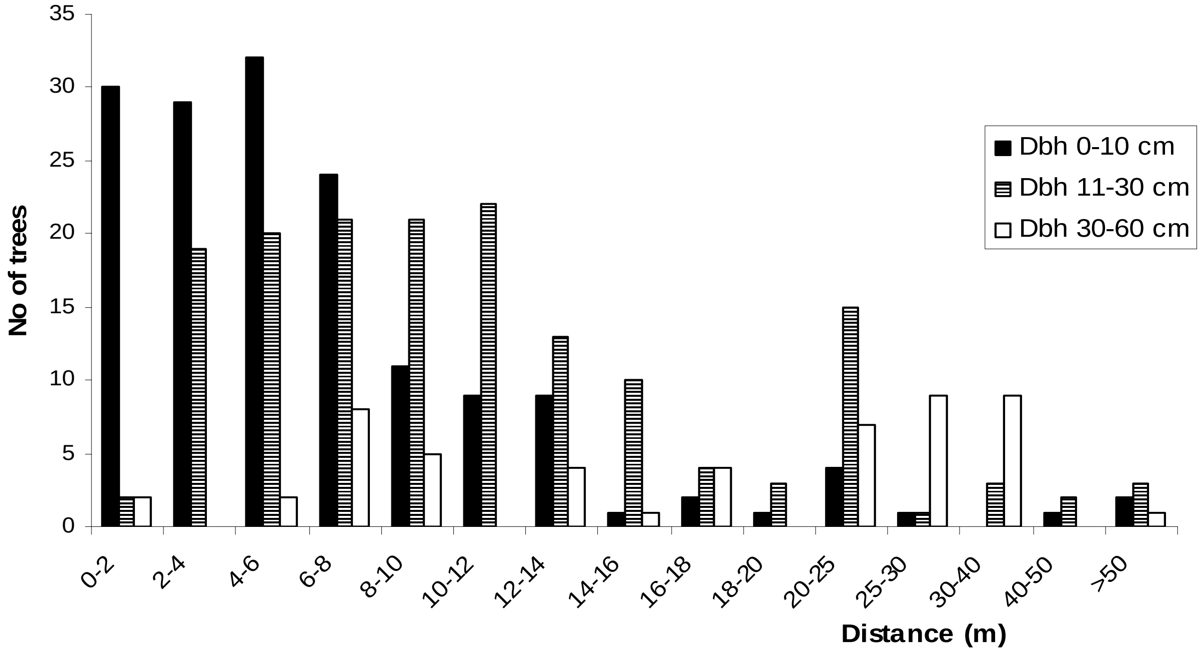

Fig. 5 NN-distances for all trees in the study area. The X-axis contains the NN distance categories with the number of trees per category represented on the Y-axis. The three size classes (small, intermediate and large dbh) are represented by black, stripped and open bars respectively.

DISCUSSION

Light is an important ecological factor which plays a major role in the recruitment of saplings the forest. Both light quality and quantity changes as light passes through the canopy (Bazzaz 1996).

Based on the results for light intensity (Figs. 1 and 2), it would appear that there is an increase in the range and mean light intensity reaching the forest floor as one moves from west to east in the study area. The high numbers of young saplings found in zone E, where the light intensity was highest, suggest that light plays a major role in the recruitment of *C. guillauminii* saplings. This compliments the observation that there were no trees < 10 cm dbh found in zones A and B, where light range was relatively low. A high light range, regardless of the mean value, suggests a very heterogeneous light environment where there would invariably be some areas suitable for colonization of a light-demanding sapling.

Zone C, where the maximum light intensity reaches 20% and above, supports large numbers of saplings. The maximum intensity for zones A and B is around the 16% mark suggesting the minimum amount of ambient light required by *C. guillauminii* saplings is somewhere between 16 and 20 percent. However, this requires additional light sampling effort at those specific areas where saplings are found. The distribution map shows the exact location of those clusters of saplings for future studies.

There are other factors that could possibly explain the age distribution from zone A to E. The geography of the study area changes quite drastically in both topography and soil make-up. This invariably creates a landscape that varies in the levels of water, nutrients and soil quality that is available. One possibility is that the growth rate of the *C. guillauminii* is slower in the light-rich area because of impoverished soils and that age is in fact not related to the diameter of the trunk. This has yet to be investigated.

However, we believe this not to be the case because of the observation of a single tree of intermediate dbh growing directly out of and ant nest of *A. swammerdami*. The lifespan of nests of *A. swammerdami* rarely exceeds 25 years (Böhning-Gaese *et al.,* 1996) and the tree clearly started growth after the nest had been established (a common scenario of *C. guillaumini* germination is in the "garbage pile" of ant nests). This would suggest that the tree was no more than 25 years old. It had attained a dbh 13.1 cm and a height of 6 to 8 metres. The age of a 9 metre *C. guillaumini* tree with a dbh of between 12 and 15 cm is estimated to be around 21 years (Deleporte *et al.,* 1996) which conforms to our predictions. Therefore, we believe that we are justified in asserting that our results strongly suggest that high light ranges coincide with high numbers of young trees and that *C. guillaumini* is a light demanding sapling.

The distribution in space of all the *C. guillauminii* trees (Fig 4) in the study area suggest that young and intermediate trees (dbh class 0-10 cm and 11-30 cm respectively) were clumped towards the area where the canopy cover was open and level light intensity is high. This clumping was confirmed in the nearest neighbour analysis showing a higher degree of clumping in the sapling stages than in the intermediate age classes. The position of these clumps of sapling trees is generally quite a distance from any of the older and intermediate trees to have been dispersed by ants (i.e. greater than a few metres). Although there were coinciding clumps of intermediate and young trees where dispersal could have taken place by ants, the presence of high numbers of isolated saplings at the edge of the study area suggests that bird dispersal is the main driver of recruitment in *C. guillauminii*. Whether these trees are offspring of isolated old trees in surrounding high canopied forest or closer intermediate-aged trees has yet to be determined.

Average dispersal distance for birds of *Commiphora* seeds has been quoted at only 0.9 meters (Farwig *et al.,* 2004). This is understandable when one considers the large number of wasted seeds that fall to the forest floor as birds feed. However, we do not believe this to represent successful dispersal that results in germination and recruitment. Our results show clumps of sapling stage *C. guillauminii* trees that are isolated by up to 100 metres from reproducing adults and intermediates.

Therefore, according to our results, it would appear more likely that it is the seeds that pass through the digestive system of bird, and are dispersed over long distances, have a better chance of reaching potentially new microhabitats or indeed new habitats entirely. This is particularly important for isolated old individuals in dense, light poor forests.

CONCLUSIONS

Our prediction for large numbers of *C. guillauminii* trees at the sapling stages in areas of high light intensity was supported by the data that was collected. We therefore conclude that germination and growth of *C. guillauminii* saplings require high levels of ambient light.

The population age structure and distribution across the study area suggests that rare, long-distance dispersal events are the main driver in the recruitment of new *C. guillauminii* trees. This study downplays the importance of short-range primary and secondary dispersal events in the recruitment of *C. guillauminii*.

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