NATURAL REGENERATION OF *Minquartia guianensis* IN PRIMARY AND SECONDARY RAINFOREST IN COSTA RICA

HONORATA GAJDA

NORWEGIAN UNIVERSITY OF LIFE SCIENCES
DEPARTMENT OF ECOLOGY AND NATURAL RESOURCE MANAGEMENT
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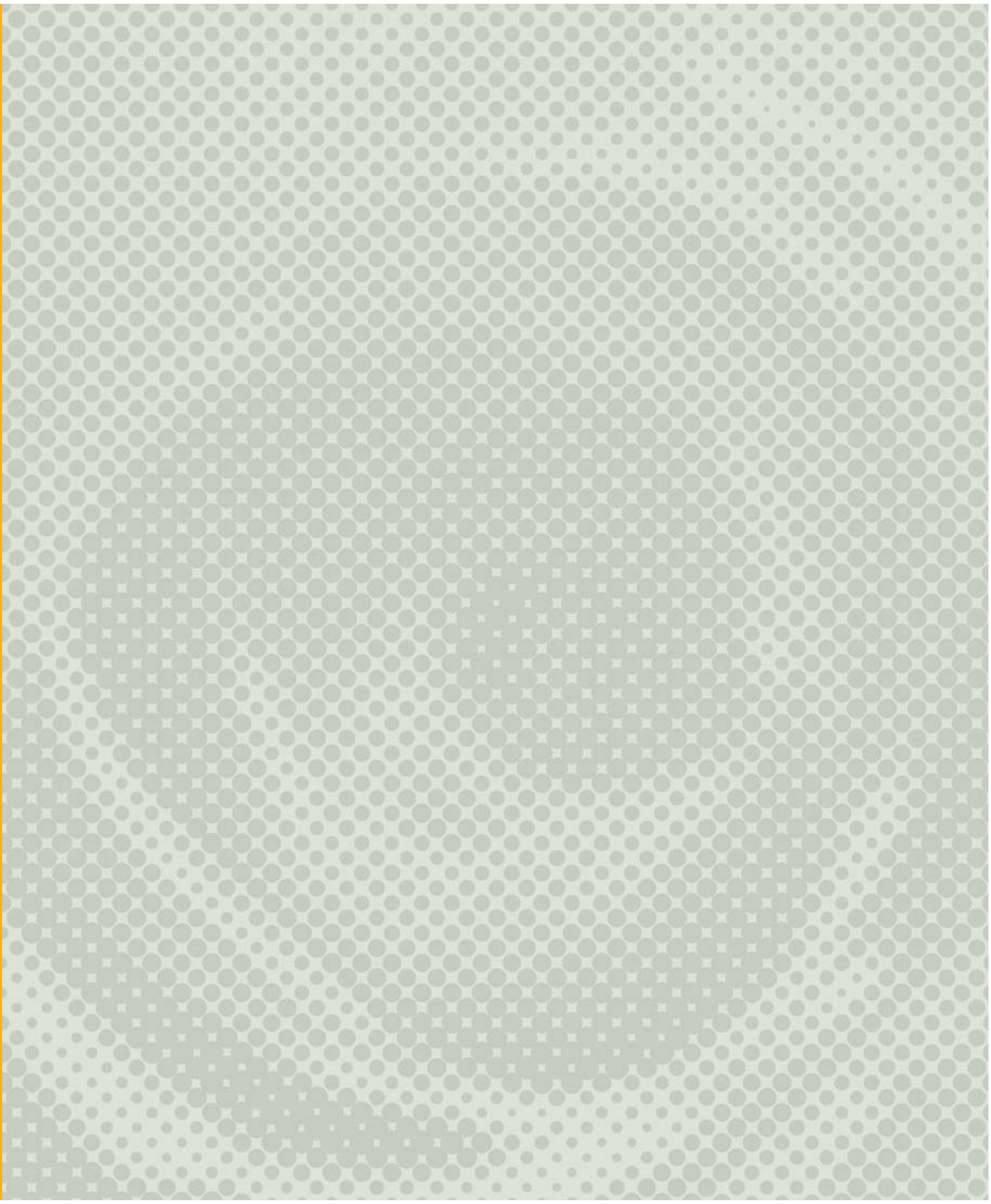

In memory of my beloved grandfather,
Jerzy Gajda

ABSTRACT

Huge land areas of tropical rainforests are being cleared every year. Once they are abandoned, species richness and structural stand characteristics may recover through secondary succession. It is, however, unclear if species composition will recover to its previous floristic composition, as old-growth forest species are poor colonizers. This study focuses on the natural regeneration of an old-growth forest tree species; *Minquartia guianensis*. The study was conducted in primary and secondary forest sites in La Tirimbina Rain Forest Center, Costa Rica. Measurements of individuals from four size classes were recorded, with emphasis on abundance, spatial distribution pattern, habitat preferences (crown illumination, topography, drainage), and physical condition. A total of 951 individuals were sampled in six 1 ha plots; three primary and three secondary forest plots. The number of adult trees was higher in primary forest than in secondary forest sites, while the number of progeny was highest in secondary forest. Habitat preferences were displayed by all size classes. In secondary forest the percent of damage increased with decreasing tree size. In primary forest the percent of physical damage did not differ significantly among the size classes. Clustering and association of progeny with adult trees was higher in secondary forest than in primary forest. The distribution pattern was less clustered with increasing tree size. Positive association of progeny to adult trees decreased with increasing tree size. The ecological processes influencing the spatial distribution of progeny and adult trees were independent.

The successful regeneration of this primary forest species in secondary forest can be attributed to the advantageous effect of remnant trees on seedling establishment and growth, and low rates of land degradation after land abandonment. In order to assist natural regeneration in deforested land areas, and to recover some of the species composition of mature tropical rain forests, it is advisable to leave seed trees of the desirable species after clear-cutting, or to plant seeds or seedlings of old-growth forest tree species in the shadows of shrubs, pioneer trees or remnant trees.

SAMMENDRAG

Store landområder av tropisk regnskog blir hogd ned hvert eneste år. Artsrikdommen og bestandsstrukturen kan gjenopprettes gjennom sekundær suksesjon i disse avskogede områdene. Det er derimot usikkert om artssammensetningen vil nå sin opprinnelige tilstand, da treslag fra gammelskog viser dårlig foryngelsesevne i åpent landskap. Dette studiet fokuserer på naturlig foryngelse av *Minquartia guianensis*, et treslag knyttet til gammelskog. Studiet ble gjennomført i primære og sekundære skogområder i La Tirimbina Rain Forest Center, Costa Rica. Det ble foretatt målinger av planter fra fire størrelsesklasser, der det ble lagt vekt på antall, romlig distribusjonsmønster, habitatpreferanser (lysforhold, topografi og drenering) og omfang av fysisk skade. Totalt ble det registrert 951 individer på seks prøveflater à 1 ha. Antallet frøtrær var høyere i primærskog enn i sekundærskog, antallet avkom var derimot høyere i sekundærskog. *M. guianensis* viste tydelige habitatpreferanser. Planter i sekundære skogområder viste sterkere tendens til klumpete distribusjonsmønster enn i primære skogområder. Distribusjonsmønsteret endret seg fra klumpet til tilfeldig fordelt med økende trestørrelse. Tendensen for klumping rundt frøtrær var synkende med økende trestørrelse.

Den vellykkede foryngelsen av denne gammelskogsarten i sekundære skogområder, kan tillegges de gunstige forholdene for etablering under gjenstående trær, i tillegg til lite degradert jordsmonn i de sekundære skogsområdene. For å fremme naturlig foryngelse av gammelskogsarter i avskogede landområder, anbefales det å etterlate frøtrær av ønskelige treslag. Hvis disse ikke er til stede, rådes det å plante frøplanter av gammelskogsarter i skyggen av busker og trær for økt etablerings suksess.

ACKNOWLEDGEMENTS

This thesis is a result of successful cooperation with Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) and the Department of Ecology and Natural Resource Management (INA), Norwegian University of Life Sciences (UMB).

It has been a great experience to wonder in the tropical rain forests of Costa Rica. Every day of the field work was a new adventure, and I am still in awe of the rich biodiversity of these ecosystems. Experiencing the early morning sun shining through the thick canopy, the sound of cicadas and singing frogs filling the air, stroke of the wing of colorful birds, and the stature of old-forest trees, has been unforgettable.

This study would not be possible without the help of my field assistant Vicente Herra, whose help was invaluable, and his knowledge of the forest was of great value for me. I am grateful to La Tirimbina Rain Forest Center for allowing me to carry out my investigation in the park and for their interest in my study. I wish to thank Bryan Finegan, for his valuable advice and help with the make up of the objectives of this study, and all the people in CATIE who were of great help throughout my fieldwork. I owe great thanks to my main supervisor, Mikael Ohlson, for his patience and help during the writing of this thesis, and my supervisor Stein Moe for his last comments on the paper. I would like to thank my Henrik for his moral support and encouragement in times when things didn’t seem to bright, and his patience with me. Maren, for her good spirits and optimistic mood, and for her motivation that helped me finish this thesis. And Cathrine for having faith in me, and her priceless advices and comments on the thesis. Thanks to all my friends for their encouragements, and to my family who haven’t seen me much during this semester.

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Ås, 14 May, 2009

Honorata Gajda

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1. INTRODUCTION

Huge land areas of tropical rainforests are being cleared for crop fields and pasture every year (FAO 2006). These land areas are subsequently abandoned due to changing economies and land degradation (Holl & Kappelle 1999; Thomlinson et al. 1996). An important question arising is: Will tropical forest fully recover in abandoned land areas such as these?

The land area covered by secondary forest on former cleared land is steadily increasing in the tropics (Hammond 1995). Today many countries have larger areas covered by secondary forest than primary forest (Brown & Lugo 1990). Species richness and structural stand characteristics often recover rapidly through secondary succession (Ewel 1980; Finegan & Delgado 2000; Holl & Kappelle 1999), however, it may take centuries before the floristic composition of old-growth forest recovers, if it ever does (Ewel 1980; Finegan 1996; Guariguata & Ostertag 2001). Tropical forests are thus among the most fragile ecosystems in the world (Ewel 1983). Old-growth forest species are often poor colonizers (Uhl 1987), and the recovery of the species composition of these ecosystems may be impeded by lack of forest seeds due to the absence of nearby seed sources, reduced animal seed dispersal into disturbed land areas, seed predation and short seed longevity (Holl & Kappelle 1999). Factors such as disturbance intensity, land use history, size of deforested land area and the proximity to remnant forest, all have a major influence on the recovery potential of these abandoned lands (Moran et al. 1996; Uhl et al. 1982; Uhl et al. 1988). Few studies have shed light on the regeneration of primary forest species in secondary succession, and more knowledge is needed to establish the resilience of tropical rain forests.

This study focuses on the regeneration potential of a primary forest species in primary and secondary tropical lowland wet forest. *Minquartia guianensis,* also called black manwood, is a slow growing tree which is treasured for its high quality wood (Flores 1994). The natural populations of this species are consequently depleted in many areas throughout the neotropics (Nebel 2001). The present study was carried out in selectively logged primary forest stands and 20 - 45 year old secondary forest stands in north eastern Costa Rica. The regeneration of *M. guianensis* was studied for all size classes (from seedlings to canopy individuals), through abundance counts, spatial pattern analysis, and a habitat preference study.

Microhabitat conditions have an impact on tree establishment, growth rates and successful recruitment to the adult stage (Dovciak et al. 2001). Microhabitat thus has an important effect on regeneration potential and abundance of trees (Ohlson & Zackrisson 1992). In my study I have investigated the microhabitat preferences of *M. guianensis* and explored potential preference changes throughout the life cycle of the species. In addition, an assessment of the physical state of *M. guianensis* individuals was carried out, as physical damage is a process often disregarded in many studies, but its potential impact on regeneration of slowly growing species may be of great importance (Clark & Clark 2001).

The distribution pattern of trees is a result of several pattern generating processes, such as seed dispersal, competition and environmental heterogeneity (Barot et al. 1999; Seabloom et al. 2005; Sterner et al. 1986). Several theories exist regarding the processes shaping patterns. It is believed that dispersal limitation will created aggregated patterns, habitat uniformity will create random patterns, while competition may cause regular patterns (Barot et al. 1999; Bivand et al. 2008). Spatial pattern analysis was applied to infer the regeneration history of *M. guianensis*, providing information about the ecological processes of importance in the regeneration of this species.

The three main objectives of this study were to: 1) determine the abundance of *M. guianensis* in primary and secondary forest, 2) determine microhabitat preferences and the role of physical damage in regeneration, and 3) investigate the spatial distribution of different size classes and their spatial association to adult trees.

2. METHODS

2.1. Species description

Minquartia guianensis, black manwood, belongs to the *Olacaceae* family (Olax family), tribe *Couleae* (Sleumer 1984). The natural distribution of the species range from lowland and premontane forest, to lower montane forests of the neotropics (Flores 1994; Sleumer 1984). It can be found in primary, secondary and gallery forests on both flood plains and terra firme, with an altitudinal distribution at 0-1000 m.a.s.l. It prefers humid climate and alluvial acid clay or sandy soils (Flores 1994; Hunter 1991; Sleumer 1984). *M. guianensis* is a slow growing, shade tolerant, evergreen canopy tree species which may reach 30 m and achieve 180 cm in diameter, however, large trees are rarely found and the maximum observed diameter in the Sarapiquí region has been 82 cm (Clark & Clark 1992; Finegan et al. 1999; Flores 1994; Hunter 1991; Nebel 2001; Sleumer 1984). Due to slow growth rates, 55 year old individuals may still be categorized as saplings (Clark & Clark 1992).

Figure 1. Adult individual of *M. guianensis* (photo: Gajda)

M. guianensis is a hermaphroditic species, with bisexual flowers (Sleumer 1984), and reaches maturity at diameters between 20 to 30 cm (pers. obs.). Flowering occurs usually from October to January. The small, creamy flowers are pollinated by beetles, bees and birds (Flores 1994). Fruits are produced mainly from January to March and reach maturity usually after 6 months (Flores 1994). The fleshy, purple fruits with big seeds are dispersed by omnivorous and frugivorous birds, bats, monkeys and small rodents (Flores 1994; Hunter 1991). However, many seeds as well as seedlings may be found close to the crowns of seed trees (Flores 2002; Nebel 2001). Parrots, parakeets, peccaries and squirrels may act as seed predators (Flores 1994). Germination is slow and can be inhibited by dehydration or temperature decrease (Flores 1994). If humidity levels are high and stable, seeds will germinate in both shade and direct sunlight (forest floor and pasture) (Flores 1994). Seedling growth is slow and mortality rates are high. Seedlings exposed to direct sunlight become generally stronger, due to earlier initiation of stem secondary growth (Flores 1994).

M. guianensis has exceptionally durable wood, which display natural resistance to fungal and termite attacks. Resistance to natural degradation can be ascribed to its high wood density and presence of toxic compounds in the wood (Bultman & Southwell 1976; Flores 2002; Sleumer 1984). Even after 80 years in contact with the ground the wood may show minor damage (Hunter 1991). The tree is appreciated for its high quality timber and has therefore high commercial value (Clark & Clark 1992; Sleumer 1984). It is used in heavy constructions such as railroads, marine constructions, bridges, houses, poles, fences etc. Today *M. guianensis* is a threatened species due to its slow growth rates and intensive logging (Flores 2002; M.Sc. Delgado 2007; Nebel 2001).

2.2. Site description

The study was conducted in the Caribbean lowlands of northeastern Costa Rica, Province Heredia, County Sarapiquí, in La Tirimbina Rain Forest Center (10°24´N, 84°06´W). The natural vegetation in the area is classified as tropical premontane wet forest according to the Holdridge Classification of the World Life Zones (Holdridge et al. 1971). The canopy tree *Pentaclethra macroloba* and the subcanopy palms *Welfia regia, Iriartea deltoidea* and *Socratea exorrhiza* are the dominant forest species (Finegan & Camacho 1999; Guariguata et al. 2000). La Tirimbina Rain Forest Center is located in the Sarapiquí River basin at 160-220 m.a.s.l. The topography is dominated by low hills separated by many small streams (Hunter 1991). Soils are humid, tropical soils classified as highly weathered Ultisols. They have volcanic origin, derived from lava flow, dominated by andesitic basalt. The soil profile is relatively deep, dominated by well drained, acidic clays with low fertility (Finegan & Camacho 1999; Fisher 1995; Hunter 1991; Sollins et al. 1994). Mean annual precipitation is 3,962 mm, with the driest period occurring in February to April and the wettest period occurring in June-July and November-December (Sanford et al. 1994). Air temperature is stable throughout the year with mean annual temperature of 24.5 °C (Vera et al. 1999). The temperatures, however, varies greatly on a diurnal basis with a maximum daily temperature of 37 °C and minimum nighttime temperature of 16°C (Sanford et al. 1994). Logged primary and secondary forest, protected old-growth forest, pastureland and various plantations such as rubber, cacao, pepper and ornamentals are found in the area (Finegan & Camacho 1999; Guariguata et al. 1997).

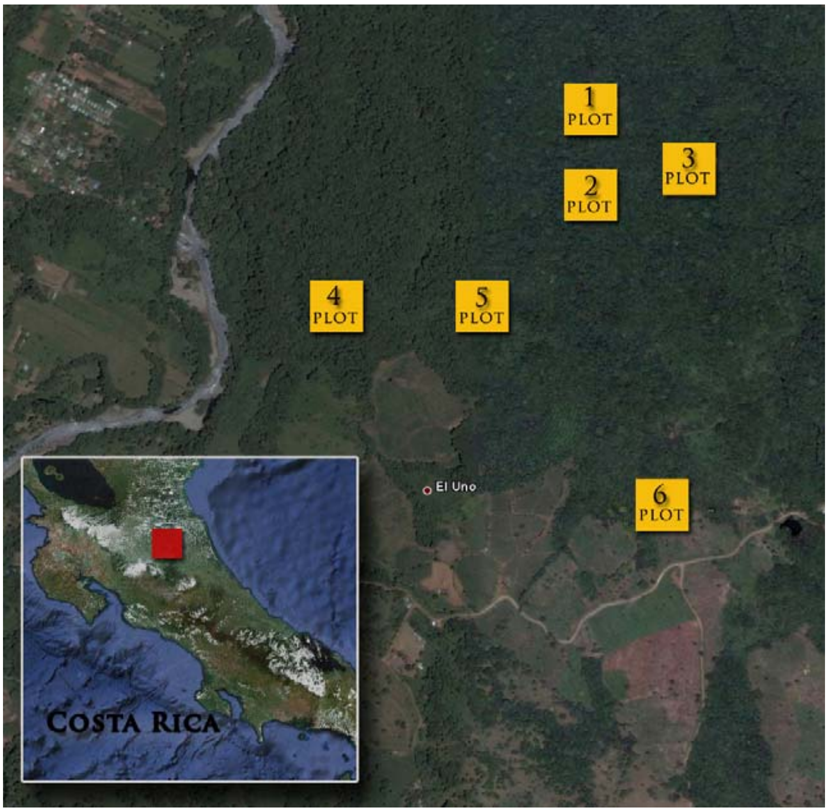

Figure 2. Map of the study area and the locations of the six sample plots, three primary forest plots (plot 1, 2, 3), and three secondary forest plots (plot 4, 5, 6) (Google Map).

The study was conducted within six 1 ha permanent sample plots, of which three were in primary forest and three in secondary forest (Figure 2). All plots were subdivided into 25 20*20 m subplots, marked with rows and columns, except plot 6 which was subdivided into100 10*10 m subplots. The primary forest plots, labeled plot 1, 2 and 3 were situated 80 m apart, and were mainly surrounded by primary forest. These plots were part of a silvicultural study and they have been lightly logged during 1989 -1990, with no post-harvest silvicultural treatment (for more detail see Finegan and Camacho (1999)).

The secondary forest plots were labeled plot 4, 5 and 6. Plot 4 and 5 were cleared thoroughly 45 years ago, but not burned, to make way for rubber (*Hevea brasiliensis*) and cacao (*Theobroma cacao*) plantations. The area was, however, never used and was immediately abandoned, and constitute today of a 45 year old secondary forest stand (Finegan 2007; Herra 2007). These two plots were positioned approximately 70 m apart and bordered in large areas to primary and secondary forest. Plot 4 bordered to a palmito de pejibaye (*Bactris gasipaes*) plantation in the south-east. Plot 5 bordered to the same palmito de pejibaye plantation and to abandoned rubber and cacao plantations in the south. Even though these plots share similar land use histories they are different in species composition (Finegan 2007).

Plot 6 was cleared and only lightly grazed for some years before it was abandoned about 20 years ago (Capers et al. 2005; Chazdon 2007). Plot 6 represented thus a 20 year old secondary forest stand. This plot was isolated from primary forest and was situated adjacent to secondary forest, pasture and *Acacia magnum,* rubber and ornamental (genus: *Dracaena*) plantations (Herra 2007).

2.3. Data collection

All individual of *M. guianensis* above 30 cm height were recorded within six 1 ha permanent sample plots, including dead trunks with a diameter greater than 20 cm. The study was conducted during the period from August to November 2007. The sampling protocol included measurements of height, diameter at breast height (DBH) and subplot coordinates.
Trees were categorised into four size classes according to Robin Chazdon's sampling protocol (Capers et al. 2005) and personal communication with Bryan Finegan:

1) *Parental trees:* DBH ≥ 20 cm.
2) *Juvenile trees:* DBH = 5 - 19 cm.
3) *Saplings:* DBH = 1 to 4.9 cm. Higher than 130 cm.
4) *Seedlings:* Stem diameter ≤ 1 cm. Stem height= 30 - 130cm.

Progeny will be used as a collective term for seedlings, saplings and juvenile trees. Stem diameter at breast height (DBH) was measured at 130 cm above ground. Calipers were used to measure diameters smaller than 4 cm and diameter tape was used for diameters larger than 4 cm. The protocol for measuring DBH followed the standards in Camacho (2000) and Clark and Clark (1992); measurements were done above stem irregularities, and lianas and vines were excluded, when branched stems were observed only the thickest stem was measured. Height was measured for all individuals with a DBH smaller than 1 cm, or with a stem height below 130 cm. Metric tape was used to measure the height from the stem base to the highest live meristem (Clark & Clark 1992; Clark et al. 1993; Dr. Finegan 2007).

Physical state and microsite variables such as crown illumination, topography and drainage conditions were measured for all progeny classes; seedlings, saplings and juvenile trees at the site where they were found. Crown illumination was the only microsite parameter registered for adult trees. Flowering and fruiting was also recorded when observed. Physical state was evaluated by categorizing each individual into healthy or damaged individuals. Damaged individuals were individuals with leader dieback or breakage (Clark & Clark 1992). Topographic position was categorized as peak, slope and nadir (Svenning 1999). Soil drainage conditions were categorized into poor and good drainage conditions. Muddy areas or slight depressions were classified as areas with poor drainage conditions, and areas where water did not accumulate were classified as good drainage conditions (Svenning 1999).

Clark and Clark's (1992) modified Dawkin's crown illumination index was used when estimating the crown illumination for progeny and adult trees. This modified index has three additional categories that captures the light spectrum where most seedlings and saplings are found in more detail (category 4, 5 and 6). The seven categories for crown illumination were: emergent crown, completely exposed to vertical and lateral light (1), crown fully illuminated from above (2), crown partially illuminated from above (10-90%) (3), crown lit only from the side: High lateral light with one big canopy opening or lots of medium canopy openings (4), medium lateral light with some medium canopy openings (5), lower lateral light with no big or medium canopy openings (6) and crown with no significant direct illumination (7) (Camacho 2000; Clark & Clark 1992; Clark et al. 1993; Finegan et al. 1999). The advantage of this method is that it can be used to estimate the crown illumination of trees of various heights by an observer on the ground (Clark & Clark 1992).

2.4. Statistical Analysis

Minitab® 15 Statistical Software (Minitab Inc.) and R version 2.8.1 (www.r-project.org) were used to perform statistical and spatial analysis. Significance level was set to 0.05.

Man-Whitney *U* test was used when testing for abundance differences of *M. guianensis* between primary and secondary forest plots. Two-way analysis of variance (ANOVA) was used when testing for differences in habitat preference and physical damage between size classes and primary and secondary forest. Tukey's post-hoc comparison was used to investigate which topographic category was preferred among the size classes.

Spatial pattern analysis

For preliminary exploration of the dataset a visual display of the distribution of *M. guianensis*, in the different forest plots was given by a density plot. Density plot is a density-based method which describes the distribution by giving a density of trees at all locations of the study area (Baddeley 2008; O'Sullivan & Unwin 2003). Ripley's K-function (Ripley 1977) with Monte Carlo simulations was applied to test whether the distribution of *M. guianensis*, within the forest plots was random, clumped or regular. This is a distance-based method which describes the average number of trees within a set of given distances of any tree (Bivand et al. 2008; O'Sullivan & Unwin 2003). The tested null hypothesis stated that the distribution of *M. guianensis* was caused by a homogeneous Poisson process, also called Complete Spatial Randomness (CSR). Under CSR trees are independent of each other and distributed at random and uniform over the study area (Baddeley 2008; Bivand et al. 2008).

Ripley's K-function was transformed into an L-function, which stabilizes the variance and makes visual interpretation of the graph easier. The L-function has the value of zero for random distribution. Values above zero suggest a clustered distribution, while values below zero suggest a regular distribution (Baddeley 2008; O'Sullivan & Unwin 2003). Due to random variability even the L-function of a completely random pattern will seldom have the exact value of zero (Baddeley 2008). Monte Carlo test is thus applied to generate the typical range of values in a random distribution (Baddeley 2008; O'Sullivan & Unwin 2003). The significance level of the pointwise Monte Carlo test was defined as: $\alpha = 2/(M+1)$ (Baddeley 2008). To achieve alpha 0.05, 39 simulations were run. Observations above the simulation

envelope affirm a clustered distribution, while observations below the simulation envelope assert a regular distribution.
No edge correction methods were applied, because each simulation was subjected to the same edge effect as the observed data (O'Sullivan & Unwin 2003). In order to investigate possible changes of the spatial pattern during the life cycle of *M. guianensis*, Ripley's K analysis was run separately for all four size classes; adult and juvenile trees, saplings and seedlings.

Spatial association analysis

Cross K-function was applied when testing whether adult trees influence the distribution of progeny. The cross K-function is a distance cross function which is a modification of Ripley's K-function. The function counts the number of progeny within different distances of each adult tree (O'Sullivan & Unwin 2003). The null-hypothesis of a homogeneous Poisson marked point process states that adult trees do not have any influence on the distribution of progeny. Monte Carlo test was used for assessing the significance level of the test, with 39 simulations based on the homogeneous Poisson point process. Observations above the simulation envelope signify clustering of progeny around adult trees while observations below the simulation envelope suggest inhibition of progeny growth near adult trees.

In order to investigate if the association pattern of progeny to adults changed during the life cycle of *M. guianensis*, a cross K-function was applied separately for all three progeny classes.

Spatial pattern generating analysis

Cross K-function randomization test was used when testing if the underlying distribution-processes of progeny and adult trees were independent. The null-hypothesis of independence of components states that the underlying distribution processes of progeny and adult trees were independent (Baddeley 2008). The test randomly changes the positions of each marked pattern independently of each other (Baddeley 2008) with a maximum displacement distance at 100 dm. The points that were shifted outside the plot window were not taken into account in this analysis.

3. RESULTS

3.1. Abundance

In total, 936 living and 15 trunks were observed in six 1 ha plots; 198 trees in primary forest and 754 trees in secondary forest. In secondary plot 5 and 6 no living adults were encountered, however trunks of dead trees were registered. The abundance of adult trees was significantly higher in primary forest than in secondary forest (one-tailed Man-Whitney *U*= 15, *P*=0.04). However, the number of progeny was significantly higher in secondary forest than in primary forest (one-tailed Man-Whitney *U*=6, *P*=0.04, Figure 3).

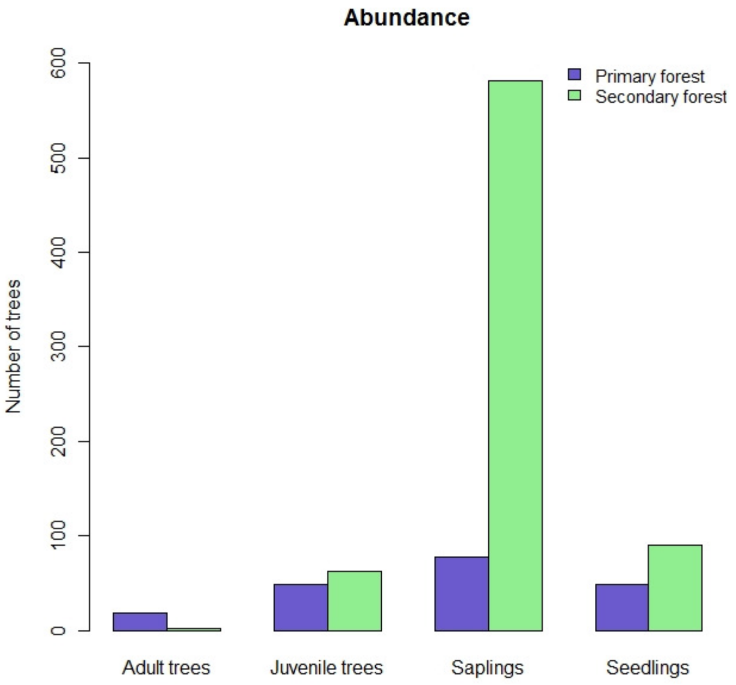

Figure 3. The abundance count of living *M. guianensis* individuals in primary and secondary forest for the four size classes; adult and juvenile trees, saplings and seedlings.

3.2. Habitat preferences

No trees were observed in crown illumination category 1; *emergent crown*. Different size classes grew under different light conditions (two-way ANOVA; *F*= 2.54, df=15, 128, *P*=0.003, Figure 4), with the smaller size classes growing under decreased light intensity (Figure 4). Crown illumination preferences did not differ significantly between primary and secondary forest (two-way ANOVA; *F*= 1.18, df=5, 138, *P*=0.32).

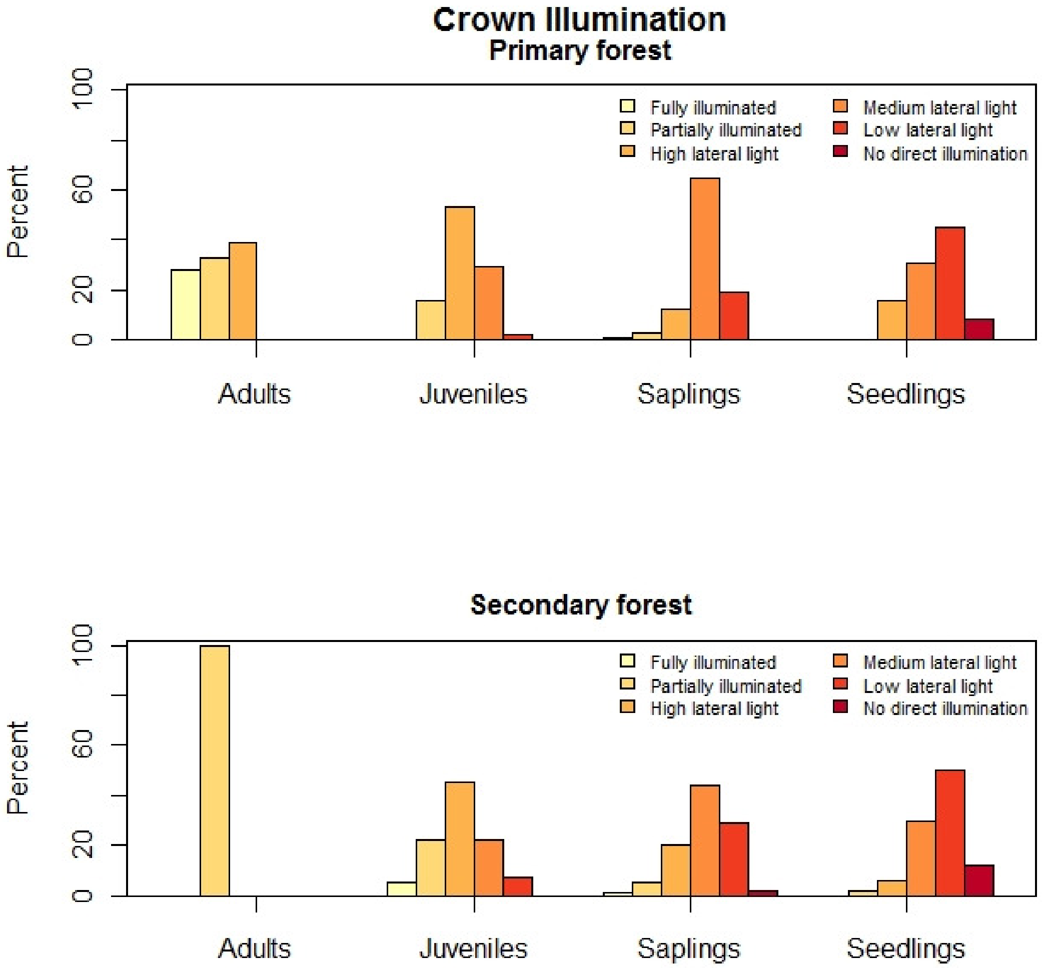

Figure 4. Percent of *M. guianensis* within the different crown illumination categories, observed in primary and secondary forest for all size classes.

Significantly more trees were found on slope than on peak and nadir, in primary forest (Tukey's test t=2.84, *P*=0.03 and t=-3.52, *P*=0.007, respectively, Figure 5), whereas no significant differences between topography classes was found in secondary forest. Topography preference did not change significantly between size classes (two-way ANOVA;

F=1.02, df=4, 49, *P*=0.41). Topography preferences were not significantly different between primary and secondary forest (two-way ANOVA; *F*=1.26, df=2, 51, *P*=0.29).

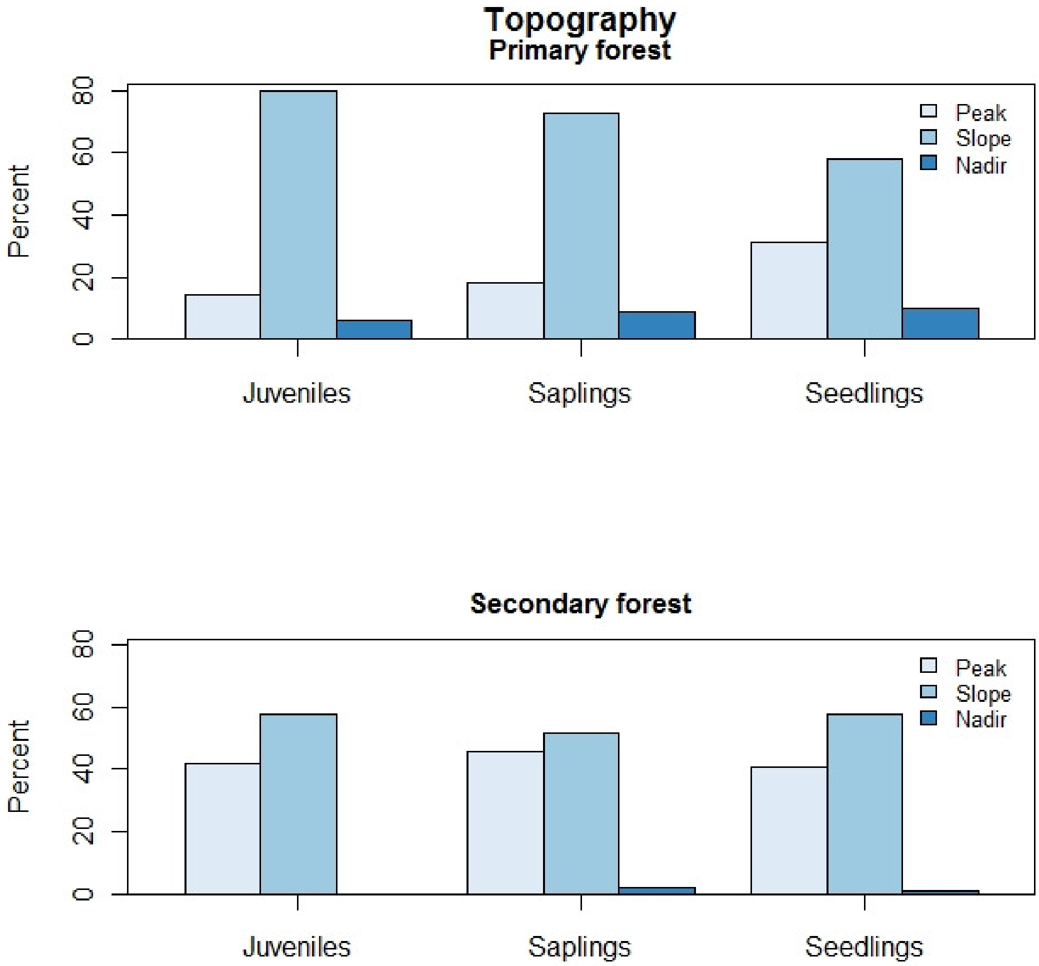

Figure 5. Percent of *M. guianensis* progeny growing within the different topography categories, observed in primary and secondary forest.

All *M. guianensis* individuals were growing in the microsite category; good drainage conditions, thus displaying a preference for well drained soil.

3.3. Physical state

The percent of healthy individuals was significantly higher than that of damaged individuals for all *M. guianensis* individuals in both primary and secondary forest, with the exception of seedlings in secondary forest (two-way ANOVA; F=69.59, df=1, 34, P< 0.0001, Figure 6). Physical state varied between the different size classes (two-way ANOVA; F=3.68, df=2, 33, P=0.04), but did not differ significantly between primary and secondary forest (two-way ANOVA; F=0.01, df=1, 34, P=0.94). In secondary forest the percent of damage increased with decreasing tree size, this pattern was, however, not visible in primary forest (Figure 6).

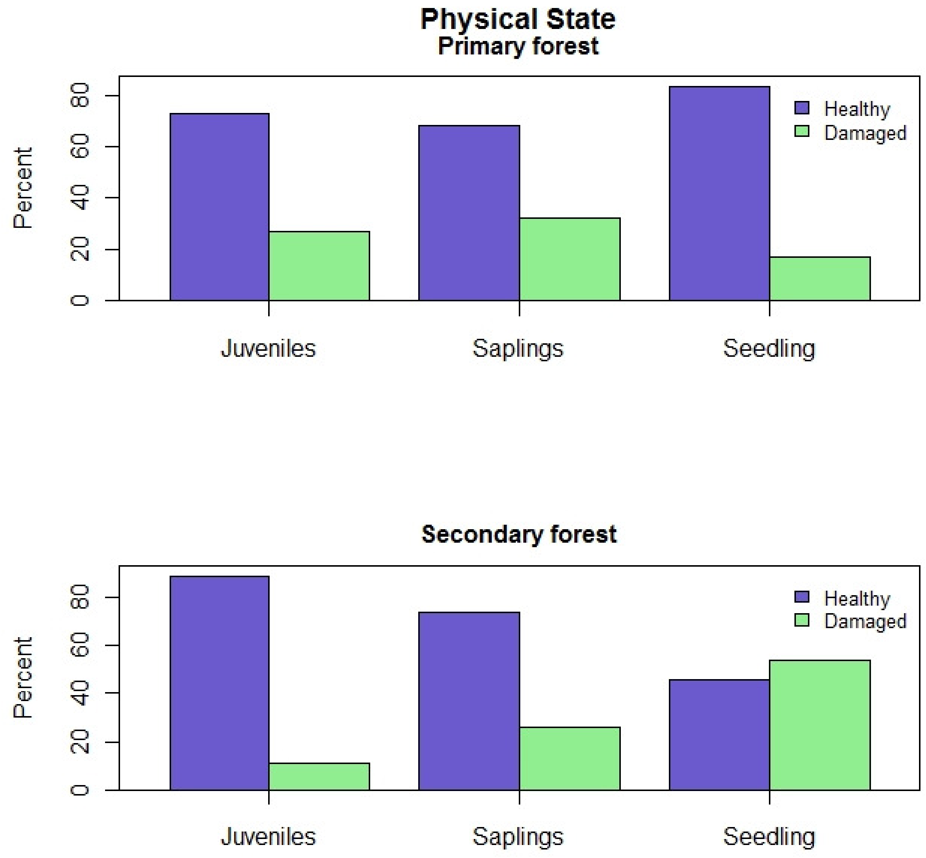

Figure 6. Percent of *M. guianensis* with and without physical damage for the three progeny classes: juveniles, saplings and seedlings in primary and secondary forest.

3.4. Spatial distribution

The densities of trees were higher in secondary forest plots than in primary forest plots (Figure 7).

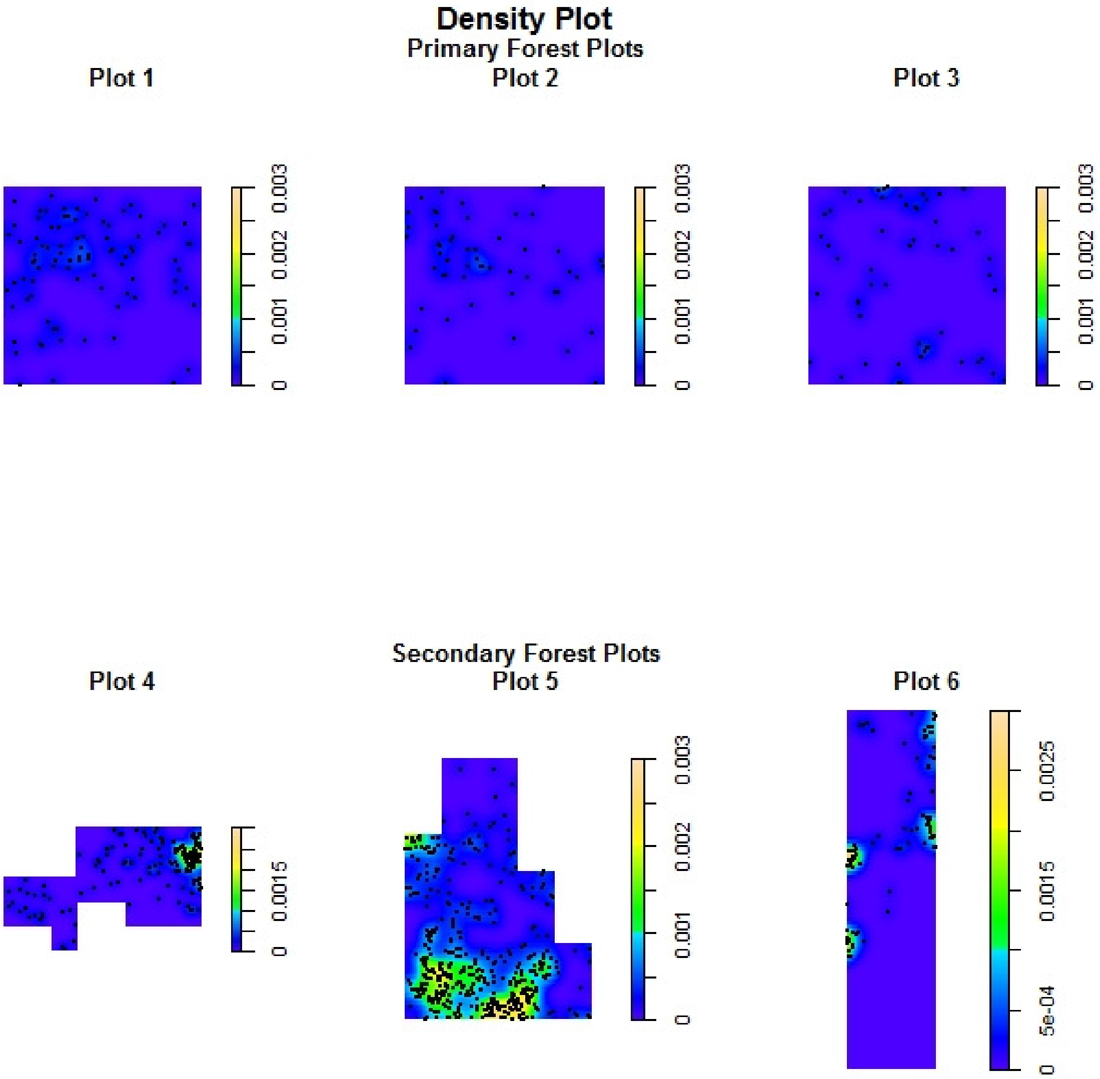

Figure 7. Density plots illustrate the density and distribution pattern of *M. guianensis* in primary and secondary forest plots with plotted observation points.

Spatial pattern analysis

Ripley’s K analysis was implemented when exploring the distribution pattern of *M. guianensis* in primary and secondary forest. Pattern changes throughout the life cycle of *M. guianensis* were analyzed by investigating the distribution pattern of each size class separately. In the following, a series of graphs were used to analyze the distribution pattern of *M. guianensis.* Detailed explanations of how the graphs should be interpreted are given in the figure text of Figure 8.

The distribution of *M. guianensis* displayed an overall tendency for clustering (Figure 8). However, the distribution pattern varied between secondary and primary forest, being more clustered in secondary forest than in primary forest (Figure 8).

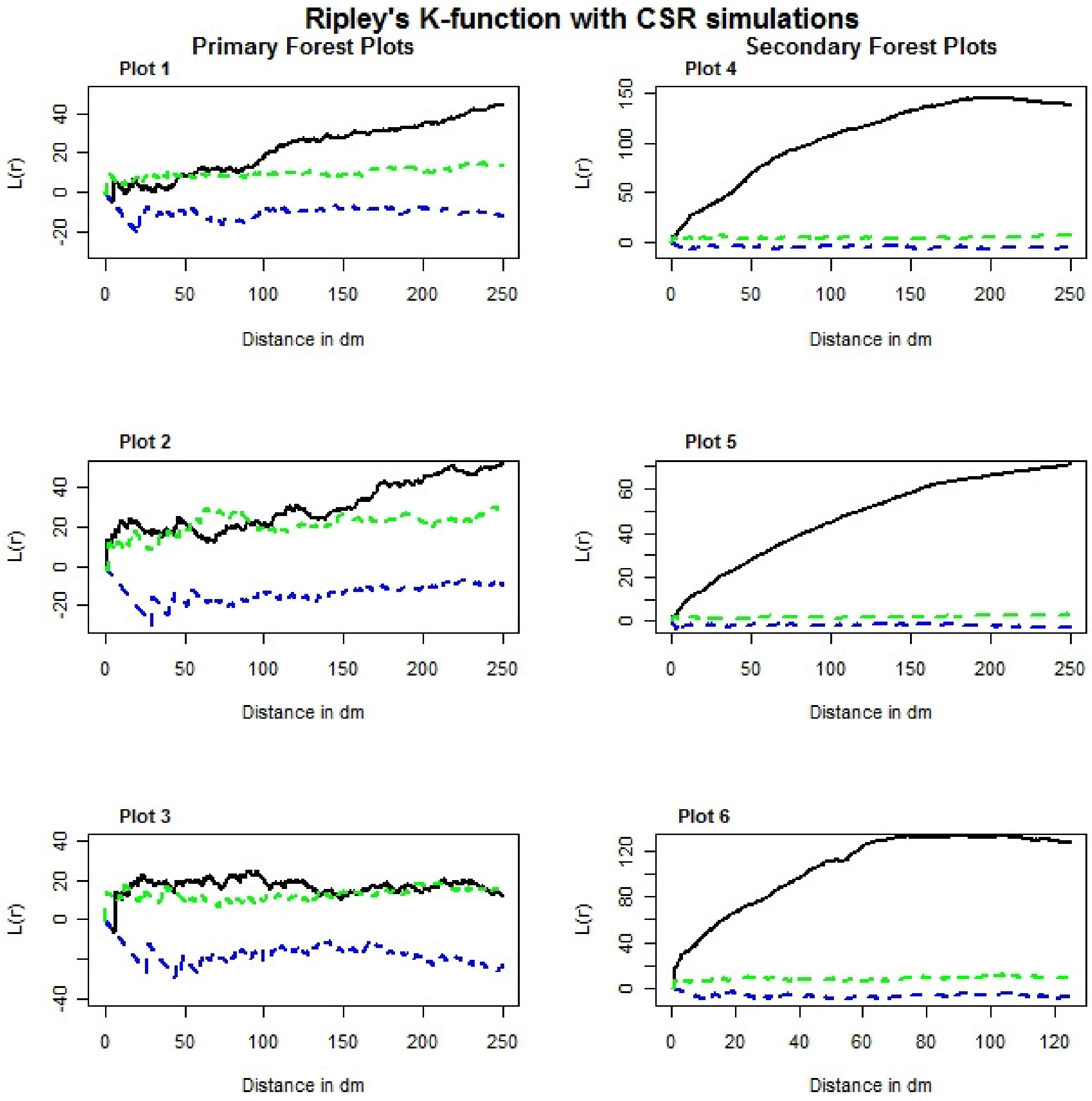

Figure 8. Ripley's K analysis of the distribution of *M. guianensis* in primary and secondary forest plots, with simulation envelope created by 39 CSR simulations. L(r) is standardized Ripley's K-function. With a significance level of pointwise Monte Carlo test: 0.05. In areas where the empirical K-function which represents our observations (the black line), is outside the simulation envelope (the area between the green and blue line), the null hypothesis of CSR is rejected. If the observation values are above the green line, the distribution is significantly clustered. If the observation values are below the blue line the distribution pattern is regular. When the observed values are within the simulation envelope, the distribution pattern is random.

Seedlings displayed a clustered distribution pattern in both primary and secondary forest plots (Figure 9). The tendency for clustering was stronger in secondary forest than in primary forest (Figure 9).

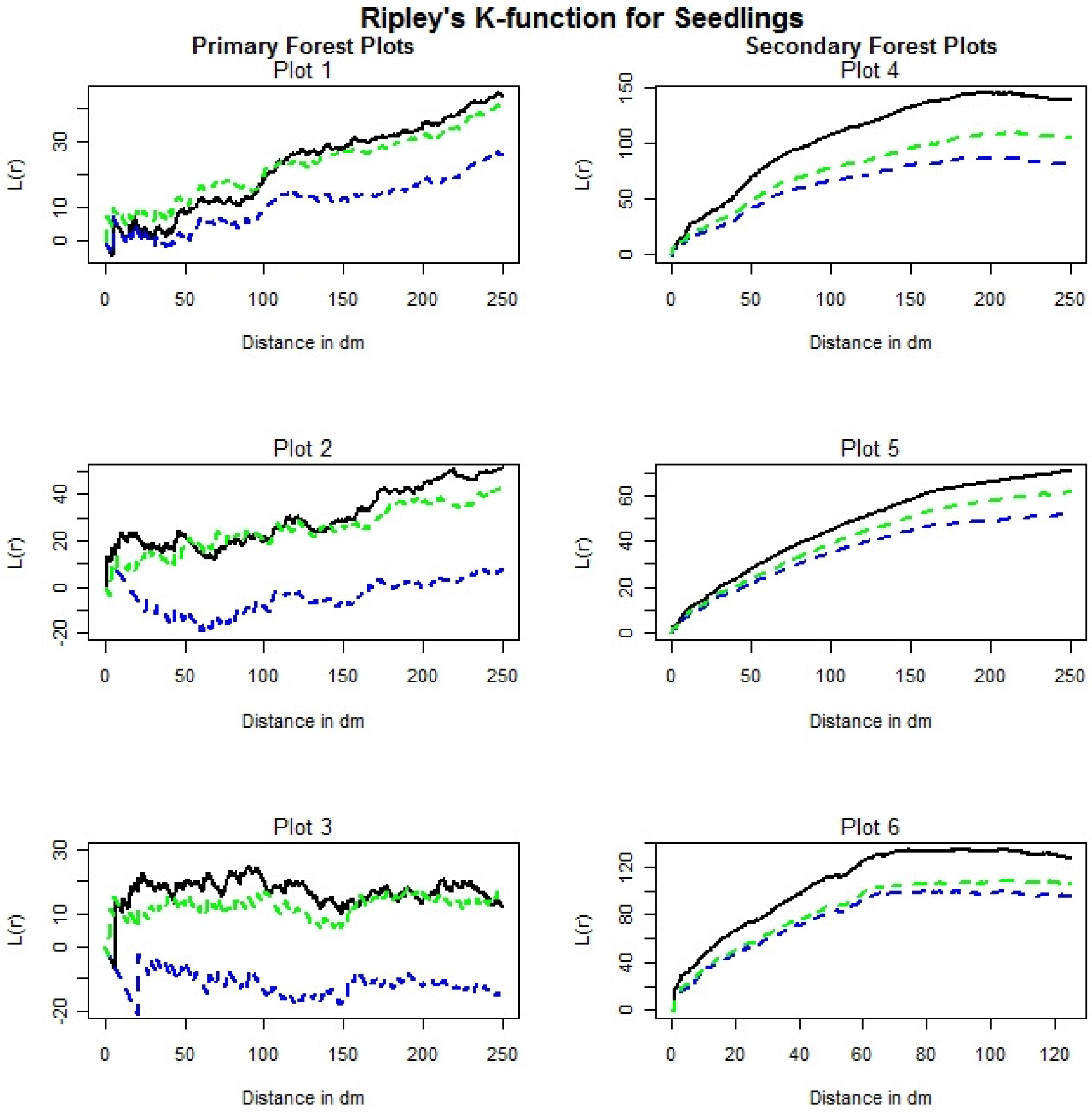

Figure 9. Ripley's K analysis of the distribution of *M. guianensis* seedlings in primary and secondary forest plots, with simulation envelope created by 39 CSR simulations. L(r) is standardized Ripley's K-function. (See **Figure 8** for graph interpretation).

Saplings displayed a clustered distribution pattern in all secondary forest plots (Figure 10).

In primary forest the distribution pattern varied among the three primary forest plots. In primary forest plot 1, the saplings were significantly clustered at distances above 100 dm. In plot 2 saplings displayed strong, but not significant clustering tendencies. In primary forest plot 3 the distribution of saplings was completely random, except for significant clustering at 30 dm distance (Figure 10).

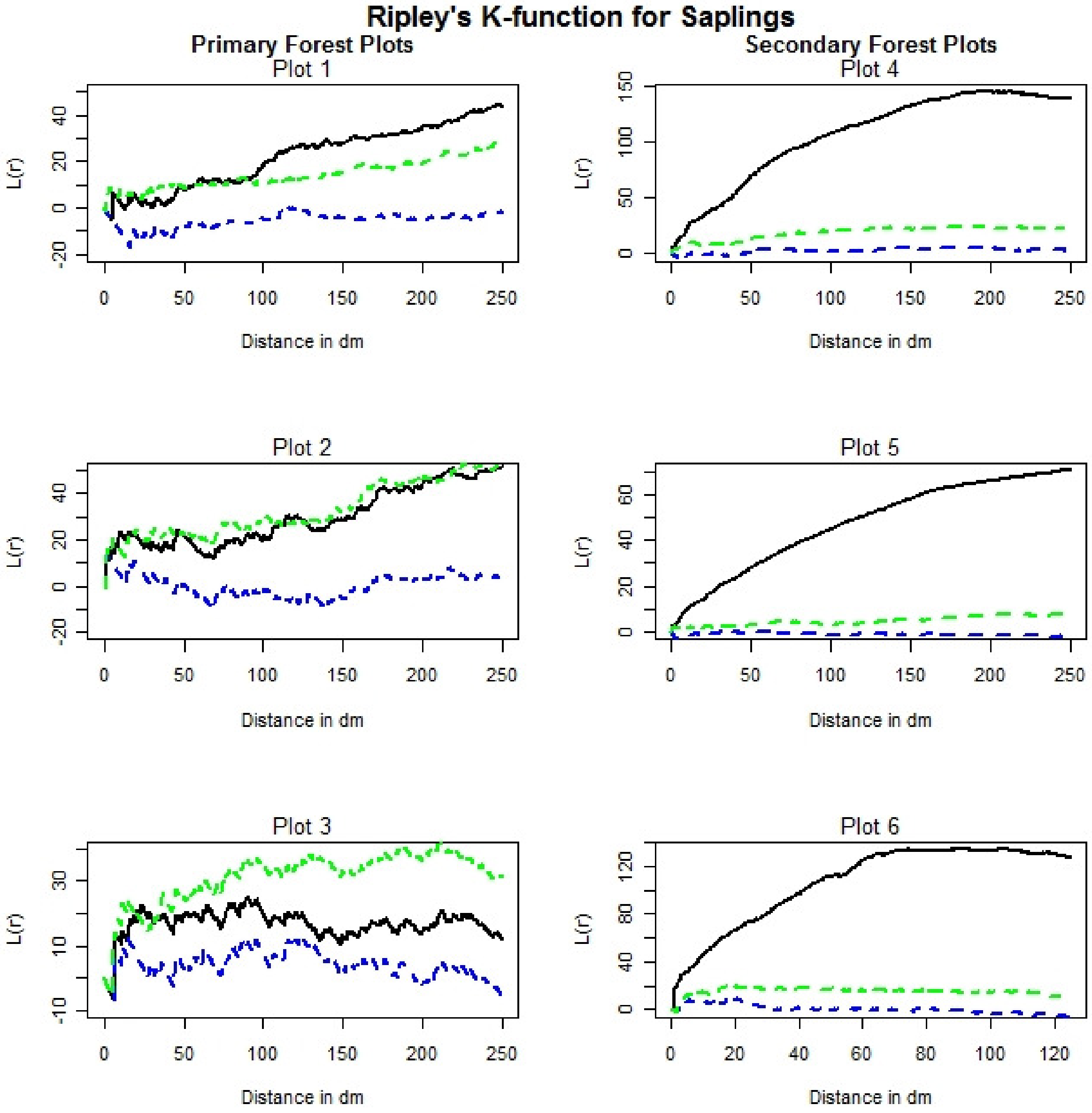

Figure 10. Ripley's K analysis of the distribution of *M. guianensis* saplings in primary and secondary forest plots, with simulation envelope created by 39 CSR simulations. L(r) is standardized Ripley's K-function. (See **Figure 8** for graph interpretation).

Juvenile trees displayed overall a less clustered distribution pattern than that observed for both seedlings and saplings (Figure 11). In primary forest juvenile trees displayed a tendency for regular distribution at distance below 50 dm, which indicate inhibition between these individual (Figure 11).

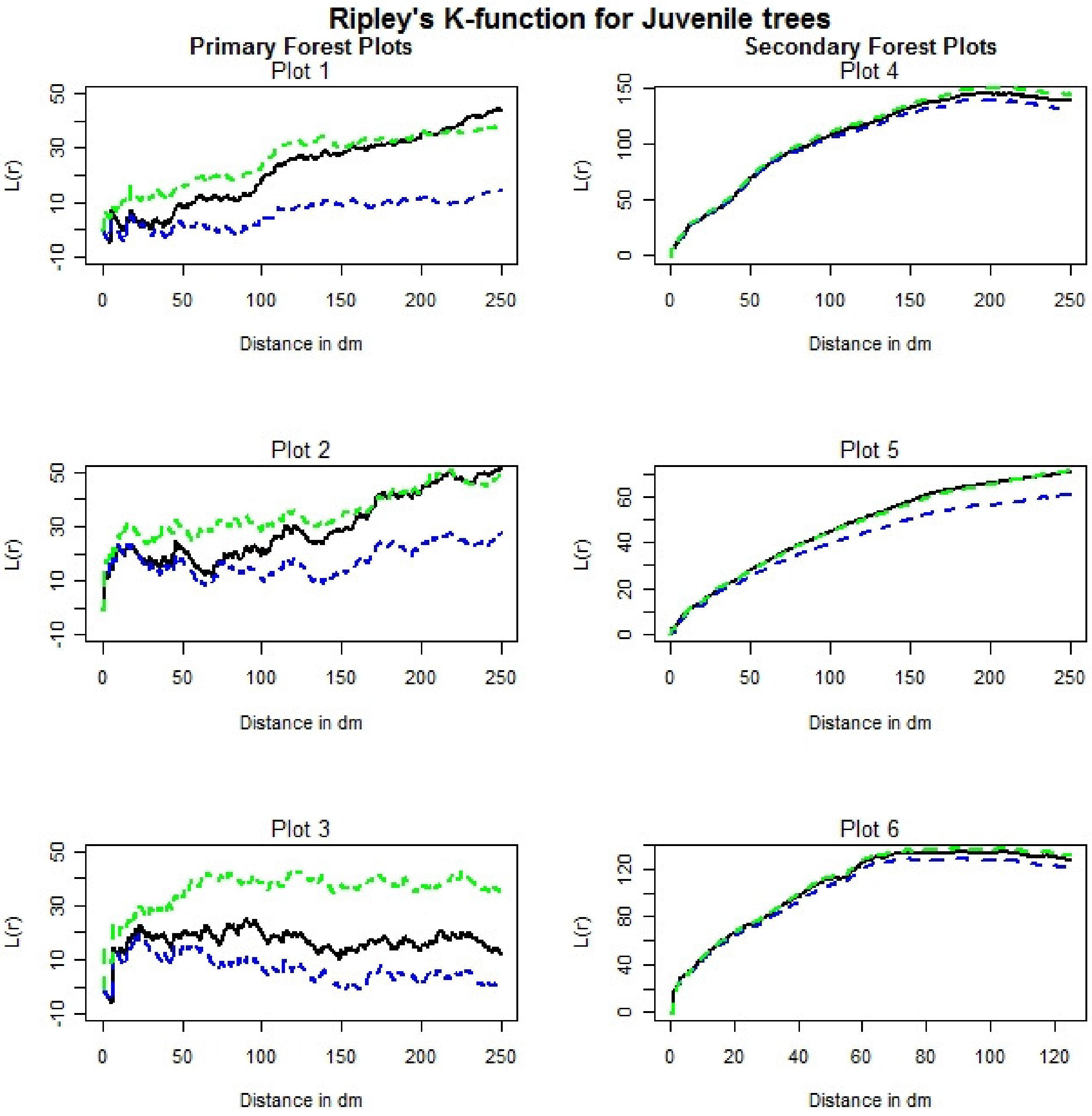

Figure 11. Ripley's K analysis of the distribution of juvenile trees of *M. guianensis* in primary and secondary forest plots, with simulation envelope created by 39 CSR simulations. L(r) is standardized Ripley's K-function. (See **Figure 8** for graph interpretation).

The distribution pattern of adult trees was similar to juvenile trees, being more random than the distribution of both seedlings and saplings. Adult trees in all primary plots displayed a tendency for regular distribution at distance below 50 dm (Figure 12). In secondary forest plot 4 only two adult trees were observed. Analysis of the distribution pattern in this plot was thus limited. In secondary forest plot 5 and 6 no living adult trees were observed. The analysis in these plots is based on the distribution of trunks.

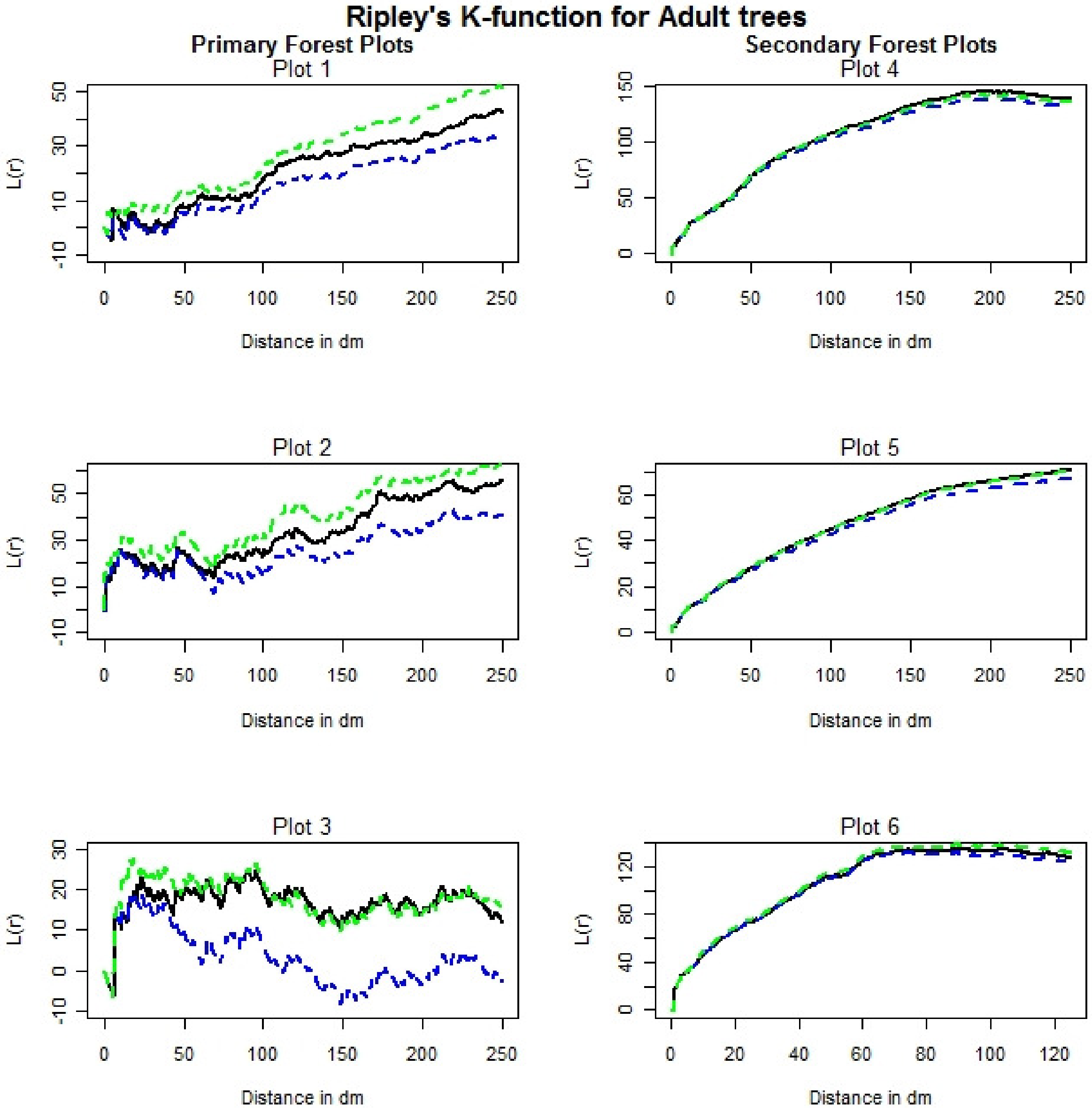

Figure 12. Ripley's K analysis of the distribution of adult trees of *M. guianensis* in primary and secondary forest plots, with simulation envelope created by 39 CSR simulations. L(r) is standardized Ripley's K-function. (See **Figure 8** for graph interpretation).

Spatial association analysis

Cross K-function was applied when testing whether adult trees and trunks influenced the distribution of progeny. In primary forest plots no spatial association between adult trees and progeny was present (Figure 13). In secondary forest plots progeny was significantly clustered around adult individuals (Figure 13).

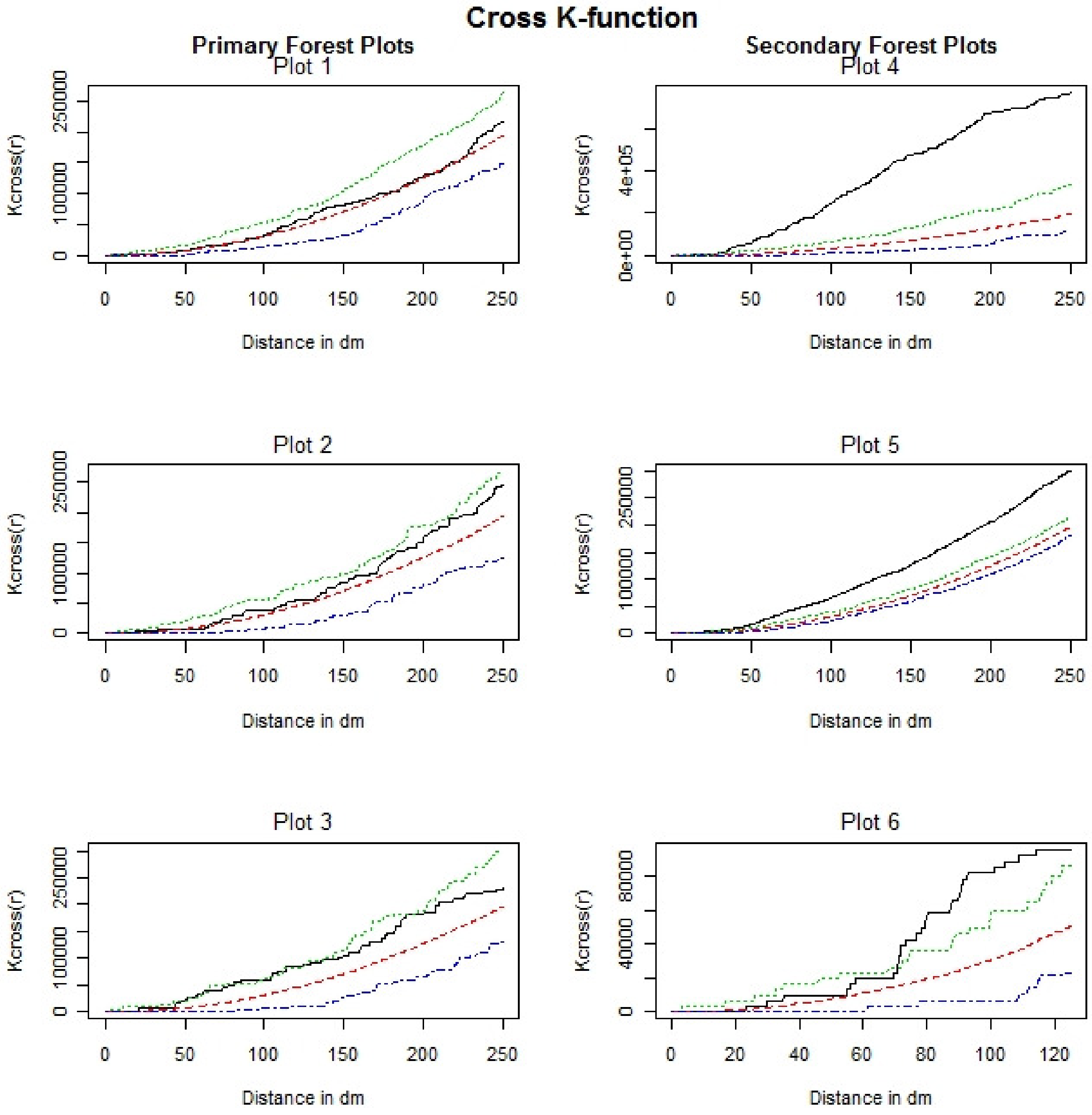

Figure 13. Cross K-function analysis of the distance between adult individuals of *M. guianensis* and progeny in primary and secondary forest plots. With simulation envelope created by 39 CSR simulations giving a significance level of pointwise Monte Carlo test at 0.05. Observations above the simulation envelope imply clustering around adult trees while observations below the simulation envelope suggest inhibition of growth near adult trees. Observations contained within the simulation envelope imply no significant relationship between adult trees and progeny.

Cross K-function was applied separately for all three progeny classes; seedlings, saplings and juvenile trees, when testing if the association pattern change during the life cycle of *M. guianensis*. The association pattern between seedlings and adult trees in the primary forest plots ranged from random (plot 1), not significant clustering trend (plot 2) and significant clustering (plot 3) (Figure 14). Seedlings in secondary plot 4 and 5 displayed significant clustering, while no spatial association between seedlings and adult trees was found in secondary forest plot 6 (Figure 14).

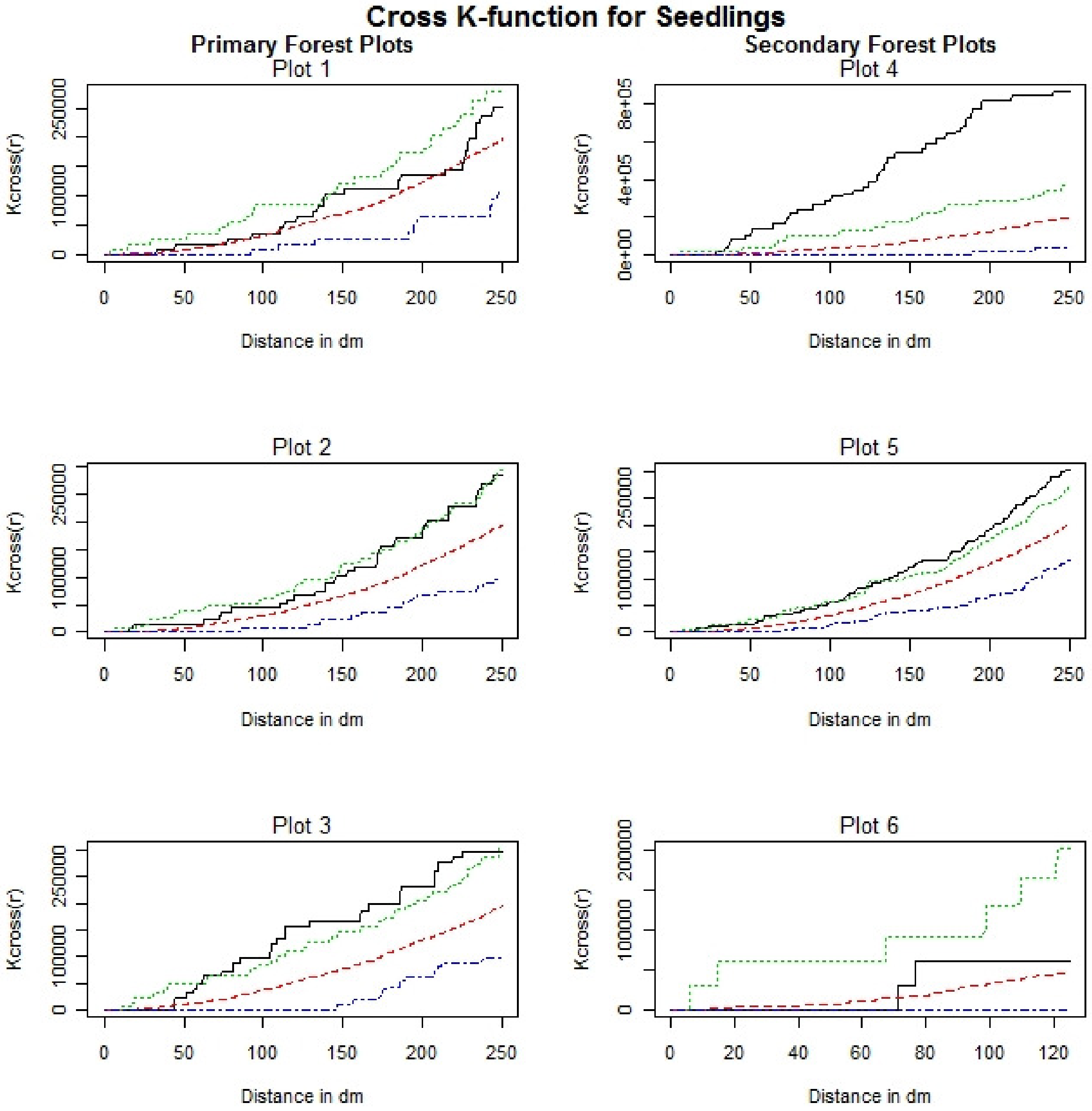

Figure 14. Cross K-function analysis of the distance between seedlings and adult individuals of *M. guianensis* in primary and secondary forest plots. (See **Figure 13** for graph interpretation).

There was no association between saplings and adult trees in primary forest plots (Figure 15). Saplings were significantly clustered around adult individuals in secondary forest plots (Figure 15).

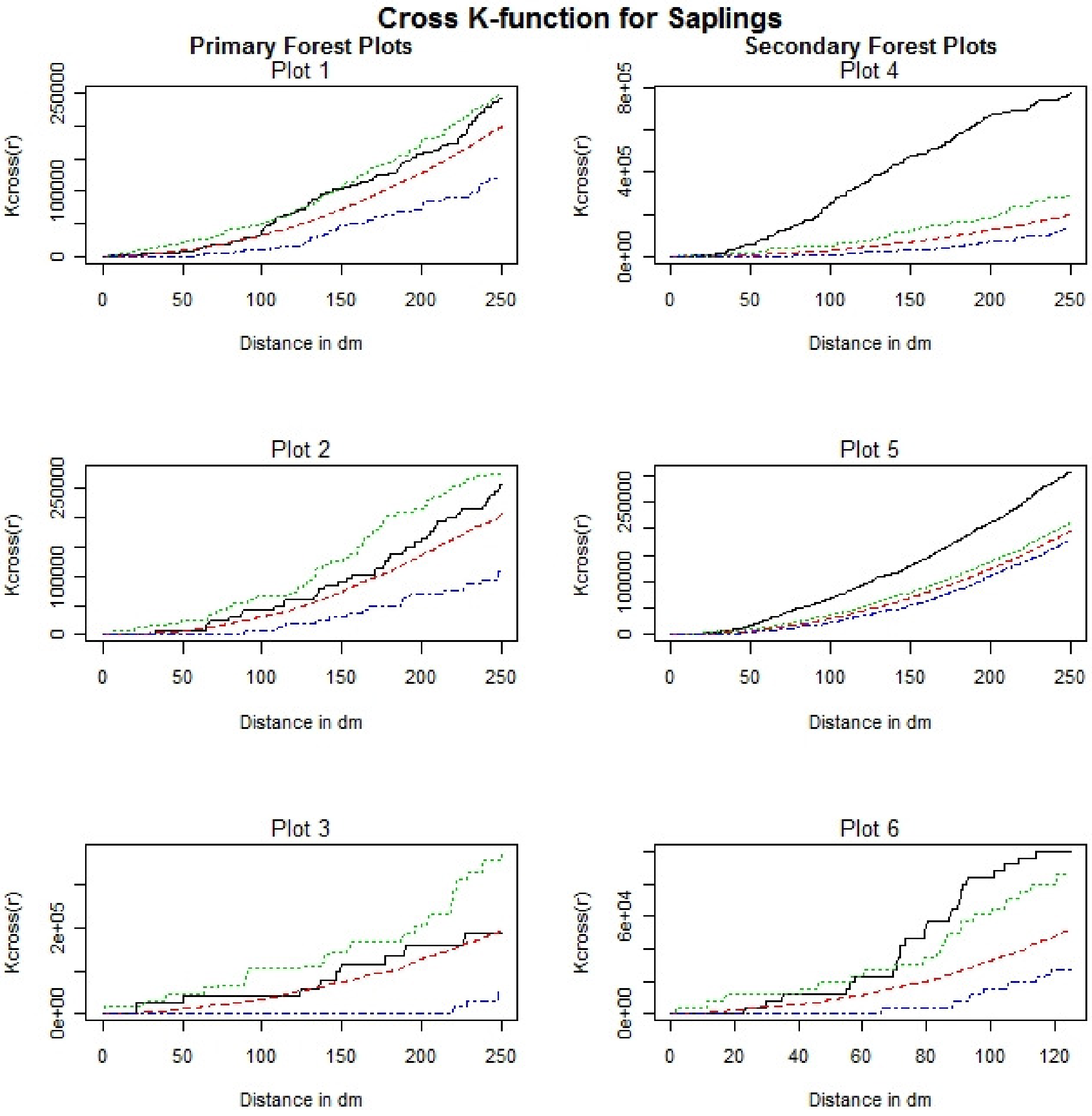

Figure 15. Cross K-function analysis of the distance between saplings and adult individuals of *M. guianensis* in primary and secondary forest plots. (See **Figure 13** for graph interpretation).

No significant associations were observed between juvenile and adult trees in primary forest plots, a tendency for inhibition by adult trees was, however, visible (Figure 16). In secondary forest plot 4 and 6, no associations between juvenile and adult trees were present. In secondary forest plot 5 juvenile trees were clustered around adult trees (Figure 16).

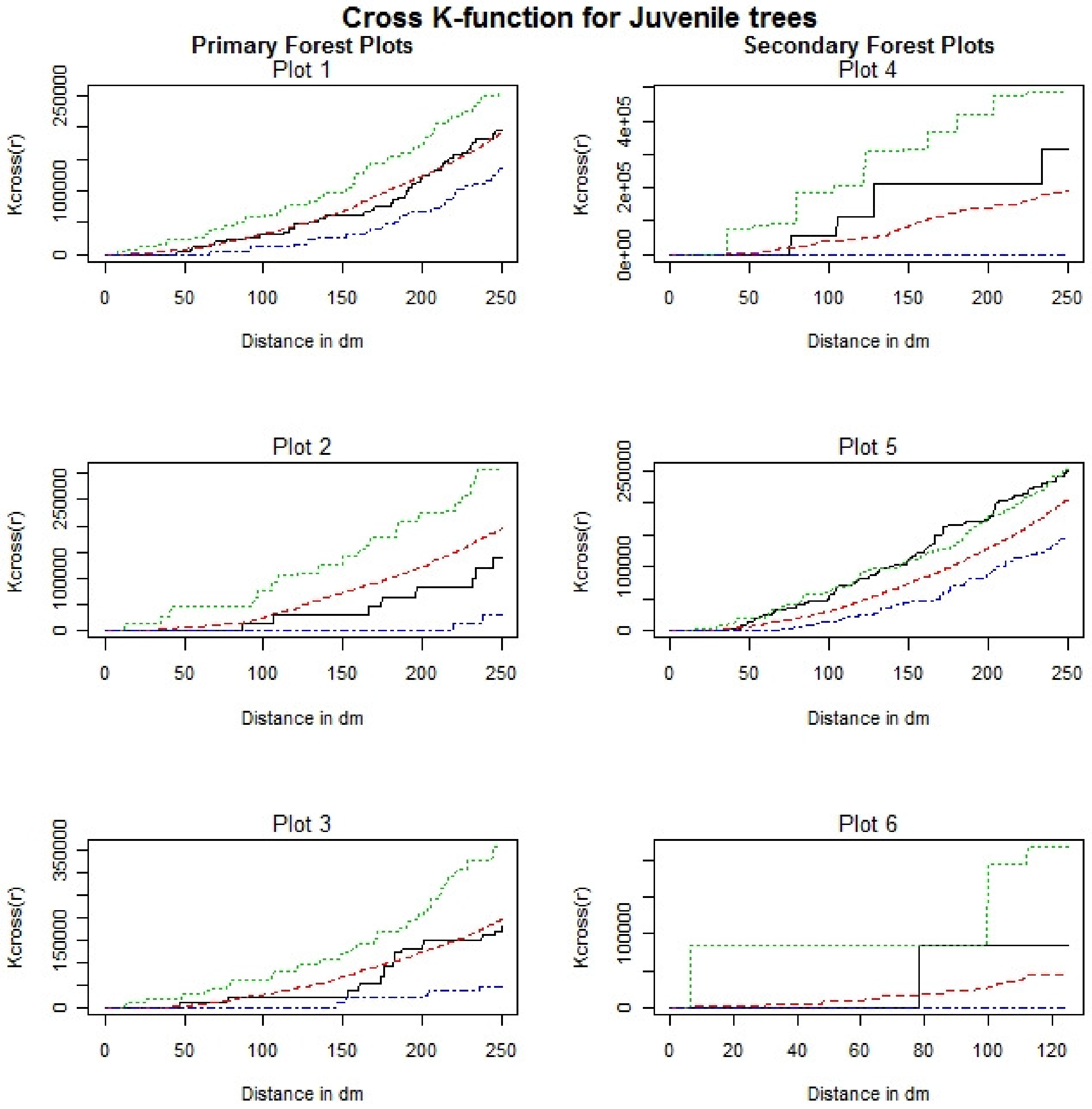

Figure 16. Cross K-function analysis of the distance between juvenile trees and adult individuals of *M. guianensis* in primary and secondary forest plots. (See **Figure 13** for graph interpretation).

Independence of components

The processes influencing the spatial distribution of progeny and adult trees were independent (Figure 17).

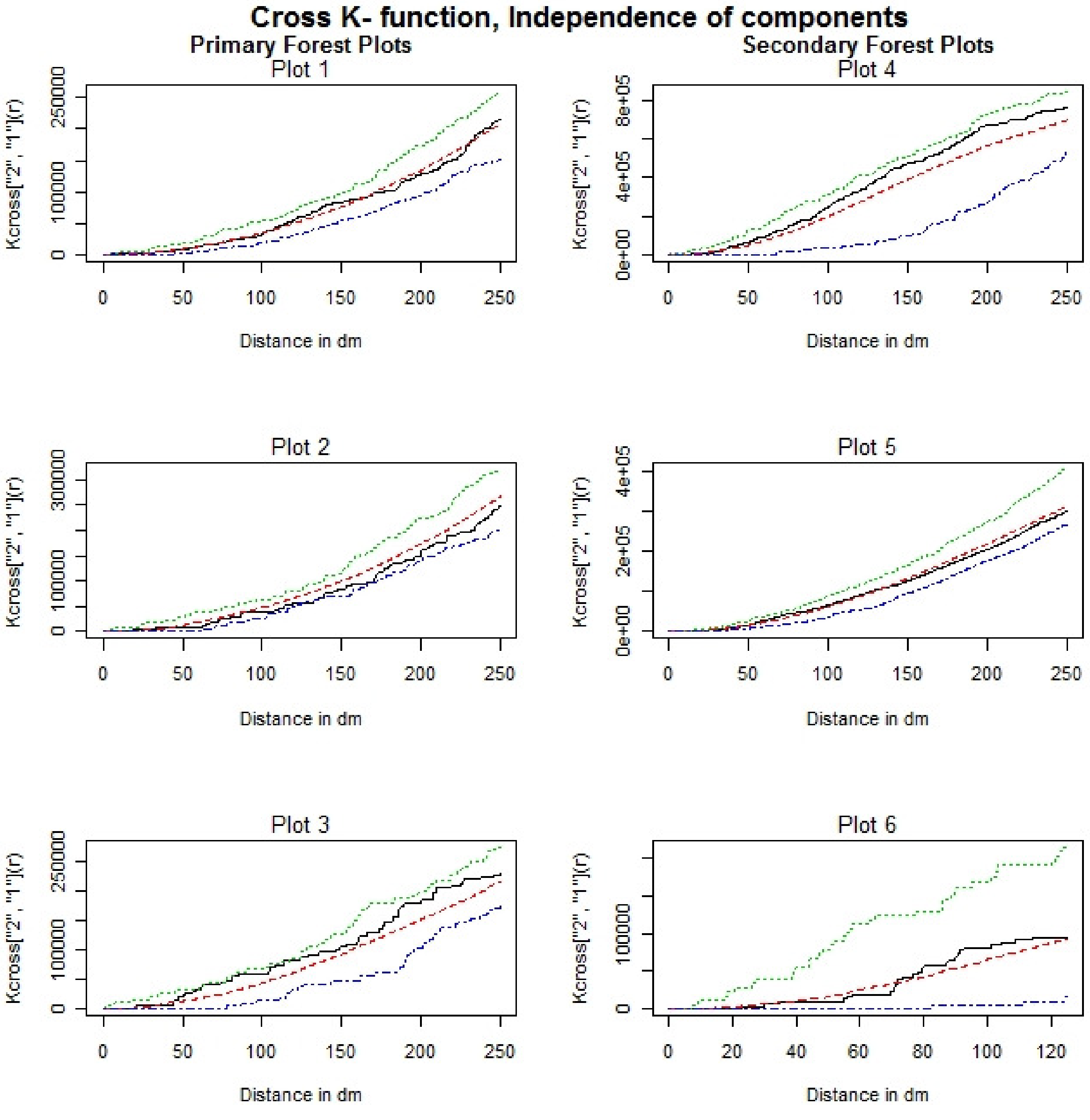

Figure 17. Cross K-function analysis of the underlying pattern generating processes for progeny and adult trees of *M. guianensis* in primary and secondary forest plots. Simulation envelope created by 39 simulations of the null-hypothesis of independence of components. With a significance level of pointwise Monte Carlo test at 0.05. Observations contained within the simulation envelope signify that the underlying distribution processes of progeny and adult trees are independent.

4. DISCUSSION

I draw four main conclusions from the results of my study. First, greater abundance of the progeny of *M. guianensis* in secondary forest than in primary forest was attributed to favorable microclimatic conditions in the initial period after land abandonment. Second, habitat preferences displayed by *M. guianensis* point out the importance of microsites on the successful establishment and growth of this species. Third, the impact of physical damage increased in populations with limited recruitment. In the end, spatial pattern analysis revealed the importance of remnant trees on the regeneration of *M. guianensis* in secondary forest sites.

4.1. Abundance

The number of progeny was significantly higher in secondary forest than in primary forest, these results contradict with other studies which report impeded forest regeneration and slow establishment of primary forest species in abandoned land areas (Aide & Cavelier 1994; Gómez-Pompa et al. 1972; Holl 1999; Hooper et al. 2005; Uhl 1987). There are several ecological processes that govern natural regeneration and thus have a direct effect on abundance. These are seed availability, seed dispersal, seed predation, seed germination and seedling growth and survival (Holl et al. 2000). One or more of these regeneration processes did diverge between the primary and secondary forest sites, causing greater abundance in secondary forest. The main difference between these forest sites, having a major effect on the regeneration processes, is their land-use history. Primary forest sites have been lightly logged, and secondary forest sites have experienced severe disturbance through clear-cutting.

It may seem that higher abundance of progeny in secondary forest cannot be explained by differences in seed production at the site, as there were significantly more living adult trees in primary forest than in secondary forest plots. In natural forest, adult trees of *M. guianensis* produce considerable amounts of fruits, however, trees growing in direct sunlight reach fertility earlier and seem to have greater fruit production (Nebel 2001). Only two living trees were observed in one of the secondary forest plots (plot 4), thus enhanced fruit production due to better light conditions after forest clearing, could only explain greater progeny abundance in this secondary plot. However, taking into consideration that it was a common practice to leave commercially important species after clear-cutting (Herra 2007), it is likely that some of the trunks observed in the secondary forest plots, were cut some years after the deforestation event, and thus had the chance to produce considerable amounts of fruits in the time before they were harvested.

It is unlikely that enhanced rates of seed dispersal from neighboring forest could explain greater abundance of *M. guianensis* in the secondary forest plots. Animal seed dispersal is limited in deforested land areas, as many forest animals are reluctant to move into the open (Cardoso da Silva et al. 1996; Guevara et al. 1986; Holl 1999). Remnant trees have, however, been found to enhance seed rain in open areas with rates similar to those found in primary forest (Guevara et al. 1986; Guevara & Laborde 1993; Uhl et al. 1988). However, since they increase seed dispersal to the same levels that are present in primary forest, it can be concluded that their beneficial effect on seed dispersal cannot explain greater abundance in secondary forest stands as opposed to primary forest.

Lower rates of seed predation in deforested land areas may have caused greater abundance of *M. guianensis* in the secondary forest plots. This statement is supported by Aide and Cavalier (1994), who reported lower seed predation rates in abandoned pastures than in forest patches. If remnant trees were present at these abandoned sites, lower seed predation beneath these trees, as was observed by Holl and Lulow (1997), could also explain higher abundance in secondary forest. Hammond (1995) and Nepstad et al. (1991), on the other hand documented higher seed predation rates in abandoned pastures and young secondary forest, than in primary forest. Other studies have revealed that the highest predation risk in given habitats vary between years and the species under study (Holl & Lulow 1997; Notman & Gorchov 2001; Willson & Whelan 1990). There is thus no consensus about the rate of seed predation in cleared land areas. Although seed predation is important in early plant establishment, its effects may be ameliorated by different survival rates at post germination life stages (Notman & Gorchov 2001). Species with low seed predation rates can experience high seedling mortality and vice versa, and thus the effect of seed predation on regeneration and abundance might not be as clear as expected (Janzen 1971; Notman & Gorchov 2001).

Enhanced germination rates in cleared land areas may have caused higher abundance of progeny in secondary forest than in primary forest. Seeds of *M. guianensis* can germinate in both shade and direct sunlight, thus both in open land areas and on the forest floor (Flores 1994; Nebel 2001), and germination rates are reported to be generally quite high (Flores

1994). According to Young et al. (1987), deforestation stimulate germination from the seed bank, and up to 85 % of the present seeds may germinate after such events. These elevated germination rates can be attributed to favorable changes in light and temperature (Garwood 1989). On the other hand, the short viability of most seeds of tropical trees (Cubiña & Aide 2001; Hopkins & Graham 1987), and the sensitivity of *M. guianensis* seeds to dehydration (Flores 1994), may have decreased the germination rates in open areas where microclimatic conditions may be more stressful than beneath the forest canopy (Holl et al. 2000). Holl (1999), however, recorded equal germination rates beneath pasture shrubs and grasses as in primary forest. The effect of germination on abundance of *M. guianensis* is thus unclear.

Greater abundance of progeny in secondary forest can be attributed to lower mortality rates of seedlings in these plots. When the seedlings escaped the high mortality rates in the early phase of establishment in the secondary forest plots, these young trees experienced greater chances of survival due to declining mortality with increasing size (Clark & Clark 1992). Butterfield (1995) and Hunter (1991) reported high mortality rates for *M. guianensis* progeny in direct sunlight in open land areas. Nebel (2001) and Vieira (1996), on the other hand, reported successful establishment and higher diameter growth rates in full sunlight than in shade. Both Nebel (2001) and Vieira (1996) underlines though that moderate shade was advantageous in the establishment and growth of *M. guianensis*. The discrepancy between the previous studies can be explained by different conditions under which seedlings of *M. guianensis* were planted. Butterfield (1995) and Hunter (1991) both cleared the sites before planting, and Butterfield added herbicides to the planting site. Thus, no shrubby vegetation or grasses were dominant. Nebel (2001), on the other hand, planted *M. guianensis* seedlings in between agricultural crops in the first years of his study.

The advantageous conditions under which seedlings of *M. guianensis* were planted in Nebels's (2001) agroforestry trials, are comparable with the initial site conditions after deforestation in the secondary forest plots. All three secondary forest plots in this study can be categorized as moderate land-use sites, subjected to gentle disturbances only. In sites such as these, where the land is not heavily degraded, and burning has not been implemented, rapid regeneration of pioneer trees and shrubs has been reported (Finegan 1996; Guariguata 1999; Guariguata & Ostertag 2001; Uhl et al. 1988). According to Nebel (2001), light shade present beneath the canopy of pioneer trees has an advantageous effect on seedlings and saplings of

M. guianensis. Seedlings growing in light shade, can be expected to have reduced mortality rates due to increased diameter growth in better light conditions (Flores 1994). Forest slush, forbs, pasture grasses and pioneer trees all have a beneficial effect on the microclimatic conditions in deforested land areas, reducing solar radiation, decreasing soil temperature and water evaporation (Bazzaz & Pickett 1980; Holl 1999; Uhl et al. 1981).

The presence of remnant trees in the three secondary forest plots, would explain higher abundance of *M. guianensis* progeny due to enhanced establishment and growth beneath these trees. Loik and Holl (1998), reported higher germination and establishment of many rainforest tree species beneath remnant trees, than in primary forest and deforested land areas. These differences may be attributed to the positive effect remnant trees have on microclimatic conditions such as; light, temperature and humidity (Guevara & Laborde 1993; Loik & Holl 1998; Rhoades et al. 1998). Seedlings growing in the shade of remnant trees receive 20 times more light than they would in primary forest, and they escape the photosynthetic stress they would have experienced in the open (Loik & Holl 1998).

Herbivory did not have an important effect on the regeneration of *M. guianensis,* as signs of herbivory damage were very rare both in primary and secondary forest (Hunter 1991). According to Ewel (1980) primary forest species are less prone to herbivory attack than pioneer trees. Sleumer (1984) suggested presence of toxic secondary compounds in *M. guianensis*, which causes the leaves to be less palatable.

4.2. Habitat preferences

Crown illumination

Smaller size classes were growing in darker light conditions than larger size classes. These results are consistent with the result found by Clark and Clark (1992) for *M. guianensis* individuals in mature forest stands. The presence of seedlings and saplings in low crown illumination categories indicate that *M. guianensis* can germinate, establish and survive in the forest understory, as was observed by Clark and Clark (2001), who report that the shade tolerant saplings of *M. guianensis* could survive long periods in the forest understory with zero growth. The observation of larger size classes in brighter light conditions, indicate that individuals of *M. guianensis* recruit to greater size classes in microsites with higher illumination, as was observed by Dovciak (2001) for white pine (*Pinus strobus*) in the Great

Lakes region, USA. According to Nebel (2001), higher light levels enhance the growth rates of *M. guianensis*, while the deep shade present in the forest understory may impede growth.

A second aspect which may explain the positive correlation between crown illumination and size class is the fact that light intensity increase with increasing heights above the forest floor (Jacobs & Kruk 1988). This implies that larger size classes will inevitably receive more light simply because they are taller (Clark & Clark 1992).

Crown illumination preferences for *M. guianensis* did not differ significantly between primary and secondary forest. Several studies in Costa Rica and Panama have reported similar light conditions and stand structure characteristics in 15-20 year old secondary forest stands as those found in primary forest stands (Denslow & Guzman 2000; Guariguata et al. 1997; Nicotra et al. 1999). In consequence, the light conditions present in primary forest plots and in the 20 and 45 year old secondary forest plots, were presumably similar, thus no significant preference differences were observed.

Topography and drainage

In primary forest, *M. guianensis* displayed microhabitat preferences for inclined topography, rather than peak and nadir. These results are in agreement with Hunter's (1991) agroforestry trials in the Peruvian Amazon, where he found that seedlings of *M. guianensis* planted on slopes grew significantly better than those planted on level land. He explained this pattern by differences in drainage conditions across the topographical gradient. Cooper (1928) also registered a microhabitat preference for *M. guianensis* for well drained slopes. It has been documented by many that topography has an effect on the soil moisture gradient, and even small topographical variations can have marked effects on drainage conditions (Chapin et al. 2002; Pritchett & Fisher 1987; Svenning 1999; Tuomisto & Ruokolainen 1994). Soils on peaks may be exposed to droughts, while soils in the nadir may be water logged (Ashton 1992). *M. guianensis* individuals growing on the hill side experience thus good drainage conditions while escaping the risk of water stress. This conclusion is in agreement with the observation that all *M. guianensis* individuals displayed a preference for well drained soil.

In addition to soil moisture, topography has an effect on soil nutrients and organic matter (Chapin et al. 2002). Upslope soils usually have lower nutrient levels than soils in the nadir

(Chapin et al. 2002). Preference for uphill microsites may indicate that *M. guianensis* is not sensitive to low nutrients levels, or that the species doesn't survive the harsh competition for nutrients present in the nadir.

In secondary forest there were no significant differences between the number of individuals found on slope and hilltop. These observations could be explained in several ways. According to Clark and Clark (1994), drought is not a limiting factor for tree growth in the Sarapiquí region, as they reported highest growth rates of trees during the driest years. *M. guianensis* individuals found on peaks in secondary forest plots were thus not exposed to drought, and could establish successfully in these sites. Secondly, greater litter depth on peaks due to lower decomposition rates with decreasing moisture levels (Nakane 1975), may have had a beneficial effect on the establishment of *M. guianensis* in the early phase of succession. Thick layers of forest slash are advantageous in the establishment of *M. guianensis* due to their favorable effect on water evaporation and solar radiation (Holl 1999).

4.3. Physical state

Physical damage was present in all size classes of *M. guianensis*, and could be explained through branch-, tree- and litter-fall, which is common in the forest understory (Clark & Clark 1991). In the case of *M. guianensis*, physical damage by herbivore attack was probably not of great importance, as herbivore damage has rarely been observed for this species (Hunter 1991). The percent of healthy individuals was significantly higher than that of damaged individuals for all *M. guianensis* individuals, with the exception of seedlings in secondary forest. This pattern implies that most individuals manage to escape physical damage.

In secondary forest the percent of damage increased with decreasing tree size. According to Clark and Clark (1991), the smaller the tree, the higher is the chance of damage from branch and litterfall. Trees can escape damage through rapid growth (Clark & Clark 1991). As a consequence of the deforestation event and absence of seed trees in the secondary forest sites, it can be assumed that individuals in these plots were even aged.

Seedlings in the secondary forest plots were thus not younger, but were individuals that suffered major growth setbacks due to physical damage. Juvenile trees were the individuals that escaped damage through fast growth. According to Clark and Clark (2001), the time it takes for a *M. guianensis* tree to reach 30 cm diameter, may vary between 38 years with maximum growth rates and no physical damage, to 186 years with mean growth rates which account for physical damage. Arrested seedling growth, is a consequence of repeated physical damage, which may impede recruitment to the adult stage. In primary forest the percent of physical damage did not differ significantly among the size classes, this can be attributed to continuous recruitment from autochthonous seed rain.

4.4. Spatial distribution

Higher rates of clustering and association of progeny with adult trees and trunks in secondary forest than in primary forest can be explained by limited seed dispersal (Aide & Cavelier 1994; Barot et al. 1999; Denslow 1987; Svenning 1999). These results correspond with previous observations by Hunter (1991), who recorded high numbers of *M. guianensis* seedlings beneath remnant trees in pastures, and random distribution of seedlings in the forest understory. Due to observed aggregation of progeny around trunks in secondary forest sites, it can be concluded that these trunks were cut several years after deforestation, functioning consequently as regeneration nuclei in the secondary forest plots (Guevara et al. 1986) in the few years before they too were harvested. The strong association of seedlings and saplings with adult trees and trunks in secondary forest may in addition to limited dispersal rates, be explained by favorable microclimatic conditions present in the shade of these remnant trees (Loik & Holl 1998). Current distribution pattern of progeny in the secondary forest plots thus reflect past distribution of safe sites for germination. The progeny in these plots is expected to be of 20 to 45 years of age, and these assertions are plausible, as saplings of *M. guianensis* may be 60 years old due to the slow growth rates of this specie (Clark & Clark 1992; Nebel 2001).

Elevated rates of seed dispersal and uniform microhabitat distribution may explain the random distribution pattern of *M. guianensis* in the primary forest plots. Seed shadows created by single animal species can cause clustered distribution of seedlings at foraging and roosting sites (Cardoso da Silva et al. 1996; Jordano & Godoy 2002; Julliot 1997). The observed clustering of seedlings in the primary forest plots, whose lack of association with adult trees may indicate possible association with animal roosting sites.

The distribution pattern of *M. guianensis* was less clustered with increasing size. These results are consistent with many other studies (Barot et al. 1999; Dovciak et al. 2001; Oliver & Larson 1996; Sterner et al. 1986), which explain the following differences with density dependent mortality. Individuals growing in dense clusters experience elevated rates of mortality due to higher rates of competition for nutrients, water and light (Barot et al. 1999). With time many of the small individuals growing in clusters will consequently die, leaving fewer, more evenly distributed, older individuals (Oliver & Larson 1996). Density dependent mortality may also explain the observed decrease in association of juvenile trees with adult trees in secondary forest plots.

There are many pattern generating processes; seed dispersal, density dependent mortality and environmental heterogeneity (Barot et al. 1999; Seabloom et al. 2005). The processes influencing the spatial distribution of progeny and adult trees were independent. The distribution of progeny was probably governed mainly by seed dispersal, seed predation and the distribution of safe sites for germination (Dovciak et al. 2001). Dovciak et al. (2001) stated that microsites which are favorable for seedling establishment may not correspond with the microsites favorable for recruitment of adult trees. The previous crown illumination study, displayed a preference for patches with higher light levels for adult trees, implying that individuals recruit to the adult stage only in sites with higher light availability. Seedlings on the other hand can establish in the deep shade of the forest canopy (Clark & Clark 1992). The distribution of adult trees in contrast with progeny was thus governed by density dependent mortality through competition and the distribution of favorable microsite patches.

5. CONCLUSION

It can be concluded that remnant trees played a major role in the regeneration of *M. guianensis* in secondary forest. Higher regeneration rates in secondary forest can be attributed to the advantageous effect of remnant trees on microclimatic conditions present beneath their canopies and lower seed predation rates in their vicinity. Furthermore, the successful regeneration of this primary forest species in secondary forest can be ascribed to the fact that these land areas were not heavily degraded, and propagules were present at the site at the time of the disturbance. If, however, these sites had experienced long history of land use, and neither propagules nor remnant seed trees were present, the regeneration of *M. guianensis* would be limited, or absent.

In the light of these findings, it is advisable to leave seed trees of *M. guianensis*, as well as other old-growth forest tree species, in deforested land areas in order to assist natural regeneration. In areas where no adult trees are present, seeds or seedlings should be planted in the shadows of shrubs, pioneer trees or other remnant trees to restore populations of *M. guianensis* and other old-growth forest tree species.

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