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Canopy Demographics at the Firestone Reserve, Costa Rica

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Canopy Demographics at the Firestone Reserve, Costa Rica

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Abstract:

Though Costa Rica has suffered numerous bouts of deforestation to its valuable tropical rainforest area, especially in the 1970s, it has become a leader in its efforts to regenerate and restore its rainforest. However, studies and protocols for the assessment of forest regeneration are urgently required. Research has shown that the percentage of light penetrating the canopy floor, or light fraction, is a good indicator of rainforest maturity. In this study, digital rectilinear photography and a global positioning system receiver were used to survey the Firestone Reserve in Costa Rica in order to measure the light fraction differences between primary/riparian forest, bamboo plantation, secondary hardwood plantation, and natural secondary regrowth. The images were used to calculate light fractions with the software program ImageJ. Using ArcGIS, a kernel density plot was created, along with a map organizing the light fractions in the vegetation types. Significant differences in light fraction were found between bamboo and all other vegetation types, between secondary natural regrowth and secondary hardwood plantation, and between secondary natural regrowth and primary/riparian forest. No significance was noted between primary/riparian and secondary hardwood plantation, or between primary/riparian and secondary forest. Inaccuracies of the study could be due to the high amount of variance, low sample size, or high levels of sunlight that distort the photographs. Nevertheless, the study provided useful information concerning the differences between vegetation types and has implications towards regrowth and recovery of the rainforest.
Introduction:

In order to minimize human impacts on global climate change, recent policies have been implemented that emphasize the usefulness of tropical forests: they provide services to the environment, according to the World Bank, by means of hydrological advantages, lower sedimentation, disaster prevention, biodiversity preservation, and carbon absorption (Kalácska et al. 2004). While landowners participating in sustainable activities are compensated for their efforts, much of society does not receive monetary reward for conserving the environment. Therefore, people do not have an incentive to consider the unspoken value of the rainforests nor to make cognizant and sensible decisions on their activities. For these reasons, in many locations, especially in the resource-rich tropical rainforests, environmentally destructive activities continue and the environment suffers long-term, fatal damage in exchange for a small, short-term gain.

Costa Rica experienced its maximum extent of deforestation in the early 1970’s and has since seen progressive recovery due to deliberate reforestation efforts and abandonment of agricultural lands (Rosario-Bixby and Palloni 1996; Aide and Grau 2004). During this decade, 4% of the forest area, or 1% of the total Costa Rican land territory, was destroyed each year (Rosario-Bixby and Palloni 1996). The large amount of deforestation correlated with vast population growth. After World War II, Costa Rica’s population grew from less than 800,000 to over 3 million people; this increase was a result of multiple factors including improved healthcare and immigration. Simultaneously during the population boom, 50% of the primary forest was cleared. It is predicted that unless substantial action is taken to decrease population growth, the rainforest is expected to be completely depleted in 50 years. Although it might be too late, the nation’s
environmental agencies have recognized the true value of tropical rainforests and are taking steps to preserve the remaining land and recover the land already used or harvested. Deforestation has numerous negative effects on the environment and its inhabitants including reduction of biodiversity, soil erosion, climate change, and air pollution. More significantly, especially in Costa Rica’s case, most of deforestation is anthropogenic. A majority of the deforestation resulted from the large increases in banana exports, cattle ranching, wasteful logging, and government homesteading policies.

Nevertheless, Costa Rica now recognizes the importance of its priceless vegetation and has become an international leader in its attempts to conserve its precious rainforest.

Costa Rica has made a substantial effort to provide incentives to its developers by creating monetary benefits for sustainable development. Since the Costa Rican rainforest has an exceptional ability to absorb carbon dioxide gas, their new “Certified Tradable Offsets (CTOs)” program, implemented in 1998, allows for the international marketing of the rainforest’s resources (“Certified Tradable Offsets” 2010). It has contributed $150 million dollars over the last 10 years to promote forest management, one of which is by the selling of CTOs, which are certified reductions in net carbon emissions equivalent to one ton of carbon absorbed by Costa Rican trees. In this agreement, programs can develop the land in exchange for purchasing CTOs (Kalácska et al. 2004), meaning that an investor pays an amount to deforest a certain area of land which is equivalent to the number of tons of carbon dioxide gas that the trees in that plot would absorb. Numerous foreign investors have showed interest in the program to fund their businesses established in Costa Rica: Norwegian hydropower businesses have heavily invested in CTOs at low prices, and the United States buys CTOs to benefit Costa Rica’s Protected Areas Project.
(“Certified Tradable Offsets” 2010). The profits from the CTO program allow Costa Rica to buy back rainforest areas from private owners to preserve and restore it. Using CTOs can also help Costa Rica compare different methods of rainforest conservation. By estimating the reduction of carbon emissions in each activity through the amount of CTOs purchased, one can evaluate the advantages and disadvantages of sustainable development mechanisms. Nevertheless, these actual values are lacking due to a limited number of accurate ecological studies (Kálacska et al. 2004).

With the expansion of tourism and textile businesses, Costa Rica has experienced a large amount of migration away from rural lands and from mountainous regions to urban areas (Aide and Grau 2004). Since the need for deforestation for cattle grazing and slash-and-burn agriculture has been reduced, and since the amount of large-scale agriculture has increased tremendously, migrants seeking more lucrative jobs abandon their properties. The urban immigration allows for the areas left behind to be recovered. Conservation and social research and policy should help subsidize urban life for the migrants, promote recovery for the abandoned lands, and attempt to find the best way to recover the depleted agricultural land and preserve the remaining primary rainforest.

In addition to policies like CTOs, Costa Rica has also facilitated the increase of mixed-tree plantations, which have both economic and environmental advantages (Redondo-Brenes, Chiu and Snow 2010). By planting 5-8 different species of trees, including trees natural to the rainforest, mixed-tree plantations help remove pressure from natural forests to support a large number of species competing for limited habitat. Not only do they provide a place for wildlife to live, but the artificial forests also improve soil conditions, sequester carbon, and attract seed dispersers. This policy differs from the
CTO program, which allows unsustainable development if the CTO is purchased; a mixed-tree plantation is a sustainable project meant to benefit the surrounding natural rainforest and its inhabitants. Though these benefits were proved to function only on a small-scale level, the use of native species for mixed plantations nevertheless mimics the natural environment while allowing sustainable tree harvesting; perhaps these “minimal” benefits will improve in the future. All of these projects have furthered Costa Rican efforts for sustainable living. However, a majority of these projects remain unproven due to the lack of evidence supporting their effectiveness (Kalácska et al. 2004). Current ecological studies attempt to quantify the deforested areas and their ability to regenerate once they are allowed to recover.

A promising way of measuring the recovery of formerly-deforested rainforest is by measuring the penetration of light beneath the canopy. Since mature primary rainforest canopies permit little light penetration (Clark et al. 1995), canopy maturity should inversely correlate with the amount of light reaching the forest floor. Additionally, forest areas with large amounts of light penetrating the canopy would cater best to saplings that need increased light for regeneration. On the other hand, increased light availability subsequently amplifies the regeneration of secondary growth. The increase can result from a natural disaster, such as hurricanes or landslides, or from human activities such as bamboo harvesting and oil drilling. By examining secondary forest through a light availability study, one can demonstrate how a forest regenerates from a disaster (Bellingham et al. 1996). Light availability can also be used for photosynthesis and evaporation studies, which are indicators of net primary production. The amount of light penetrating a canopy also has important implications for the nature of the vegetation
and its relationship with species richness, wildlife habitat and behavior (Paletto and Tosi 2009).

However, direct calculation of the presence of light penetration is a time consuming and costly process. Photographic methods were determined to be the most efficient method of measurement for estimating light penetration, since a camera can be easily transported to a large number of sites for efficient surveying (Anderson 1963). The recent appearance of digital cameras and software programs to measure light intensities allow for rapid analysis of photographs (Thimonier, Sedivy and Schleppi 2010).

The most commonly-used way of measuring light penetration is by hemispherical canopy photography (HCP), in which a photography vertically-oriented camera is used to estimate understory light beneath the forest canopy’s tree and shrub layer but above herbs and seedlings. By taking the photograph using a fish-eye lens, an $180^\circ$ view can be captured. Properly calibrated HCP’s can quantify direct and indirect light radiation entering through the openings of the canopy (Bellingham et al. 1996).

After obtaining hemispherical photographs, the amount of direct and indirect light penetrating the canopy layer can be calculated by measuring the number of photons directly and indirectly entering the gap per unit time at different angles though a series of equations, which gives the Leaf Area Index (LAI) (Chen and Chilar 1995). LAI is a dimensionless unit, representing the total area of leaves divided by their underlying ground surface area. It is an appropriate indicator of the surface canopy cover, since leaves are an interface between atmosphere and ecosystem. Measuring LAI is important since the value has an effect on certain physical and biophysical interactions between the surface and the atmosphere, such as light and precipitation interception,
evapotranspiration, CO$_2$ fluxes and dry deposition (Chen and Chilar 1995; Thimonier, Sedivy and Schleppi 2010).

HCP has several drawbacks, though, including the high cost of the equipment, the sensitivity to orientation and leveling, and an inability to handle plots with steep landscape slopes. Hemispherical photography was not used in this study, since the question of the study was simply if light was entering the canopy, not specifically whether the light was direct or indirect. Positioning and leveling the HCP camera would be too time-consuming in order to photograph all quadrants of the reserve. Additionally, high relief in the primary/riparian areas and the secondary hardwood plantation forests would be disadvantageous for hemispherical photography. A more cost-effective, efficient method of surveying and photographing the reserve would be the ideal method to estimate light penetration.

In this study, rectilinear photography, i.e. vertical photography with a regular wide-angle lens, was used to measure the amount of light penetrating the canopy. The photographs were analyzed using a program called ImageJ, which avoids the complex, time-consuming and sometimes inaccurate LAI calculation. LAI calculations are affected by non-flat leaves, which dominate tropical forests; measurements of LAI can only be estimated by assuming a projection coefficient of non-flat leaves as a constant of 0.5 (meaning the LAI was half for non-flat leaves) (Chen and Black 1992). However, analysis using ImageJ is a simple solution to avoid the tedious calculation of LAI, since it rapidly processes the image to provide the percent of light entering the canopy.

The landscape where the method was tested was the Firestone Center for Restoration Ecology (FCRE). The FCRE was originally a lowland tropical rainforest,
which was converted into farmland for cattle grazing during the 1950s and 1960s. Since 1993, the FCRE was allowed to recover, and it was also reforested with native and exotic bamboo species (Redondo-Brenes, Chiu and Snow 2010). The property is divided into various hardwood, banana, peach palm and bamboo plantations, most of which are still harvested, in addition to naturally regenerating secondary forest and primary/riparian areas (Redondo-Brenes, Chiu and Snow 2010). Since Pitzer purchased the reserve in 2005, faculty and students have traveled there to perform Ecology studies (“Firestone Center” 2009).

The term light fraction was defined as the percent forest area that is not occupied by overstorey cover, or tree crowns. This means that light can penetrate the forest floor to facilitate new growth. By comparing light fraction in different types of forests, such as primary versus secondary forests, one can make inferences about the productivity of the area as well as develop insight on certain interactions between the surface and the atmosphere (Chen and Black 1992).

Specific Aims

The objective of this study was to compare light fractions between four vegetation types on the reserve: bamboo plantation, secondary forest (including natural secondary regrowth and hardwood plantation), and primary/riparian forest through a basic rectilinear photography survey. Locations of the photographs were elected by random sampling within each 1-hectare grid square of the 60-hectare reserve in order to avoid the subjective selection of “good” gaps. A minimum of 10 photographs were to be taken in each complete 1000m² quadrant. After analyzing these images on ImageJ, the ArcGIS program was used to create maps that indicate the photographic locations along with the
corresponding vegetation type. The primary goal was to find significance between the
light fraction and each vegetation area. It was hypothesized that the primary/riparian area
would have a significantly lower light fraction than the secondary natural regrowth and
artificial bamboo forest, since the primary/riparian area has not been disturbed and has a
significant amount of time for canopy trees to grow and compete for light. However,
since the secondary hardwood plantation is artificially created to mimic the natural forest,
it will not differ from the primary/riparian light fraction. Significance was also
hypothesized between the secondary forest types and the bamboo forests, due to the
difference in vegetation. Due to the fast-growing nature of bamboo and natural secondary
regrowth, and because high light fractions indicate high amounts of productivity, it was
predicted that these two vegetation types would have the highest light fractions. Notable
differences between different types of forest can confirm varying productivities of
tropical forests and have insights towards their regeneration. Another goal of the study
was to evaluate rectilinear photography as an appropriate technique for measuring light
fraction.
Methods

Study Site
The research was performed at the Firestone Center for Restoration Ecology in Costa Rica, a 60-ha reserve in the Barú district of southwestern Costa Rica (Redondo-Brenes, Chiu and Snow, 2010; Fig. 1). This tropical lowland moist forest is dominated by secondary growth, since a majority of the land was cleared for cattle grazing, and then beginning in the early 1990’s, for tree and bamboo plantations. The rainfall is approximately 4100 m/year, and the annual temperature ranges from approximately 23 – 33°C (Redondo-Brenes, Chiu and Snow 2010). The elevation varies from circa 5m to 303m above sea level (Roberts et al. 2009). Further information about the FCRE can be found in the website (http://costarica.jsd.claremont.edu/). Measurements were taken for a total of 44 days between June 2 and July 15, 2010.
Figure 1. Location of the study area within the tropical lowland moist forest at the FCRE. Solid black lines indicate the Access Road which can be navigated by vehicles. Two main rivers run through the reserve, the Terciopelo Creek and the North Creek. The reserve is bordered by fences on the western sides by fences and on the eastern sides by fencing and by two rivers, the Quebrada Cacao and South Creek. Scale bar is in meters (Roberts et al. 2009).

**Field Measurements**

The light fractions were determined using two variations of indirect methods. The first method involved taking sets of 5 rectilinear canopy photographs using a GPS unit to note the UTM only at the starting location and determining the locations of the subsidiary points by measuring off 25 meters east, 50 meters south, 50 m west and 50 m north (Fig. 2) – this method was used between June 2 and June 6, 2010*. The second method used a Juno Trimble GPS unit at all photographic locations; this process was used between June 7 and July 15, 2010. All photographs were taken with an Olympus FE-4000 digital
camera, with the lens set at 26mm focal length. The effective field of view at 10m subject
distance is 3.46m horizontal and 2.31m vertical (Atkins 2010), or $8m^2$ of canopy area.

**Figure 2.** Walking pattern for canopy photographs between June 2 and June 6, 2010. The
ant image represents the starting point in which a GPS measurement was acquired.

Using the GPS unit and a compass, the randomly selected starting point of the
first photograph was determined by navigating to an area within the desired grid. The
“grids” were derived from a map of the reserve that was imported to the GPS unit. After
reaching the starting point, the camera was leveled with the lens facing upward at a
height of 1m using a tripod. Minimum height for the vegetation to be determined as
“canopy” was set to approximately 2m (vegetation was manually removed if the height of
the canopy was below this level). The camera was aligned so that the left side of the
image was oriented to the north. The camera was set at the maximum wide angle (26mm)
to photograph the largest amount of forest canopy possible. In order to prevent the
camera from shaking, a 10s timer was used to take the photo. The camera was set to
automatic exposure in order to derive the best contrast in the photographs. The resolution of the photos was 3968 x 2976 pixels (Fig. 3).

The process was repeated 4 more times to create a set of 5 photos, once after walking 25 paces north, then 25 paces east, then 50 paces south, then 50 paces west. However, the pacing was more of a set of guidelines, and certain conditions induced the number of paces to vary. If the number of paces was not able to be completed due to obstacles such as cliffs or rocks, the photo was taken 5m before pacing could not continue. If no vegetation was present over the point after the desired number of paces, pacing was continued until a canopy was reached.

*Between June 1 and June 7, 2010, the process was conducted with a GPS unit at the starting location of each set of five photos. The number of paces taken from the starting point remained the same (25 paces north, 25 paces east, 50 paces south, 50 paces west). The paces were predetermined by taking an average meters traveled of a few tests of 25 paces. The paces averaged 17.7 meters/25 paces, or 0.708 meters/ pace. The process was always conducted with the original photo then walking exactly 25 paces north, 25 paces east, 50 paces south, and 50 paces west. If an obstacle, such as a tree, was encountered during the pacing, the obstacle was avoided by walking around it. Pacing was continued on the other side of it, and the amount of paces through the obstacle was estimated. The exact pacing methods were used this week, rather than the subsequent weeks since the GPS location was only taken at the starting location. The GPS locations for the starting point were converted from degrees to UTM, and the locations of the other 4 photos in the set were calculated using the pace average of 17.7m/ 25 paces.*
Fig. 3. Canopy photograph of bamboo forest. Photo 206. Date taken: June 10, 2010.

**ImageJ analysis**

Each photograph underwent an ImageJ (http://rsbweb.nih.gov/ij/) analysis in order to determine the light fraction. The image was converted to an 8-bit grayscale in order to improve contrast and brightness between the canopy cover and the penetrating light. The image was thresholded (i.e. converted to a 0/1 two-point grayscale), and the image was inverted. This was done to create the optimal contrast between light fraction (rendered red) and understory canopy cover (rendered white) (Fig. 4). Because the ImageJ thresholding method corrected a majority of the sun reflection on the leaves and branches, this process improved the light fraction analysis (Paletto and Tosi 2009). The measurements were set to measure the area fraction of the image, and the image was analyzed, giving a percent representing the light fraction.
Figure 4. Canopy photograph of bamboo forest upon analysis with the ImageJ program. Photo 206. Date taken: June 10, 2010. Image analyzed June 10, 2010.

**Centroids**

Using the UTM coordinates provided by the GPS measurements, an XY coordinate (indicating the latitude and the longitude of the photo) was found for the locations of each photograph taken. In each set of 5 photographs, the average of the XY coordinates of each photo was determined, creating a centroid location, which was paired to the average light fraction for the 5 image set.

**Outlying Data**

The mean and standard error of the light fractions was taken for each set of 5 digital photographs. If a photograph exceeded 90% of the standard error, its GPS
location and light fraction were removed from the data set, and the centroid and average light fraction were calculated from the remaining data points.

**Blooming effect and Light Reflection**

When light saturation leaks onto adjacent pixels, this creates a “blooming” effect on digital photographs (Leblanc et al., 2005; Thimonier, Sedivy and Schleppi 2010). When this occurs, the light fractions were calculated as larger than their actual value since it gives the appearance of blurry or “fuzzy” areas of the canopy (Thimonier, Sedivy and Schleppi 2010). The blooming effect was corrected on *significantly* skewed images by painting over the pixilated areas using the Paint application on Windows 2000. By painting the distorted part of the image black, when it was analyzed in the ImageJ program, it would recognize it as foliage cover and not as a light fraction. It was also found at times that light would reflect onto some of the leaves, which would also make the light fraction appear larger than its true percentage. When the data was being analyzed for obvious outliers, these reflections were targeted and painted over using the Paint program before their images were analyzed on the ImageJ program. If the blooming or the reflections could not be corrected, the image was discarded.

**Creating data maps using ArcGIS**

With the ArcGIS program, along with the data taken from the GPS unit, locations of all the photographs (n=720) on the FCRE were mapped using the 2009 map of the FCRE (Fig. 1).

After the images were edited for blooming effects and outliers were removed, an additional map was created graphing the centroids (n=140) of each set of five
photographs on a map. These points were arranged (latitude longitude average) on a layer above the FCRE map.

Interpolation of the points was used in order to illustrate a continuous surface of percent light fraction in a kernel density plot. Green surface areas correspond to low light fraction, while gradual white, orange to red indicate regions with high light fraction.

In order to pair the centroid points in their respective vegetation types, the 2006 FCRE image (Fig. 5) was used, since it showed the clearest divisions between different types of vegetation. Using the GIS program, the areas in the reserve were separated to indicate bamboo, primary, riparian, and secondary (including the specific sub-categories hardwood plantation and natural regrowth) forests. In order to identify the riparian area, the GIS program was set to select the river and add 15 m to each side. The centroid points were placed onto a layer above the map indicating the vegetation types, and the points were grouped into the separate vegetation categories.
ANOVA and T-Test Analysis

After the 140 centroid points were calculated and grouped in to their respective vegetation types on the ArcGIS map, a 1-way analysis of variance (ANOVA) was performed in order to determine differences between the type of vegetation and light fraction. There were 4 sample types used in the first analysis (bamboo, primary/riparian, secondary hardwood plantation, and secondary natural regrowth), and an independent, standard weighted-means analysis was used. For the results that were determined to be significant, a Tukey HSD analysis was performed to find out which two specific vegetation types displayed significant differences. Similar ANOVA tests were performed comparing bamboo, primary/riparian and all of the secondary forest locations combined.
T-tests were performed to find significance between secondary hardwood plantation and secondary natural regrowth, as well as between primary/riparian and the combined secondary forest locations, between primary/riparian and secondary natural regrowth, and between primary/riparian and secondary hardwood plantation.
Results:

Data Collection
A total of 720 photos were taken in all quadrants of the reserve. At least 10 photos per hectare were taken. The ArcGIS image in Fig. 6 displays the locations of all the photos taken using both photographic methods on the reserve between June 2 and July 15, 2010. The GPS locations of the photographs indicate that the majority of the reserve was photographed, in various types of vegetation (Fig. 6).

Figure 6. Locations of canopy photographs within the Firestone Reserve, June 2- July 15, 2010 (n=720).

Kernel density plot
The kernel density plot (Fig. 7) shows a continuous gradient of the various amounts of light fraction throughout the reserve using an interpolation of the light fractions of each photo. The various colors, ranging from red to dark green, represent the
gradient of the light fractions. The red color represents the areas with the largest light fraction of the maximum 58%, followed by orange, white, light green, and dark green representing the areas with the least light fraction of the minimum 7% (Fig. 7). The areas with the largest light fraction are represented on the western corner of the density plot, while the areas with the smallest light fraction tend to be located near the rivers and on the southwestern area of the reserve (Fig. 7).

Figure 7. Kernel density plot of the light fractions (n=720). Image prepared November 26, 2010.

Grouping the centroids using ArcGIS

All of the photos were analyzed using the ImageJ program, and average light fraction was recorded. After the images were edited for the blooming effect, light
reflection, and outlying data was discarded, the centroids were calculated, generating a total of 140 points. After each group of photos was condensed into centroid points, the GIS map was created to indicate the various vegetation types on the reserve (Fig. 8). The light green color on the western corner indicates bamboo forest, light purple indicates primary forest, light blue indicates riparian, peach indicates secondary forest (excluding secondary hardwood plantation and secondary natural regrowth), sea green on the southwestern area of the reserve indicates the secondary forest sub-category hardwood plantation, and the lilac color towards the middle of the reserve indicates the secondary forest sub-category hardwood regrowth (Fig. 8). When the GIS layer distinguishing vegetation types was combined with the GIS layer indicating the 140 centroid points for average light fraction, the locations were able to be classified into the different vegetation types (Fig. 8). It was found that 16 locations were identified as bamboo, 24 as primary/riparian forest, and 100 as secondary forest (with 8 as hardwood plantation and 11 as natural regrowth) (Fig. 8).
ANOVA and Tukey HSD analysis

The greatest average light fraction was in bamboo forest, followed by secondary natural regrowth, all secondary forest values, primary/riparian, then secondary hardwood plantation (Table 1). The average light fraction was 36.00% for bamboo, 27.45% for primary/riparian, 28.68% for all secondary locations, 26.55% for secondary hardwood plantation and 30.31% for secondary natural regrowth (Table 1). When bamboo, primary/riparian, hardwood plantation and natural regrowth were analyzed using an ANOVA test, there was a significant difference found between the four vegetation types (Table 1; ANOVA, p < 0.0001). These results were further analyzed by a Tukey HSD test to determine which vegetation types displayed significant differences. The bamboo forest
had a very significantly greater light fraction than primary/riparian and secondary hardwood plantation (Table 1; Tukey HSD, p<0.01). Bamboo forest was also observed to have a significantly greater light fraction than secondary natural plantation (Table 1; Tukey HSD, p< 0.05). No other significant differences were noted using the Tukey HSD test. There was also a high level of variance noted for each of the vegetation types, especially in bamboo plantation and natural secondary regrowth (Table 1).

**Table 1.** Relationship between vegetation type and average light fraction (±SE and variance) (n=140).

<table>
<thead>
<tr>
<th></th>
<th>Bamboo (n=16)</th>
<th>Primary/Riparian (n=24)</th>
<th>Secondary (n=100)</th>
<th>Hardwood Plantation (n=8)</th>
<th>Natural Regrowth (n=11)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean light fraction (%)</strong></td>
<td>36.00 ± 1.17</td>
<td>27.45 ± 0.77</td>
<td>28.68 ± 0.40</td>
<td>26.55 ± 1.049</td>
<td>30.31 ± 1.2475</td>
</tr>
<tr>
<td><strong>Variance</strong></td>
<td>43.77</td>
<td>14.05</td>
<td>15.68</td>
<td>8.80</td>
<td>17.12</td>
</tr>
</tbody>
</table>

**T-test analysis**

A two-tailed T-test indicated that secondary natural regrowth had a significantly larger light fraction than secondary hardwood plantation (Table 1; T-test, p<0.05). The T-test did not find significance between primary/riparian and secondary forest (Table 1; T-test, p>0.05). Similarly, when primary/riparian forest was compared to the secondary forest sub-categories, no significance was discovered with hardwood plantation (Table 1; T-test, p>0.05). However, when primary/riparian forest was compared to secondary natural regrowth, primary/riparian displayed a significantly lower light fraction when a one-tailed T-test was performed (Table 1; T-test, p<0.05), and a slightly significant lower light fraction when a two-tailed T-test was performed (Table 1; T-test, p<0.08).
Discussion:

Surveying the reserve

In order to quantify the amount of light penetrating canopy floors in closed and open canopy areas, a large number of studies have employed various photographic techniques in tropical wet and moist forests, and these methods have been evaluated for effectiveness (Anderson 1963; Bellingham et al, 1996; Clark et al. 1995; Kalácska et al. 2010; Paletto and Tosi 2009; Thimonier, Sedivy and Schleppi 2010). It has been determined that despite differences in the mechanisms of photographing the canopies and analyzing the results, the data have yielded consistent results (Clark et al. 1995). The data acquired in this study, similarly, also corresponds to data acquired in prior research: the light fraction entering the canopy floor mostly varied between 8% to about 45% (excluding bamboo plantation which was not surveyed in prior research) (Fig. 7), was very similar to the percentages noted in the Clark et al. (1995) study, which ranged between 5% and 40%. Additionally, less than 30 images were discarded from the original set of 720 photos, and less than 10 were edited using the paint program. Due to its comparability in light fraction data to other photographic methods, a relatively small need for image discarding and editing, and improved speed, cost and efficiency, rectilinear photography seems to be an appropriate method for measuring light penetration.

A majority of the Firestone Reserve was photographed (Fig. 5) in all of the quadrants, proving that the survey was comprehensive for the four main vegetation types on the reserve: bamboo plantation, primary/riparian, secondary hardwood plantation and natural secondary regrowth. Since the methodology of photographing the area involved selecting at random a point in the desired quadrant located by the GPS and taking set
numbers of paces in a specific pattern, subjective classifications of light fractions were avoided. Because of the random sampling of the reserve, the data can be deduced to larger-scale interpretation (Clark et al. 1995). Additionally, using rectilinear digital photography on the sloped Firestone Reserve seemed to be more advantageous and efficient than hemispherical photography. The large amount of sloping, especially in the riparian area of the reserve, did not limit the data collection nor the determination of light fraction since only a vertical, directly upward shot was taken. On the other hand, hemispherical photography in these areas would have shown skewed results.

When the light fractions of each photograph were organized in the kernel density plot (Fig. 7), the results accurately matched the hypothesis. The red color, indicating a high light fraction, was most prevalent in the bamboo forest and natural secondary regrowth areas on the western part of the reserve (Fig. 7). The darker green areas, which signify areas with low light fraction, were mostly present in areas around rivers and in the secondary hardwood plantation area on the southeastern area of the reserve, which also confirms the hypothesis that both of these vegetation types would have lower light fractions (Fig. 7).

**ANOVA, Tukey HSD, and T-test interpretations**

ANOVA, Tukey HSD and T-test both confirmed and negated the significance of the differences in light fractions between the four vegetation types. The area classified as bamboo had a higher light fraction than primary/riparian and all classifications of secondary forest, proven by the ANOVA and Tukey HSD analysis (Fig. 8; Table 1), which supports the hypothesis. Because bamboo has a characteristically rapid rate of growth by its method of exponentially increasing its number of shoots per plant and does
not use a dense leaf system for photosynthesis and growth, it was expected that an increased amount of light would penetrate through the bamboo canopy and towards the floor (Table 1).

A T-test indicated that the secondary hardwood plantation had a significantly lower light fraction than natural secondary regrowth, which is an accurate differentiation between artificial and natural secondary forest, respectively (Table 1). While primary forest tends to have several canopy layers that block light penetration from reaching the canopy floor, larger trees and stumps (which is also characteristic of hardwood plantations), secondary forest grows in a thicket-like, sunlight-loving structure, with a smaller amount of trees or large stumps (Marks 1995). The thicket structure would allow more light to penetrate for high levels of productivity and fast recovery, whereas an artificial hardwood plantation would grow large, leaf-bearing trees that would more aggressively compete for sunlight. Though older natural secondary growth forest would eventually develop larger canopy trees, the Firestone Reserve is a young forest with immature natural secondary growth and would not exhibit this type of older growth.

Similarly, T-test results yielded no difference between primary/riparian forest and secondary hardwood plantation (Table 1). The purposeful planting of canopy trees in the secondary hardwood plantation mimics the surrounding old-growth rainforest, which predominantly consists of large canopy trees as well. Since the two forests have similar, large trees growing and competing for light, there was no difference expected between the two vegetation types. This result also has positive implications towards mixed-hardwood plantations mimicking the natural habitat. Since the hardwood plantation has no significant differences in light fraction from the natural old-growth forest, perhaps the
area imitates the natural habitat in a way that would be suitable for wildlife inhabitants (Redondo-Brenes, Chiu and Snow 2010). Because the light fractions of primary/riparian forest and the hardwood plantations are similar, this does not explain the reasoning for the lack of wildlife habitat in the mixed-plantation forests. The reason wildlife do not amply inhabit the mixed-plantation forest could possibly be due another factor, perhaps one that has so far went unnoticed. A similar light fraction between natural forest and an artificial plantation, along with similarities in other biological factors, could be used as a determining factor of whether an artificial environment could be used as wildlife habitat.

On the other hand, primary/riparian forest was found to have only a slightly significant lower light fraction than natural secondary regrowth in a T-test analysis (Table 1). Although a significant result was expected in the hypothesis, it is believed that with a larger sample size- natural secondary regrowth was only classified within 11 centroid points- the difference in light fractions has a greater chance of being significant. Clark et al. in his 1995 study noted that “The number of samples necessary to describe structural features of a landscape with given accuracy is proportional to the variance of the variable of interest”. Since the average light fraction for each vegetation type had a large amount of variance, a larger sample size is needed for a more accurate study (Table 1). This study erred in acquiring large sample numbers due to the low number of centroid points for secondary natural regrowth (n=11) and secondary hardwood plantation (n=8) despite a high amount of variance (Table 1). This resulted from the random sampling of the reserve, since the vegetation types were designated after the photographs were acquired. It is suggested that the vegetation types be classified using ArcGIS before the field measurements are conducted; this way more photographs can be taken in areas with a
specific vegetation type that is condensed into a smaller area unlikely to be photographed by random sampling. Random sampling can still occur in each vegetation type by locating with a GPS to any point within the vegetation.

Additionally, when all of the secondary growth locations were combined and a T-test was conducted, no difference was noted between primary/riparian and secondary forest (Table 1). This could be the result of the large number of variance within the two samples, but it could also be a result of separating the two vegetation types. Since the designations between primary and secondary forest were estimated by using GIS to map out the areas from the 2006 birds-eye map of the reserve (Fig. 5), it is likely that the categorization between the two vegetation types was inaccurate. Additionally, the designation of secondary forest was too broad since it includes both natural (regrowth) and artificial (hardwood plantation) types of secondary forest, which are very different environments, as proven by the T-test which indicated a significant difference between the two vegetations (Table 1). Again, it is recommended that additional photographs be taken in the primary/riparian areas and in the specific secondary forest subcategories (hardwood plantation and natural regrowth) due to the high amount of variance in the results and low availability of these vegetation types in the reserve. It is also recommended that additional photos be taken in the Hacienda Barú, which has additional areas of primary/riparian and natural and artificial secondary growth, in order to provide additional useful data for this study.

**Effect of weather on rectilinear photography and light fraction**

When the images were analyzed on ImageJ, it was noted that the most inaccurate light fraction calculations resulted on days with high levels of sunlight. It was most likely
on sunny days that the “blooming effect” would result, or that light would reflect on parts of the vegetation, which indicates a higher light fraction than the true value. This is one particular disadvantage of using rectilinear photography as opposed to hemispherical photography. Blurring pixels on a rectilinear, digital photograph, after analysis with ImageJ, would induce a higher light fraction because rectilinear photography captures diffuse as well as direct light radiation. Digital rectilinear photography not only makes light fractions appear larger than they really are, but the same lens on different cameras may also yield significantly different light fractions (Thimonier, Sedivy and Schleppi 2010). Hemispherical photography, on the other hand, is more adept in correcting this flaw since it only observes light that directly penetrates the canopies (Bellingham et al. 1996). Even on a clear day, high level clouds (or presence of a single cloud) can also produce variations in the light fractions using rectilinear photography. It seems as though a cloudy day is ideal; on these days, the photographs exhibited less blooming and/or light reflection, which yield less need for image editing for more accurate light fraction determinations.

**Conclusions and future experiments:**

Due to its comparable calculated light fractions to other photographic methods, minimal need for image discarding and editing, and improved speed, cost and efficiency, rectilinear photography might be a more appropriate method for measuring light penetration. Bamboo plantation and natural secondary regrowth, respectively, had the highest light fractions, which correlates with their rapid rate of growth and high levels of production. Primary/riparian areas were found to have smaller light fractions than natural secondary growth. However, because hardwood plantation has similar vegetation to
primary/riparian forest, the lack of significance between the two was expected. Additionally, the lack of significance between primary/riparian and all secondary forest classifications could be due to an overly broad classification of secondary forest. This was demonstrated when secondary hardwood plantation was found to have a significantly higher light fraction than natural secondary regrowth.

This study has specific implications canopy demographics of different types of rainforest vegetations by means of varying light fractions. A majority of the hypotheses was proved by the results, meaning that measuring light fraction is a good indicator of vegetation type and productivity. Not only does it identify various light fractions between different types of vegetation, but it allows one to predict the rapid, sun-loving secondary regrowth of a rainforest after it suffers from a disaster, whether it would be natural or human-caused.

Future studies on the Firestone Reserve could attempt to find other differences between vegetation types in concert with this study. Two promising options are measuring canopy heights and diameter at breast height (DBH) and comparing these results between the different vegetation types. High canopy heights would be expected in the primary/old growth forests and hardwood plantations, since they yield large canopy trees that compete for sunlight, and lower canopy heights would be expected in secondary forest and in bamboo plantation, since these species favor higher levels of sunlight and thus do not have to grow to compete for most light. Additionally, because the secondary forest has had lesser time to recover, it is expected that it would have a lesser canopy height. Similar results would be expected for DBH, which would vary based on age and type of vegetation in the forest.
Studies could also be furthered from the Redondo-Brenes, Chiu and Snow (2010) study on mixed tree plantations. Though it is known that birds tend to habitat natural species, such as *T. amazonia*, more frequently than nonnative species such as *Tectona grandis*, perhaps light fraction is also a factor affecting their habitat selection. Though light fraction was not proved to be different between primary/riparian and secondary hardwood plantation in this study, which implies that light fraction should not affect wildlife inhabitation, more research specifically targeting this difference should be conducted. The light fraction could be compared between the different mixed-tree plantations and to primary and riparian forest. Perhaps the success of the mixed plantation for inhabiting wildlife would correlate with light fractions most similar to the light fractions of primary old-growth and riparian forests. If there is no correlation found, this would indicate that the discrepancies in wildlife inhabitation are due to another factor. This study could further research on the ecological benefits that human-modified landscapes could provide.

Finally, this study could be repeated in 5 to 10 years to evaluate how the canopy demographics have changed. Since the secondary forest will have had more time to recover, it could increase the amount of old-growth type canopy trees, which would yield a lesser significant difference between primary and secondary forest. Additional photos could be taken in Hacienda Barú to acquire more data on primary/riparian and secondary forests for light fraction calculations.
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References


