

Light interception and use strategies of coexisting tree species in a forest on
Yakushima Island, Japan

by

Jema Buenaventura Tiel-Saluña

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Abstract

Light is a critical factor for plant growth. Taller plants can pre-empt light energy and suppress growth of shorter plants, which is understood via one-sided competition. Yet, many species coexist along the vertical gradient of light in forests. Different plants employ different strategies to acquire and use the available light. Such differences influence not only the structure of the plant themselves but also of the species composition of the forest.

For this study, we aimed to quantify the differences in how plants efficiently intercept and use light in relation to aboveground growth. To do so, we used a new technique to measure leaf area density of the canopy and calculate canopy light interception in a non-destructive way.

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Chapter 1: Introduction

There are long standing questions in forest ecology, e.g. how can many different plant species coexist with each other in a forest? What mechanisms drive diversity and coexistence in forests? These questions have led to studies that come up with several ecological and evolutionary theories about diversity and coexistence. The different theories on diversity and coexistence are based on different approaches and perspectives. These approaches look at genetic factors, physiological responses to different environmental stimuli, resource competition, canopy structure, among others.

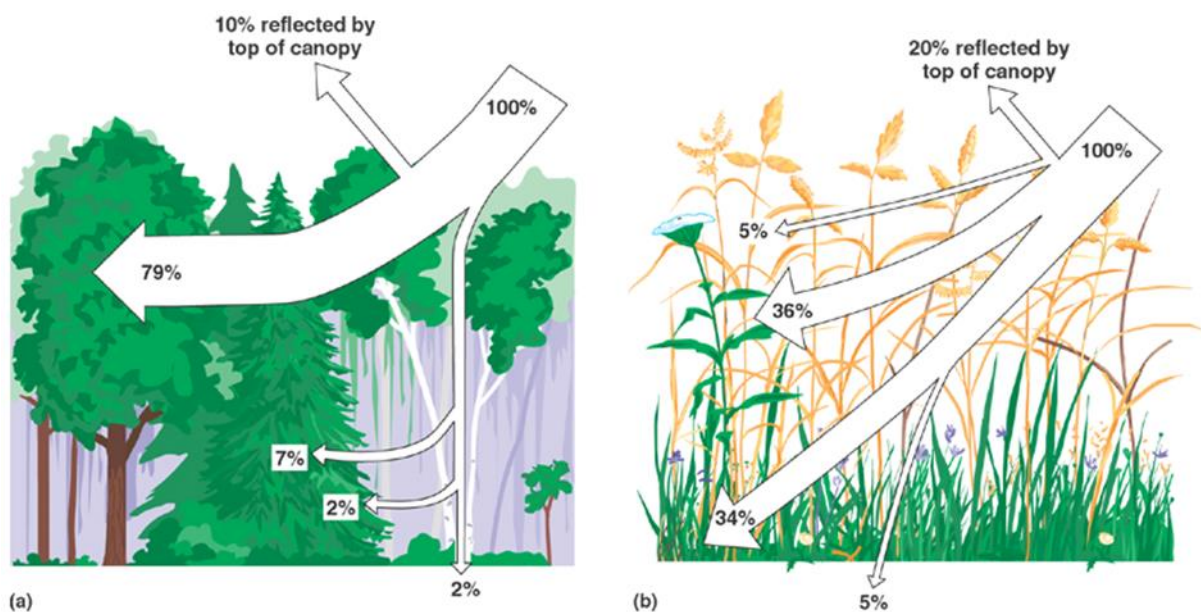
Multiple species of plants coexist in a given space and species composition changes with heterogeneity of environment and along succession stages. There are a large number of studies on coexistence mechanisms along horizontal heterogeneity, yet coexistence along vertical heterogeneity (e.g. light gradient) is much less understood. Light is essential for photosynthesis and plant growth; thus light interception strategies and effective light utilization are vital for all autotrophic plants. As such, light competition is one of the factors influencing diversity and coexistence of plants in forests.

Light attenuation

Light is the ultimate source of energy for plants driving photosynthesis. In a forest, light environment is different – both vertically and horizontally. The distribution of light within the canopy is influenced by vegetation types, leaf area index, and leaf angles (Schäfer & Dirk, 2011). Light levels are also subject to other factors such as diurnal and seasonal changes. Plant cover changes the light environment underneath it (Monsi & Saeki, 1953; Baldocchi, 2012). The type of plants making up the cover can have an effect on how much light reaches the ground (Bartemucci et al 2006). Sunlight reaching the ground through gaps in the crown or upper canopy – also referred to as sunpatch or sunflecks, depending on the duration – is important for small growing plants (Chazdon and Pearcy, 1991). For example, in dense forest stands one expects less light penetrating through the canopy. What the light environment is within a stand is important as this is related to the photosynthetic capacity of vegetation.

In forests where both tall canopy plants and small subcanopy and understory plants co-exist, mechanisms of light competition and the efficiency of light-use of plants need further understanding. Light in the forest is a resource that plants compete for (Grime, 1977). Thus, light attenuation in the canopy has been the subject of much research because of its role in determining the structure, distribution and coexistence of plants. Only about 0.5% - 5% of incident light reaches the forest floor (Chazdon and Pearcy, 1991; see Figure 1). It is thus critical that plants develop strategies to capture light. Several studies have centered on empirical growth of plants to harness light, focusing on crown architecture, plasticity, and allometric growth patterns (Kohyama, 1986; Ackerly & Bazzaz, 1995; Takahasi et al 2001; Valladares 2002; Sterck et al 2005). Other studies emphasize the differences in leaf traits or leaf nutrient use based on the physiological responses of plants to changing light environments (Wright et al 2006; Van Kuijk & Anten 2008). In addition, differences in responses to light can also be seen in plants from different functional groups (Kamiyama et al 2010; Niinemets 2010), which points to inherent characteristics that can determine how plants respond to light.

Figure 1. Light distribution in a forest (a) and in a meadow (b).



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As plants compete for light, light attenuation means that plants need to invest in height in order to capture light (Schwinning and Weiner, 1998). For example, saplings growing below

canopy need to either increase leaf area to increase photosynthetic production or increase plant height to reach better light environments (Takahashi et al, 2001). It was shown that lateral-growth species invests in crown development while vertical-growth species invests in trunk growth (Takahashi et al 2001; Poorter et al 2006). However, being tall also has its disadvantages because being tall means plants need to allocate more resources for maintenance and support (Falster and Westoby, 2003; Yadun, 2005). Nevertheless, does this mean that taller plants are indeed more efficient in capturing light than smaller plants? Furthermore, the fact that smaller substory and understory plants co-exist with taller canopy plants implies that although plants are not able to reach the top canopy they employ other strategies that could help them to survive, grow and reproduce in limited light availability under their taller neighbors (Keuskamp et al, 2010).

Light interception efficiency (LIE)

Comparing how plants utilize light resource for growth can provide insights for species coexistence in plant community. Hirose and Werger (1995) have proposed a way to compare how plants efficiently use biomass to capture light. They defined Φ_{mass} as the efficiency by which plants invest biomass in capturing light. This is also known as light interception efficiency (LIE) of plants. Φ_{mass} is the product of Φ_{area} and LAR (leaf area ratio). They defined Φ_{area} as the captured light per unit leaf area and LAR as the ratio between total leaf area and aboveground biomass. Their study showed that although tall and dominant species captured more light resulting in high Φ_{area} , their Φ_{mass} was not necessarily high. Their results also showed that this was because of the negative correlation between LAR and Φ_{area} which was interpreted as a trade-off between benefit (light) and cost (supporting biomass). This trade-off comes about because to achieve a high Φ_{area} plants need to invest on supporting biomass to place their leaves on top of the canopy to receive more light. Their study further showed that smaller subordinate species compensated for lower light capture with higher leaf area ratio (LAR). Similar mechanism so far has accounted for the variations within monospecific stands (Anten & Hirose, 1998) and young secondary forest (Selaya et al, 2008). Thus, plants can have different Φ_{mass} values – that is LIE – which can be regarded as a reflection of the different strategies that plants use to effectively capture light. This has implications in the coexistence of species in a certain stand.

Light use efficiency (LUE)

Stratification in the canopy effectuates light variability. As light travels from the top of the canopy to the floor, several layers of foliage capture the available energy. The efficiency at which plants transform captured light into biomass is referred to as light use efficiency (LUE). It has been observed that a linear relationship exists between the amount of dry matter produced by a plant stand with the amount of light energy intercepted by the foliage canopy (Monteith, 1977; Charles-Edwards [1982] as cited in Cannell, 1989). Controlled studies involving monocultures with abundant nutrient source show that plant dry matter increase over time with increased intercepted radiation attributed to an increase in leaf area (Kiniry, 1998; Mariscal et al, 2000; Merilo et al, 2006). However, only a part of the solar energy is converted to plant dry matter. This loss in energy transformation can be attributed to several factors such as respiration, quantum efficiency of photosynthesis, reduction in the net rate of photosynthesis due to limited resources such as CO₂ or water or enzymes, among others (Monteith, 1972; Cannell, 1989; Binkley et al 2004). Moreover, some studies show a decline in plant growth rate in mature forests. Niinemets (2010) argued that increase in plant size and age leads to higher leaf dry mass per unit area, lower biomass allocation to foliage, higher foliage aggregation, thus leading to decrease in both LAI and LIE. However, a study conducted by Xu et al (2012) in *Quercus*- dominated forest show that this decrease in stand biomass accumulation may simply be due to loss of large, dominant trees. Nevertheless, no studies so far have been conducted on plant growth rate in primary forests where there is limited resource and multiple species exist.

LIDAR system

The past decades saw the development of non-destructive methods of characterizing canopy structure through remote sensing technologies. One such method uses light detection and ranging (LIDAR) systems that measures distance using pulsed laser light's time of travel (Parker et al, 2004). Manual methods of canopy measurements can be laborious or may involve destructive way of collecting samples from a stand. Moreover, it also means only a limited area of stand can be measured at a given time. Newer types of sensing technology can rapidly measure distribution of forest canopy over a broad range of area (Lefsky et al., 1999). However, most remote sensing technologies are airborne or space-based which makes it

expensive (Parker et al., 2004). A ground-based portable system can offer a rapid, inexpensive assessment of stands from readily available commercial systems.

Research questions

The different light capture strategies of plants may explain the intra- and interspecific differences in growth patterns, biomass allocation, and crown structure of plants within a stand. Studies on light capture and light interception efficiency have been done on herbaceous stands and young secondary forests. This can be due to the fact that the height of primary forests makes it difficult to measure light capture from the ground. Thus, to my knowledge, this is the first study to quantify light interception and light use efficiency of tree individuals in a primary forest.

Thus, in order to further the understanding on the different strategies used by plants in a primary forest this study aims to address the following questions:

- (1) How do plants differ in light interception efficiency?
Are taller plants more efficient in intercepting light than smaller plants?
- (2) How do plants differ in light use efficiency?
Are taller plants more efficient in converting captured light energy into biomass production than smaller plants?
- (3) To what extent do the differences in light interception and light use efficiency correlate with tree height?

The first objective of this study is to see differences in light interception efficiency (LIE) of different species and individuals in a primary forest. Establishment of species in primary forests depends on their successful utilization of light as they have out-competed other species in the forests. It is expected that there are differences in LIE among species. It is predicted that taller plants would have higher Φ_{area} values than shorter plants. This is in line with Hirose & Werger's studies (1995) studies showing that taller species invest on supporting tissues (biomass) to capture light. However, in terms of light interception efficiency (LIE), shorter species would have higher LIE than taller species.

In relation to this, it is also important to measure how efficient plants are in converting captured light to biomass growth per year. In this paper, this is defined as light use efficiency

(LUE). LUE is biomass growth per total captured light per year. It is predicted that taller plants would have higher LUE than smaller plants.

In addition, it is the aim of this study to estimate leaf distribution in a non-destructive way. Recent method that has been applied to estimate leaf mass area is LIDAR (Parker et al 2004). It is an indirect and non-destructive method of estimating leaf distribution and leaf area index. In this study the reliability of LIDAR was tested in estimating leaf distribution.

Chapter 2: Methodology

Study Area



Figure 2. Yakushima Island. Red balloon marked with A indicates the position of the study site on the island.

Research plots are situated in the National Forests of Yakushima Island in the south of Japan (detail in Aiba & Kohyama 1997). The warm-temperate forests of Yakushima consist of evergreen broad-leaved trees dominated by *Distylium racemosum*. The mountain area of the island rests on granite rock while the lowland areas are covered with sedimentary rock. The island receives ample amount of precipitation which is up to 10,000 mm per year – one of the wettest area in the world. Pristine primary forests, which have largely disappeared in Japan, still remain in Yakushima. Several permanent research plots of well-developed primary forests have been established on both the eastern and western parts of the island since 1981. These plots have had minimal human disturbance for at least 150 years. The altitude of these plots ranges between 150-1200m above sea level.



Figure 3. Aiko plot, measured to 60 x 20 m. Subplots measuring 2.5 x 2.5 m marked by yellow tape.

The study site for this research project is called Aiko, a primary forest plot situated on the Eastern side of the island (N=30.380; E=130.627). It is about 150 m above sea level on a relatively flat terrain. The plot area is 60 x 20 m which was divided into 2.5 x 2.5 m subplots totaling to 192 subplots.

Plant material

Aiba and Kohyama (1997) described 14 dominant species based on abundance on Yakushima, namely: *Camellia japonica*, *Cleyera japonica*, *Camellia sasanqua*, *Distylium racemosum*, *Eurya japonica*, *Illicium anisatum*, *Litsea acuminata*, *Myrsine seguinii*, *Neolitsea aciculata*, *Podocarpus nagi*, *Rhododendron tashiroi*, *Symplocos glauca*, *Symplocos prunifolia*, and *Symplocos tanakae*. These evergreen species represent different layers along the vertical gradient, i.e. from canopy, subcanopy and understory. Aside from evergreen plants, there are also deciduous species in the area. They noted that dominant species in

primary forests at higher altitudes are different compared to those at lower altitudes. *Distylium racemosum* is dominant in primary forests at higher altitudes while *Castanopsis cuspidate* is dominant in lower altitudes (Aiba et al 2001). From the same study, they reported that species composition between primary and secondary forests differs depending on altitude. There was no difference in species composition between secondary and primary stands at lower altitudes but that it differs at higher altitudes.

For this study, there were 24 species of plants present in the plot considered for plot analysis. These plants can be categorized as canopy and subcanopy species depending on their heights (Aiba and Kohyama, 1997). Trees with diameter less than 5 cm were not considered.

See Table 1 for the complete list of plant species present in the study plot.

Canopy structure

Canopy structure was measured for each individual plant within the study area. Crown depth (in meters) – the top and bottom height of the crown, was measured using a hypsometer/rangefinder (Vertex IV, Haglof, Langsele, Sweden). Crown width (in meters) of each tree was measured by determining the short and long axes of the crown projected on the ground. Crown surface area and crown volume were calculated from these measurements assuming that crown shape is elliptic cylinder.

Aboveground biomass

The aboveground biomass of each individual was estimated using allometric equations. Total aboveground biomass (M , in kg) and total stem and branch biomass (M_{SB} , in kg), and total leaf mass (M_L , in kg) were calculated from DBH, height (H), wood density (WD) data and LIDAR data.

DBH of each individual plant was measured. These measurements were made in April 2008 and May 2011. Trees with DBH of less than 5cm were not considered for this study. Height of individual trees was measured using a rangefinder (see section on canopy structure). Wood density data come from Aiba and Kohyama (1997) and additional measurement for species without existing data.

The allometric equations used for the calculation of aboveground biomass are below. They were based on the work of Kitamura et al. (1960) and Kawanabe (1977).

Total biomass

$$\log_{10}(M) = 2.0465 \log_{10}(\text{DBH}) + 0.55 \log_{10}(\text{H}) + 0.8614 (\text{WD}) - 0.9525$$

$$R^2 = 0.986$$

Total biomass without height data

$$\log_{10}(M) = 2.6203 \log_{10}(\text{DBH}) + 1.0479 \log_{10}(\text{WD}) - 1.1059$$

$$R^2 = 0.912$$

Total stem and branch biomass

$$\log_{10}(M_{\text{SB}}) = 1.998 \log_{10}(\text{DBH}) + 0.720 \log_{10}(\text{H}) + 0.797 \log_{10}(\text{WD}) - 1.099$$

$$R^2 = 0.989$$

Total leaf mass

$$\log_{10}(M_{\text{L}}) = 1.870 \log_{10}(\text{DBH}) + 2.10 \log_{10}(\text{WD}) - 1.384$$

$$R^2 = 0.892$$

Calculation of light interception efficiency (LIE) and light use efficiency (LUE)

Light interception efficiency (Φ_{area} , and Φ_{mass}) were calculated by dividing total amount of intercepted light by total leaf area (LA) and by total aboveground biomass respectively. Light use efficiency (LUE) is a parameter defined here as biomass growth per total amount of intercepted light (in $\text{kg mol}^{-1} \text{ year}^{-1}$).

LIE, LUE, and relative growth rate (RGR)

One aim of this study is to examine whether there is a difference between tall and short plants across species in terms of light interception efficiency and light use efficiency. Plants that are efficient in interception and in using the intercepted light for growth can be seen in the carbon gain. Thus, carbon gain can be seen as an indication of the efficiency at which plants convert intercepted light. If relative growth rate (RGR) is defined as the aboveground growth rate per aboveground biomass, that is:

$$\text{RGR} = \frac{\Delta M}{M}$$

then, RGR is also indicative of how plants are efficient in capturing light ($= \Phi/M$) and how efficient they are in converting captured light into carbon gain ($= \Delta M/\Phi$). In this case,

$$\text{RGR} = \text{LUE} \times \text{LIE}$$

If tall plants are more efficient in capturing light and in converting captured light into biomass, then it is expected that they would have greater LIE, LUE and RGR values than smaller plants.

Light environment

Light distribution within the canopy was measured using LI-190SA light sensor (Li-Cor, Lincoln NE, USA) attached to LI-1400 data logger (Li-Cor). Light intensity was measured every 1m from the base up to 17m at the top of the canopy using a telescopic rod (Taketani Trading Co., Osaka, Tokyo, Japan) with the attached light sensor. Maximum length of the telescopic rod was 15 meters. Considering height of the researcher, maximum height of 17 meters was achieved by lifting the 15-meter rod. To get the average light intensity for each height, measurements were recorded after 10 seconds of light exposure at the center of each grid. Light measurements were made at every other subplot within the study area. All light intensity measurements were done under overcast sky. Relative light intensity along the height of the canopy was calculated for each grid using the light intensity above the canopy as reference. For instances where the top of canopy exceeded 17 meters, light above the

canopy from a neighboring grid was used as a reference. To calculate the daily light interception, relative light intensity was multiplied by daily average PPFD ($57.47 \text{ mol m}^{-2} \text{ day}^{-1}$) which was calculated from typical insolation in Yakushima Island ($12.575 \text{ MJ m}^{-2} \text{ day}^{-1}$, average across 1961–1967 Japan meteorological agency) and a conversion constant ($4.57 \text{ mol PPFD MJ}^{-1}$ under natural light; McCree 1972; Amthor 2010).

Leaf Area Distribution using LIDAR

Leaf area distribution (LAD) was measured using LIDAR (Light Detection and Ranging, LD-90, Riegel Laser Measurement Systems, Horn, Austria). The LIDAR technique used in this study was based on a portable terrestrial LIDAR system developed by Parker et al. (2004). LIDAR is based on the principle of measuring vertical distance by time-of-flight using pulsed laser light (see Parker et al. 2004). In their study measurements were done by walking along several transects at a constant pace and at 1m level above the ground. For this study, however, distance measurements of the canopy were collected by moving the LIDAR apparatus at a 360° angle along the horizontal plane from the four corners of each subplot while facing the center point of each 2.5 X 2.5 m grid. This was also to avoid position inaccuracies and angular deviations caused by variability in walking rate. Vertical profile for each grid was taken by measuring a total of 1000 measurements per second. Height of the LIDAR reference plane was kept at 1m above the ground.



Figure 4. Kosuke Akutsu measuring leaf distribution using the portable LIDAR system. Measurements were done at 360° degree from the center of each subplot from a height of approximately 1m above the ground.

Equations to calculate for LAD were derived from MacArthur and Horn (1969). According to the calculations of MacArthur and Horn (1969) foliage density can be derived using the following formula:

$$D(h) = \frac{-d[\ln\varphi(h)]}{dh}$$

where $D(h)$ is the density of foliage at height (h), $\varphi(h)$ the probability of no leaves over the first h meters, that is, the probability at which no leaf is intercepted (no laser interception occurred) above the LIDAR, which was above 1 meter, within the vertical column up to h .

Leaf mass per area (LMA)

Leaves were collected from different light levels of trees using a 15m-long branch cutter. Sample leaves were scanned and the digital images were analyzed using ImageJ software to

compute for leaf area of each species. Leaf samples were weighed after drying in an oven for about seven days. Leaf mass per area (LMA) was then calculated from these parameters. (LMA = 1/SLA; SLA (specific leaf area) = one-sided area of fresh leaf/oven-dry mass)

Calculation of Leaf area (LA)

Leaf area and relative light profile were calculated for each voxel, i.e. 2.5m (W) X 2.5m (L) X 1m (H), for a total of ca. 4,000 voxels. Since crowns from different individuals sometimes occupied the same space, number of crowns that occupied the center of each voxel was calculated. If more than one individual were present, leaf area and relative light data were split equally according to the number of individuals. These weighed data of leaf area and light were then integrated for each individual, resulting into total leaf area and total relative light absorbed for each individual.

Statistical Analysis

Data were analyzed using R statistical package software (version 2.15.0; R Foundation for Statistical Computing, Vienna, Austria). Significance levels of correlation between and among parameters were tested using Pearson's test. Type II regression (standardised major axis slope, Warton et al. 2006) was used to fit bivariate relationships.

Chapter 3: Results

Plant Material

A total of 205 individuals comprising 24 different species were measured in the plot. This number excludes plants with < 5 cm DBH. The most abundant species in the plot was *Distylium racemosum*, a canopy plant. Table 1 below shows the complete list of plant species present in Aiko plot.

Crown distribution

Below is a figure of the crown distribution of the 205 plants in the plot. Figure 5 shows overlapping of crowns of the different plants. What this figure also shows is that plants have different crown shapes. Most are ellipsoid; some are more or less spheroid. These factors were considered in computing for the leaf area distribution using LIDAR results.

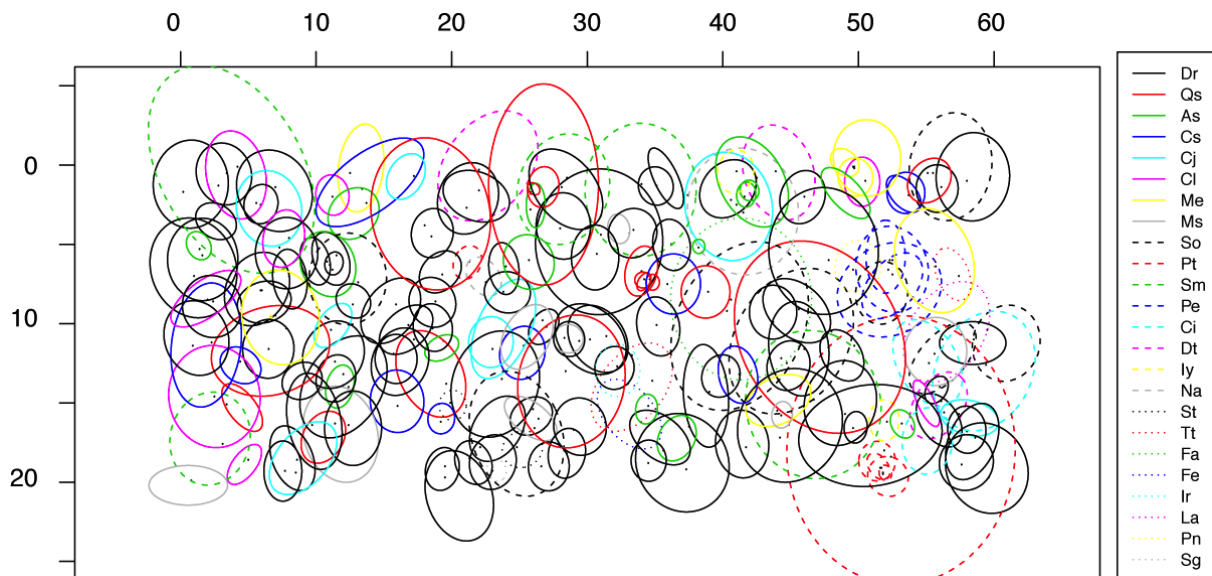


Figure 5. Crown distribution of individuals on the study plot area, top view perspective.

Table 1. Species information and characteristics of 24 species found in the study site. Abb, abbreviation of species name, N, number of individuals in 1200m²; Hmax, maximum height observed in the study site (m); Hmed, median of tree height (m); DBHmax, maximum diameter at breast height (cm); CanoSL, canopy slenderness which is the ratio of crown mean diameter to crown depth (m m⁻¹); WD, wood density (g cm⁻³); LMA, leaf mass per area (g m⁻²) and median (and 95% CI) of relative light intensity (% in reference to above the canopy) at which leaves were exposed.

| Abb | Species | Family | N | Hmax | Hmed | DBHmax | CanoSL | WD | LMA | Relative light |
|-----|----------------------------------|------------------|----|-------|-------|--------|--------|-------|-----|------------------|
| Aa | <i>Actinodaphne acuminata</i> | Lauraceae | 1 | 15.2 | 15.2 | 25.78 | 1.595 | 0.608 | 120 | 34.1 (0.7–100) |
| As | <i>Ardisia sieboldii</i> | Primulaceae | 15 | 14.5 | 11.45 | 22.73 | 1.542 | 0.624 | 103 | 3.9 (0.5–73.3) |
| Cj | <i>Camellia japonica</i> | Theaceae | 8 | 15.3 | 11.25 | 30.56 | 1.153 | 0.735 | 187 | 10.8 (1.2–93.7) |
| Cs | <i>Camellia sasanqua</i> | Theaceae | 10 | 15.6 | 7.275 | 23.94 | 0.766 | 0.691 | 152 | 3.2 (0.8–66.3) |
| Ct | <i>Cinnamomum tenifolium</i> | Lauraceae | 3 | 15.05 | 12.55 | 38.71 | 1.064 | 0.52 | 127 | 6 (0.4–100) |
| Cl | <i>Cleyera japonica</i> | Theaceae | 8 | 10.9 | 7.15 | 16.87 | 0.786 | 0.645 | 168 | 7.2 (0.6–12.3) |
| Dt | <i>Daphniphyllum teijsmannii</i> | Daphniphyllaceae | 3 | 16.25 | 15.8 | 37.88 | 1.007 | 0.582 | 164 | 47.3 (2.9–96.2) |
| Dr | <i>Distylium racemosum</i> | Hamamelidaceae | 89 | 18.8 | 9.9 | 46.19 | 1.128 | 0.914 | 207 | 8.7 (0.8–97.5) |
| Fe | <i>Ficus erecta</i> | Moraceae | 1 | 13.6 | 13.6 | 12.19 | 0.867 | 0.64 | 98 | 71.3 (23.1–91.2) |
| Il | <i>Ilex liukuensis</i> | Aquifoliaceae | 2 | 8.2 | 7.2 | 6.27 | 0.865 | 0.72 | 158 | 2.6 (1.0–2.6) |
| Ir | <i>Ilex rotunda</i> | Aquifoliaceae | 1 | 14.2 | 14.2 | 9.87 | 1.803 | 0.55 | 113 | 71.3 (4.8–71.3) |
| Le | <i>Lithocarpus edulis</i> | Fagaceae | 4 | 14 | 11.1 | 25.81 | 0.832 | 0.743 | 166 | 6.9 (1.6–61.6) |
| Mt | <i>Machilus thunbergii</i> | Lauraceae | 6 | 16.85 | 4.8 | 136.94 | 0.554 | 0.639 | 165 | 9.1 (0.8–96.9) |
| Mr | <i>Meliosma rigida</i> | Sabiaceae | 8 | 16.1 | 13.7 | 30.97 | 0.877 | 0.534 | 154 | 23.5 (1.8–100) |
| Ms | <i>Myrsine seguinii</i> | Myrsinaceae | 8 | 12.45 | 8.75 | 22 | 1.201 | 0.814 | 116 | 1.2 (0.3–37.4) |

| | | | | | | | | | | |
|----|---------------------------------|---------------|----|-------|-------|-------|-------|-------|-----|-----------------|
| Nn | <i>Nageia nagi</i> | Podocarpaceae | 1 | 8.15 | 8.15 | 9.26 | 0.821 | 0.579 | 123 | 2.7 (1.4–3.3) |
| Na | <i>Neolitsea aciculata</i> | Lauraceae | 2 | 14.3 | 12.7 | 43.29 | 1.061 | 0.637 | 145 | 7.5 (2.2–77.2) |
| Qs | <i>Quercus salicina</i> | Fagaceae | 16 | 20.85 | 10.7 | 68.75 | 1.041 | 0.925 | 140 | 37.4 (1.9–100) |
| Sh | <i>Schefflera heptaphylla</i> | Araliaceae | 8 | 17.85 | 15.05 | 49.97 | 0.76 | 0.465 | 118 | 15.5 (1.1–88.8) |
| Sm | <i>Stewartia monadelphica</i> | Theaceae | 5 | 20.9 | 19.8 | 63.38 | 0.772 | 0.71 | 103 | 69.1 (4.2–100) |
| Sg | <i>Symplocos glauca</i> | Symplocaceae | 1 | 8 | 8 | 6.21 | 1.003 | 0.591 | 79 | NA |
| St | <i>Symplocos tanakae</i> | Symplocaceae | 2 | 7.35 | 7.175 | 7.51 | 1.108 | 0.682 | 143 | NA |
| Tt | <i>Turpinia ternata</i> | Staphyleaceae | 2 | 10.4 | 8.9 | 25.31 | 0.787 | 0.48 | 101 | 4.2 (1.2–13.7) |
| Za | <i>Zanthoxylum ailanthoides</i> | Rutaceae | 1 | 16.1 | 16.1 | 32.15 | 0.189 | 0.432 | 99 | 84.7 (81.5–100) |

Height distribution and profile

Figure 6 below shows the distribution of height of all individuals measured in the plot. The maximum height measured by the rangefinder was 22 meters. This figure also shows that most plants have heights ranging from 5 meters to 15 meters.

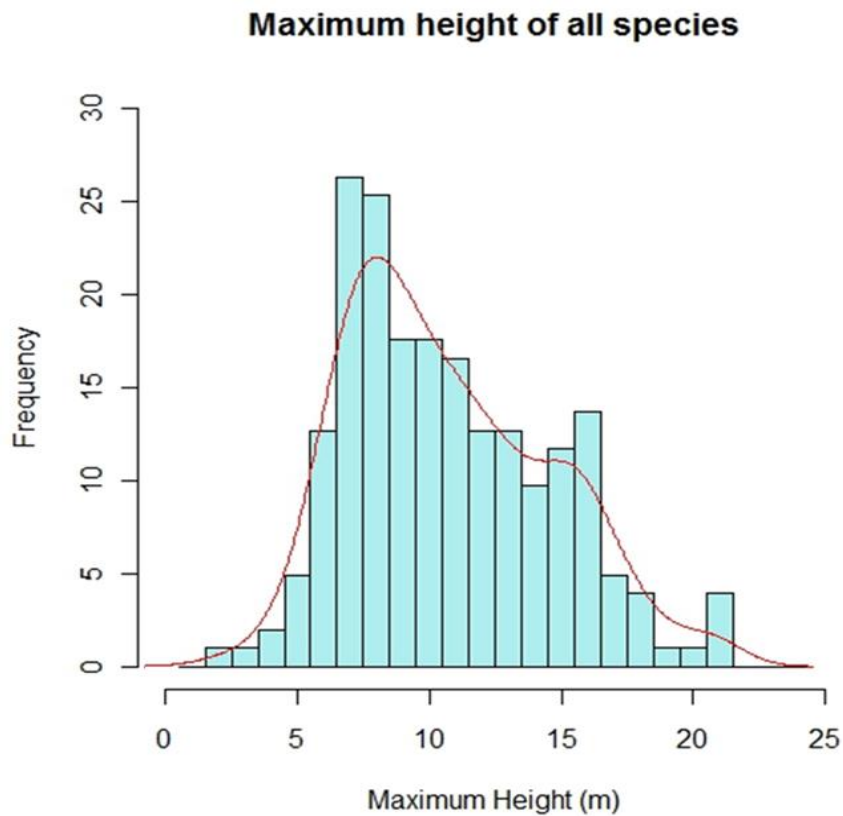


Figure 6. Maximum height, h (m) of all species on the plot.

Figure 7 below shows the different height profiles of the top 12 species in the plot. The tallest plants in the plot is *Stewartia monadelphica*, which are top canopy species. *Distylium racemosum*, the most abundant species in the plot has a height distribution that spans almost all height ranges.

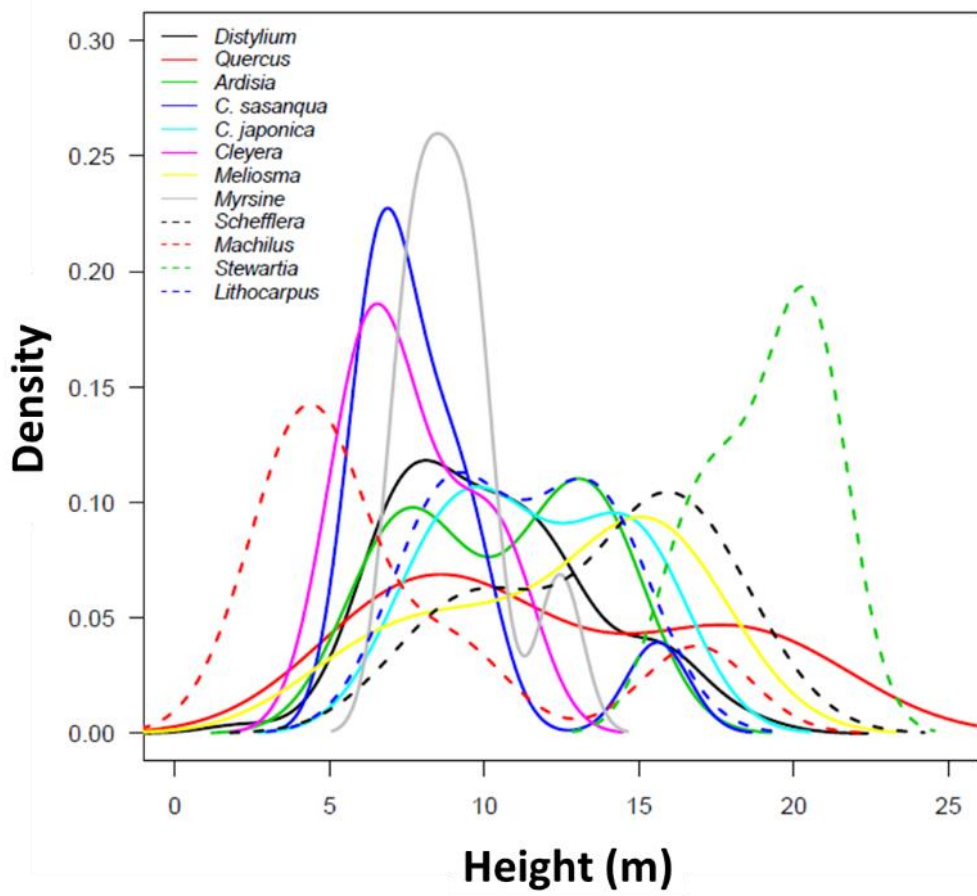


Figure 7. Height distribution of the different species in the study area.

Validation of LIDAR method

To see the usefulness of LIDAR in estimating leaf area, results were compared from LIDAR and that of allometric relationship (Fig. 8). Comparisons show that LIDAR can provide a reliable estimate of leaf area of individual plants. Therefore, LIDAR can be a useful non-destructive alternative for measuring leaf area. LIDAR can replace the vertical pole method which can be time-consuming in the field (i.e. van Kuijk & Anten 2008).

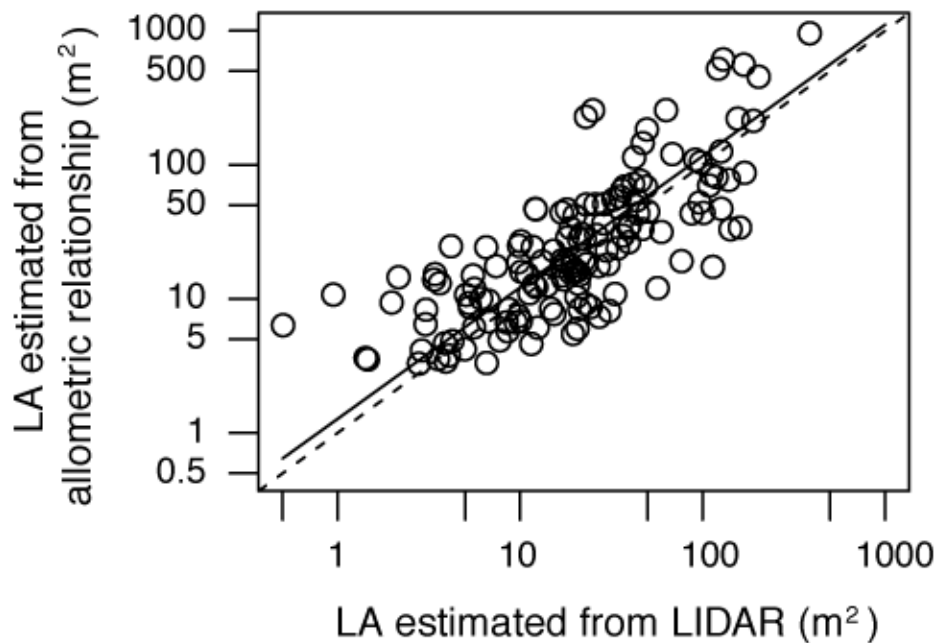


Figure 8. Comparison of LA estimated from allometric equations and LIDAR data.

Relative light density along the height

Figure 9 below shows the relative light density of the area along the vertical height. The maximum height at which light intensity was measured was at 17m. Mean relative light density measured was 1.25% at 1m above ground.

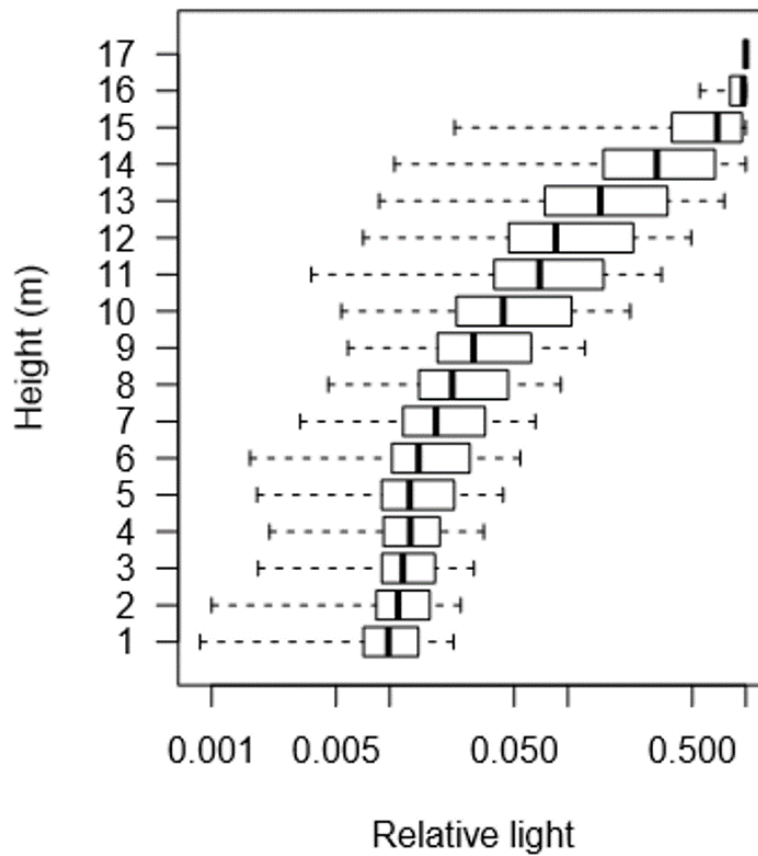


Figure 9. Relative light density vs canopy height.

Relationship of light and LA

Leaf area estimate from LIDAR rather than from allometric relationship has higher correlation with light interception ($R^2 = 0.662$ vs. 0.568 , Fig. 10). This indicates that LIDAR is a good predictor of variability in light interception in the canopy by estimating leaf area distribution in the canopy

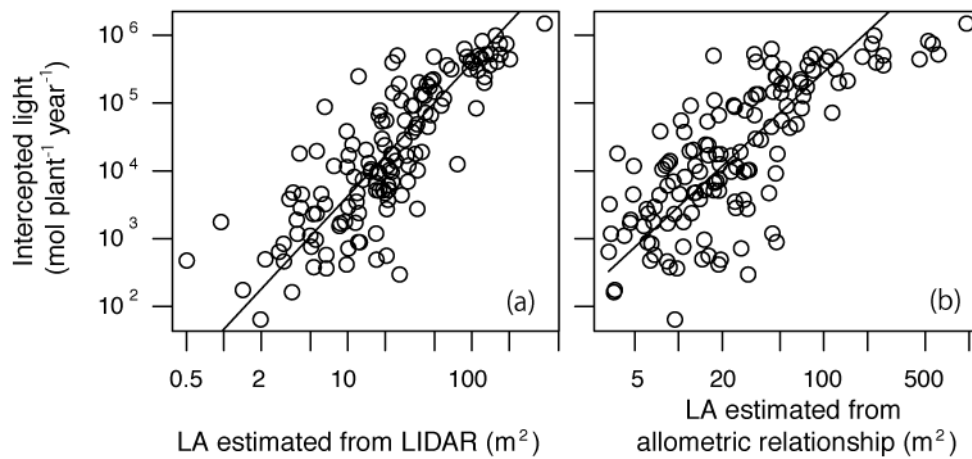


Figure 10. Intercepted light per plant (mol plant⁻¹ year⁻¹).

Foliage profile of plants

LIDAR data can provide a 3D profile of a plot (Fig. 11 and 12). Figure 11 shows the horizontal foliage heterogeneity of the plants in the 60x20m study area at heights ranging from 1.5m to 18.5m above ground. Figure 12 shows a 3D foliage profile of the plot from different slices, with denser foliage at 10-15m height. Crown geometry overlays show overlapping of foliage of trees. In some instances, tree crowns as depicted by the quadrilaterals show no foliage in some profiles. This can be due to difficulty of LIDAR to penetrate lower canopy foliage and hit top canopy leaves.

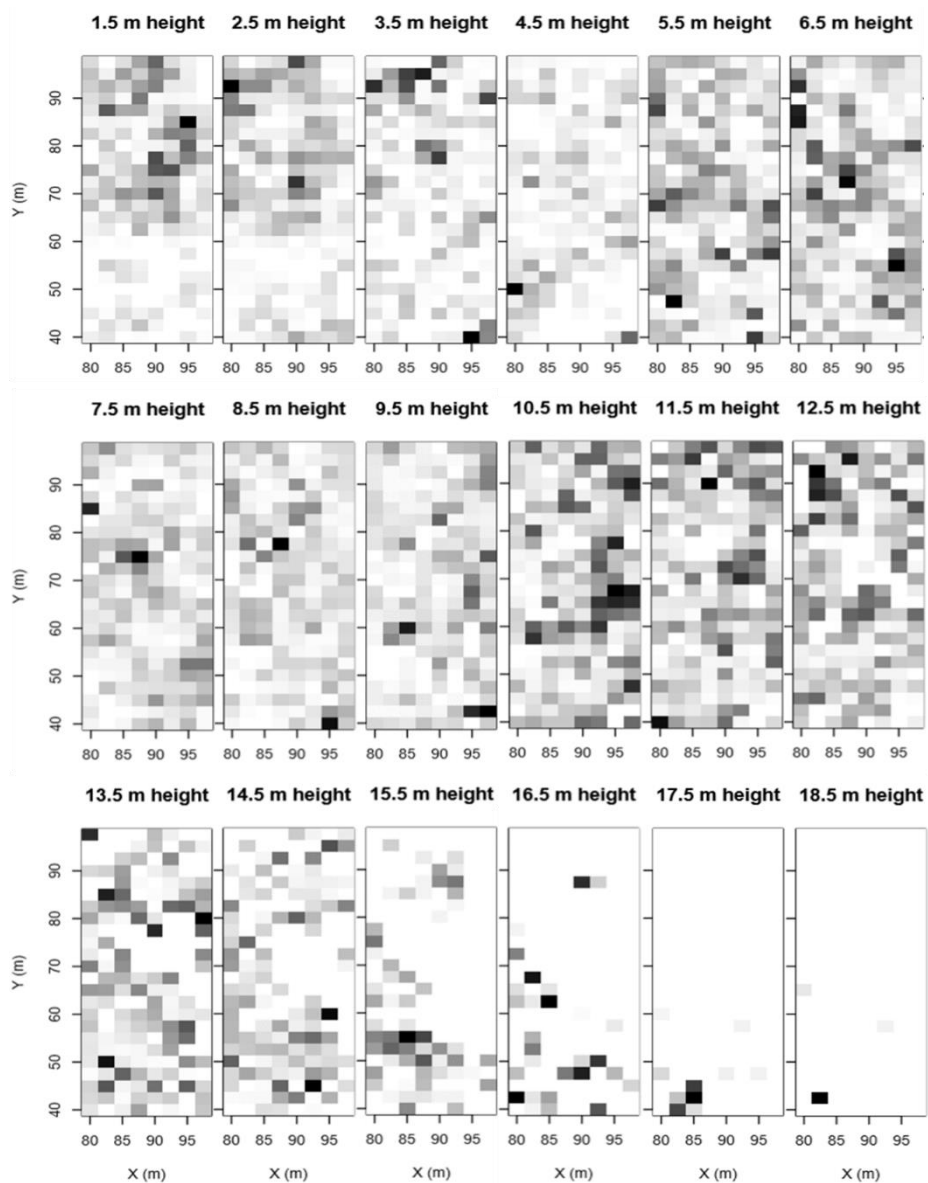


Figure 11. Horizontal foliage density profile of the study area (i.e. top view). Figures depict foliage density profile of the plot at intervals of 1m starting at 1.5m to 18.5m, where darker areas denote denser foliage.

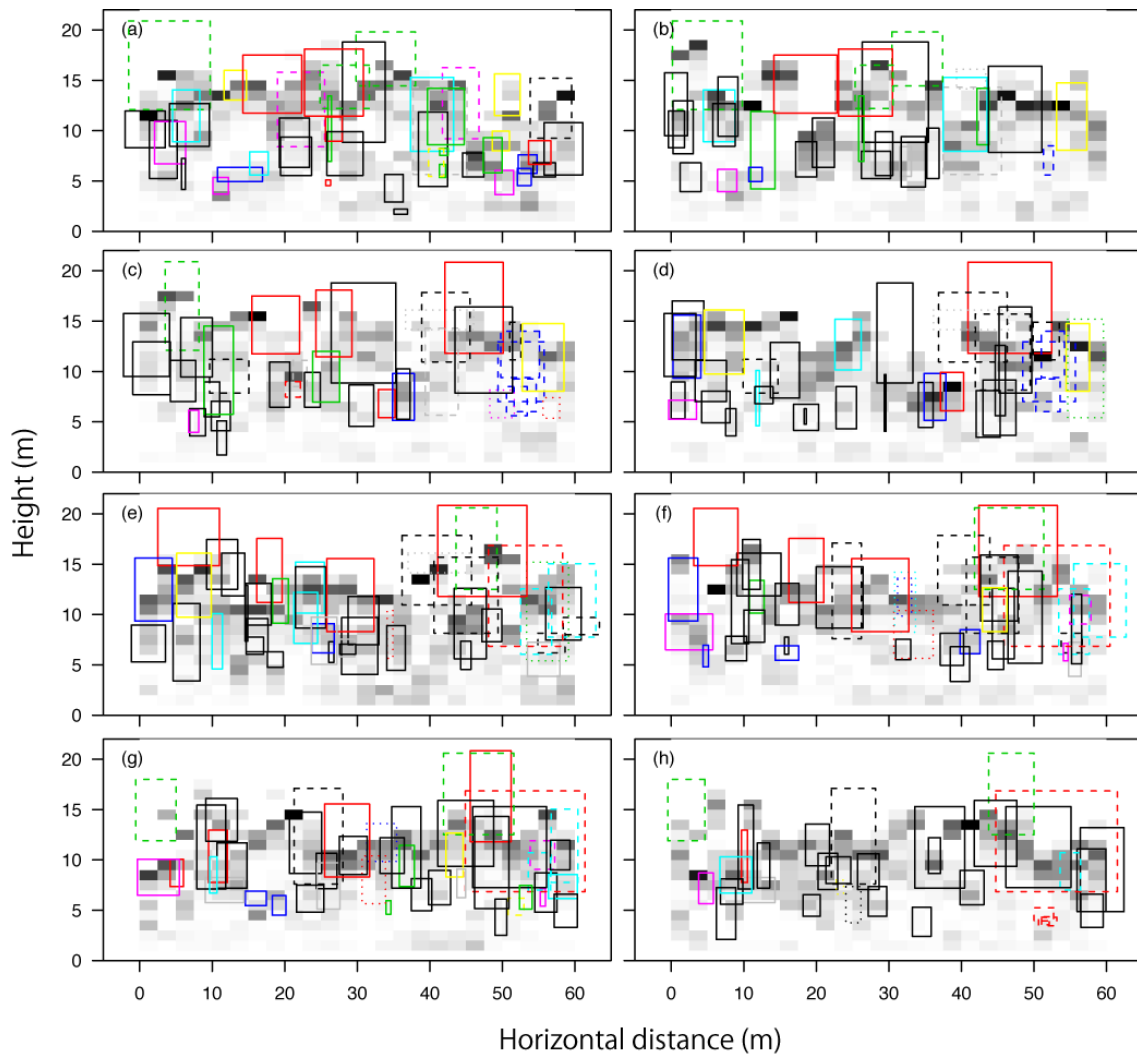


Figure 12. Foliage density profile of the study area. Figures depict foliage density profile of the plot at intervals of 2.5m starting at (a) 1.25m to (h) 18.75m. Darker areas denote denser foliage. Crown geometry is denoted by quadrilaterals on each profile slice.

Vertical light profile of plants

Figure 13 shows vertical light profile of the plot, showing the different light environments within the stand. There was a strong light attenuation within the canopy, with mean relative light intensity of 1.25% at 1m above the ground.

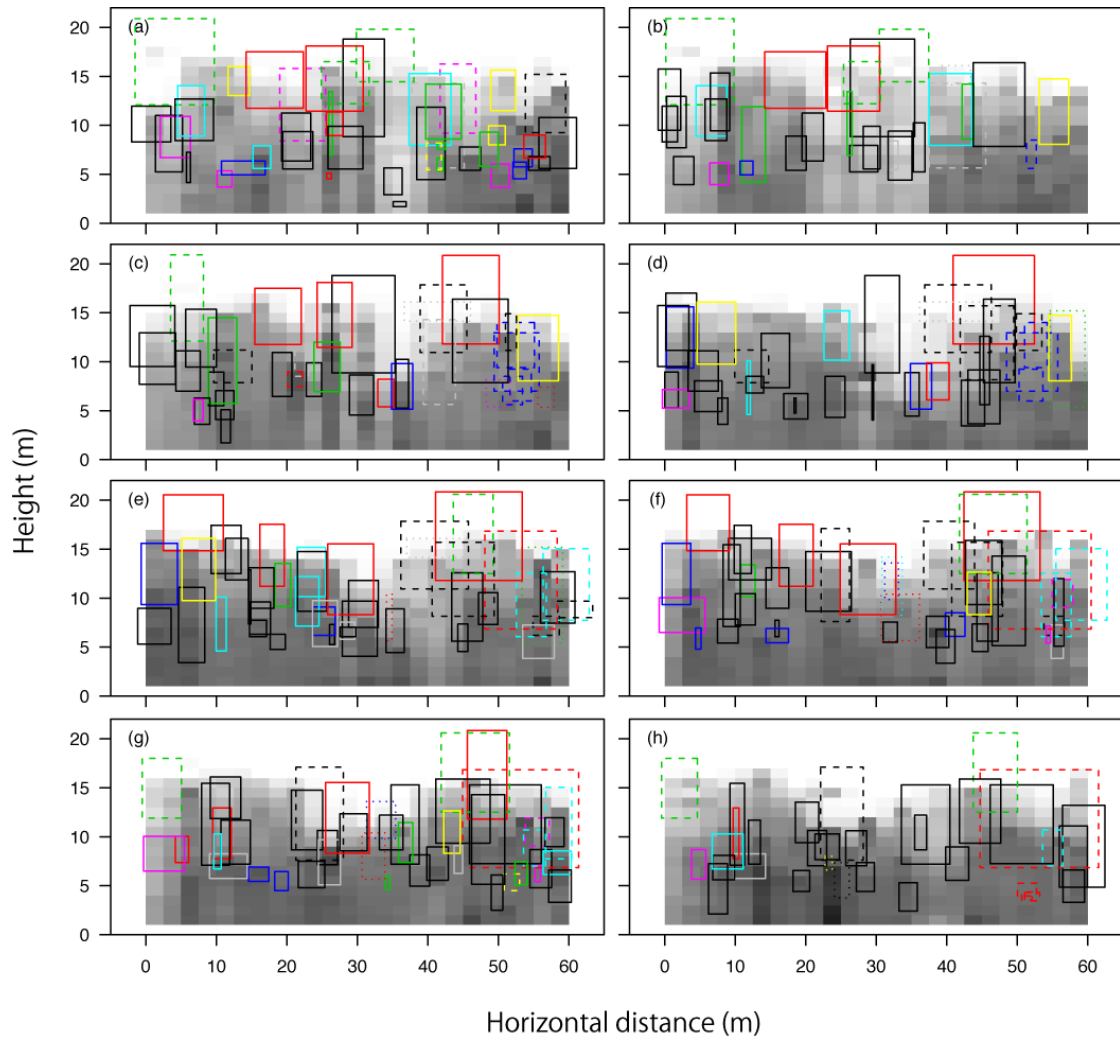


Figure 13. Light profile of the study area. Figures depict vertical light profiles of a series of slices starting at (a) 1.25 m to (h) 18.75 m. Darker areas denote darker environment.

Growth rate and relative growth rate

Figure 14 shows the growth rate and relative growth rate in relation to height of the different plant individuals and species in the plot. Results show a positive correlation between height of plants with growth rate, thus taller plants grew faster than smaller plants (Fig.14a).

Relative growth rate was not correlated with height across all individuals, thus there was no difference between tall and short plants in terms of growth for their size (Fig.14b). Positive correlation was also found between mean growth rate and mean height of species (Fig.14c). Also, no correlation was found between RGR and mean height per species (Fig.14d).

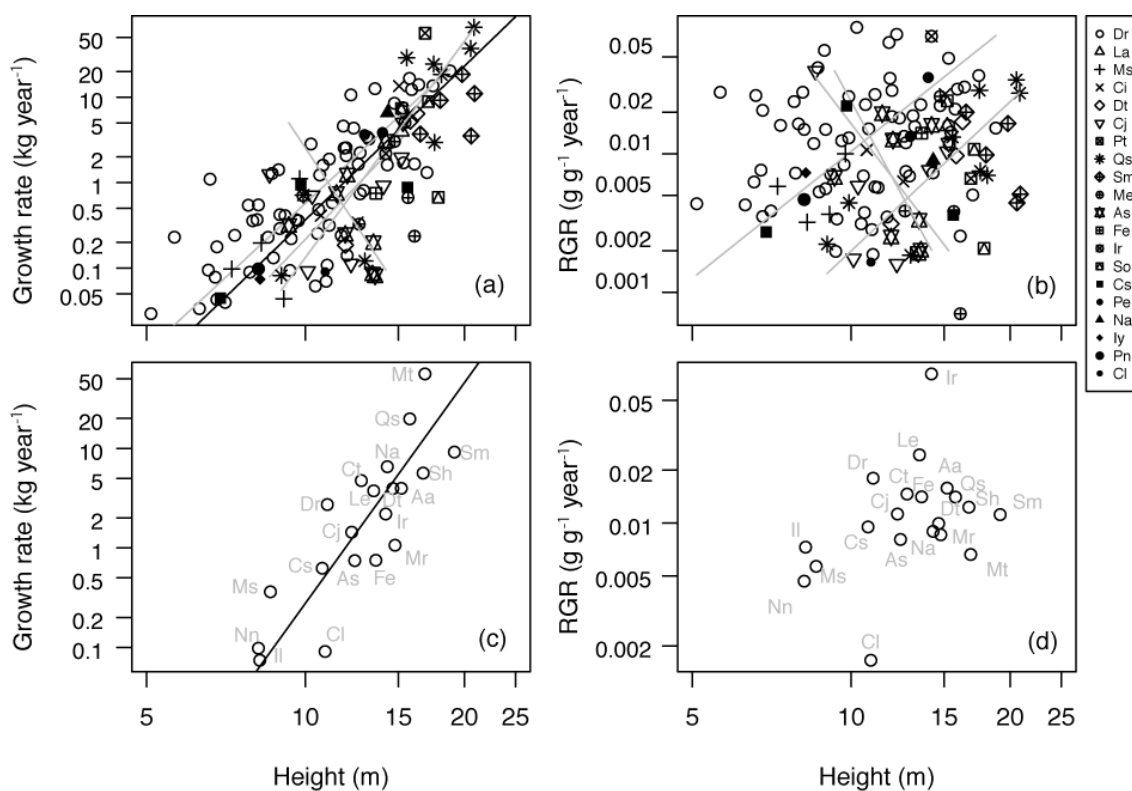


Figure 14. Growth rates and relative growth rates of the plants in the plot.

Light interception efficiency (LIE) and light use efficiency (LUE)

Figures 15, 16, and 17 shows light interception efficiency and light use efficiency among individuals and species. Results show that there was a positive correlation between height and LIE among individuals and across species (Fig. 15a, 15b, 16a, and 16b), thus taller individuals had more advantage in efficiently capturing light per unit leaf area. However, leaf area ratio (LAR) had a negative correlation with tree height across individuals and species (Fig. 15c and 16c), meaning taller individuals had relatively more aboveground biomass per leaf area. A negative correlation was also found between mean height and LUE across individuals (Fig. 15d) and across species (Fig. 16d) although the latter was not statistically significant. This means that taller individuals were less efficient than smaller individuals in converting captured light to biomass.

Figure 17 shows a negative correlation between LIE and LUE. As shown, taller plants were more efficient in capturing light per unit leaf area and per unit mass. However, in terms of light use efficiency, short plants seemed to be more efficient in using light captured and converting to biomass growth per year than taller plants.

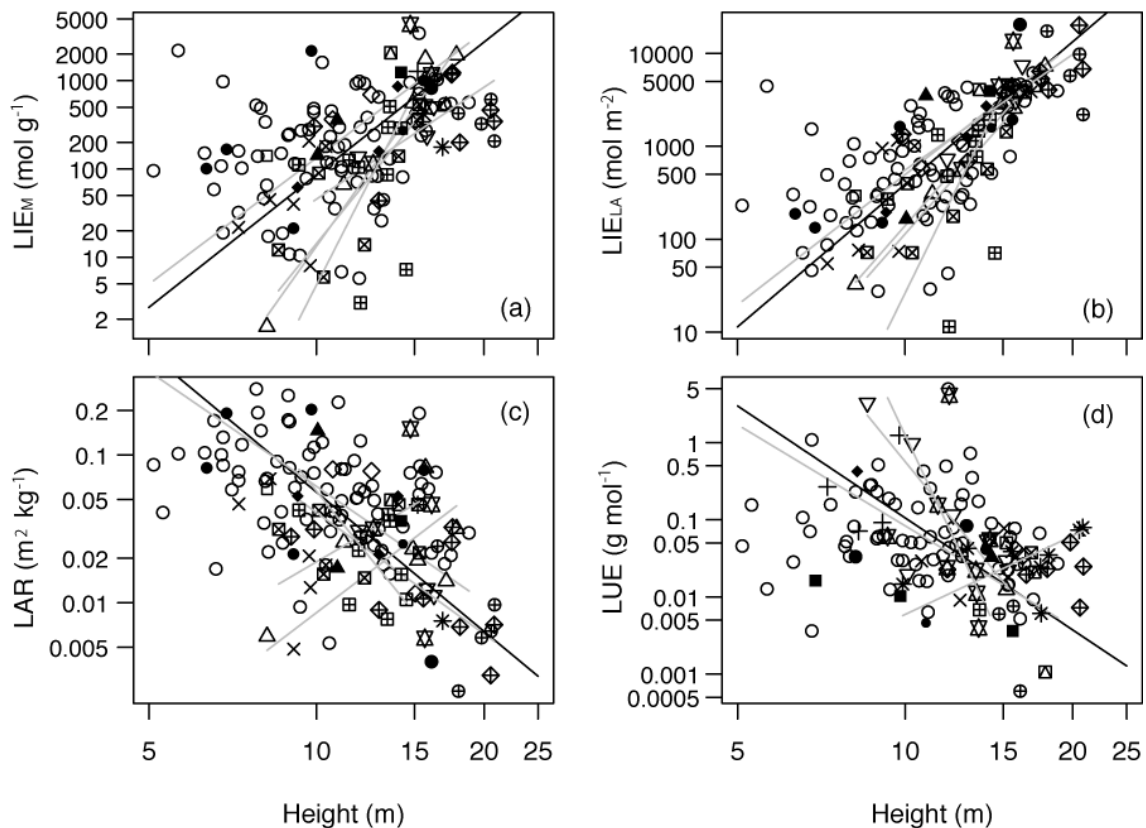


Figure 15. Light interception efficiency (LIE) and light use efficiency (LUE) of the individual plants.

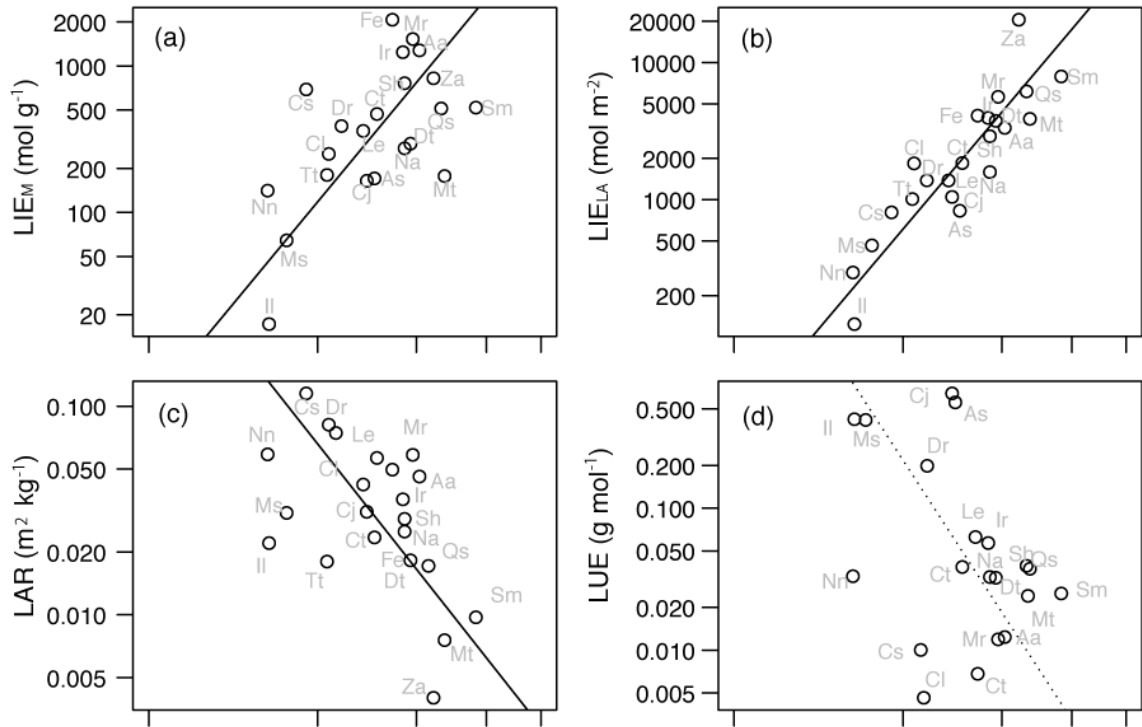


Figure 16. Light interception efficiency and light use efficiency of the species present on the plot.

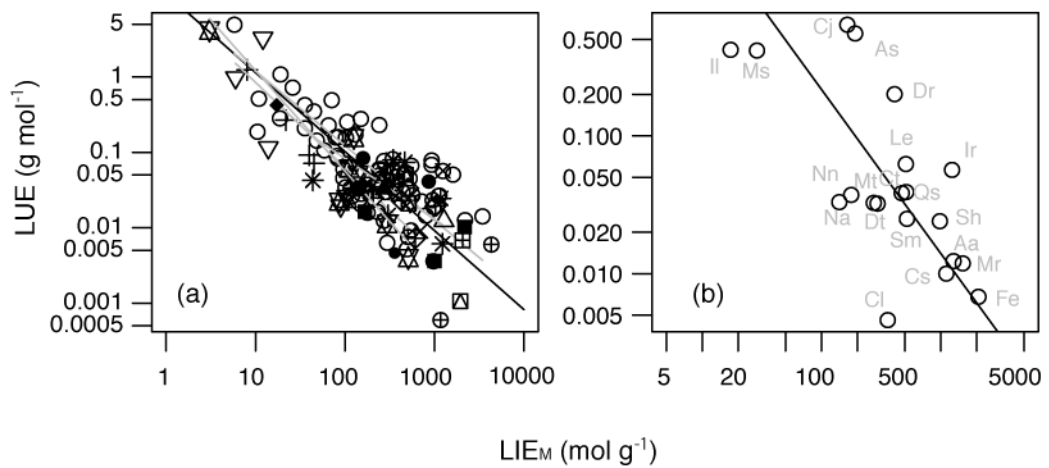


Figure 17. Inverse relationship between LIE and LUE.

Chapter 4: Discussion

Reliability of LIDAR method

This study shows that LIDAR can provide a rapid assessment of height and foliage density profiles in mature forests. Mature forests provide challenges in measuring leaf and light distribution because of height of trees, variability of structure and time. Direct measurements of LAI in forest stands are laborious and can be destructive in nature (Breda, 2003). The vertical pole method for determining canopy density and structure as described by MacArthur and Horn (1969) is impractical in many forests because of the tall stature of trees and high density of leaves (Jonckheere et al 2004). Determination of LAI through harvesting may be ideal for individual plant study but not for mature and protected forest areas. Using a system such as ground-based LIDAR provides an efficient and non-destructive way to measure foliage density and canopy structure. It can obtain thousands of data compared to point-quadrant sampling. Leaf area per plant estimates from LIDAR were linearly comparable to estimates from allometric equations (See figure 8). In addition, leaf area estimates from LIDAR were more highly correlated with light interception than that from allometric relationship (See figure 9). Data from LIDAR were also able to provide 3D profiles of height and foliage density (See figures 7, 10). LAI value (6.4, SD=1.51, n=192) obtained from LIDAR was within global estimates for temperate evergreen broadleaf forests (5.7, SD=2.4) (Asner et al 2003).

However, as with any field technique the use of LIDAR has its disadvantages. Foliage profiles (Figure 12) show some tree crown projections with no foliage. In these cases, LIDAR may have difficulty in penetrating dense or clumped foliage. This may lead to underestimation of foliage density and leaf area at the top of the canopy. This underestimation is a common source of error in leaf area determination methods in which the cited two major causes of discrepancy were clumping and contribution of stem and branches (Breda, 2003; Jonckheere et al 2004).

Differences in light interception efficiency and light use efficiency

Results of this study showed that taller plants within and across species were more efficient in intercepting light (LIE) than smaller individuals (See figures 15, 16). This seems to agree with previous studies (e.g. Hirose and Werger, 1995) that suggest that tall species have an advantage over subordinate species in receiving a large fraction of incident PPFD. This means that tall stature is an advantageous strategy in competing for light. However, other studies suggest that this difference in light interception efficiency is small (Selaya et al 2007; Vermeulen et al 2008; Van Kuijk et al 2008). This difference in findings may be due to differences in stand structure and successional traits of the study areas. Selaya et al (2007)'s and Van Kuijk et al (2008)'s studies were done on early secondary forests where available light near the forest floor was much higher (>20%) than in a mature forest floor (1.25%) such as that in Yakushima.

In terms of light use efficiency (LUE) the results of this study showed that taller individuals were less efficient in converting light energy into biomass (See figure 15d, 17). One possible explanation for this is that leaves at the uppermost layers experience cannot use strong light for photosynthesis due to saturating curve of light-photosynthesis relationship (Poorter, 2002). With limited light availability in the understory, gaps could provide sunlight that can be efficiently used for growth. Moreover, results also showed that LAR decreased with height which means that taller individuals might be investing more of their energy into aboveground biomass such as supporting stems than leaves. This may in turn explain the apparent trade-off between LIE and LUE between small and tall individuals which resulted into no difference in relative growth rates across individual size. Furthermore, this trade-off may explain smaller individuals' strategy to compensate for lower light levels. Scope of this study, however, does not consider a plant's allocation to roots whose contribution to total biomass may be around 20% (Michaletz et al. 2014).

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