Trade-off between light interception efficiency and light use efficiency: implications for species coexistence in one-sided light competition

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Summary

1. Taller plant species can pre-empt solar energy and suppress growth of subordinate species in vegetation stands, which is described through one-sided competition. Yet, in much of the world’s vegetation species of different statures coexist. This study aims to clarify the mechanisms underlying this apparent paradox.

2. We quantified how co-occurring species and individuals intercepted and used light for growth in a mature, warm-temperate evergreen forest. This was performed by determining the 3D distribution of foliage and light with a ground-based lidar system in combination with nondestructive measurements of plant growth.

3. Taller trees intercepted light more efficiently per unit of above-ground biomass than shorter trees did (=higher light interception efficiency, LIE). However, taller trees tended to have lower biomass production per unit light interception (=lower light use efficiency, LUE). Reduced LUE in taller trees was associated with their higher biomass allocation to nonphotosynthetic organs and probably with over-saturated light intensity for photosynthesis at high canopy positions. Due to the increased LIE and decreased LUE with tree heights, a trade-off between LIE and LUE was found, and this trade-off resulted in trees of different statures having similar relative growth rates.

4. Synthesis. Light competition drives trees to grow taller, and the light interception efficiency is higher in taller trees; however, this benefit comes at a cost of decreased efficiency of light use for growth. This trade-off allows trees of different statures to grow at proportionally comparable rates and may promote coexistence of tree species in one-sided light competition.

Key-words: asymmetric competition, coexistence, determinants of plant community diversity and structure, forest, light interception, light use, one-sided light competition, RGR, trade-off

Introduction

In natural vegetation, large numbers of species coexist, and understanding the mechanism underlying this coexistence is a major challenge in ecology (Silvertown 2004). Species diversity is apparent along both horizontal and vertical axes. Coexistence of plant species has been often explained by horizontal heterogeneity caused by disturbance or abiotic environments (e.g. resource availability), yet it remains largely unknown how plant species of different statures can coexist vertically (Kohyama & Takada 2012). Taller plants can pre-empt light energy and suppress light acquisition of shorter plants, and thus, light competition is one-sided, which contrasts with two-sided competition, such as soil nutrient- or water competition. One-sided competition is often related to size-asymmetric competition, which means that bigger individuals get disproportionately larger amounts of light relative to their size, than smaller individuals, leading to a progressive increase in size differences and ultimately to the exclusion of the smaller individuals (Weiner & Thomas 1986; Schwinning & Weiner 1998). Yet, the enormous variety in tree stature

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COMMONLY OBSERVED IN NATURAL VEGETATION, PARTICULARLY IN FORESTS, CONTRASTS THIS SCENARIO. APPARENTLY, SHORTER PLANTS CAN GROW, REPRODUCE AND RECRUIT IN THE SHADE OF THEIR TALLER NEIGHBOURS (KOHYAMA 1993; KOHYAMA & TAKADA 2009). THEREFORE, CLARIFYING THE MECHANISMS HOW SPECIES WITH DIFFERENT STATURES COEXIST UNDER ONE-SIDED COMPETITION IS A KEY ISSUE IN OUR UNDERSTANDING OF PLANT SPECIES COEXISTENCE.

LIGHT COMPETITION CAN BE UNDERSTOOD AS THE PRODUCT OF TWO PROCESSES: (I) HOW COMPETING INDIVIDUALS INTERCEPT LIGHT IN RELATION TO THEIR BIOMASS (LIGHT INTERCEPTION EFFICIENCY, LIE) AND (II) HOW COMPETING INDIVIDUALS UTILIZE THIS INTERCEPTED LIGHT FOR GROWTH (LIGHT USE EFFICIENCY, LUE) (SCHWINNING 1996; HIKOSAKA, SUDOH & HIROSE 1999). DESPITE THE WELL-KNOWN NOTION OF SIZE-ASYMMETRIC COMPETITION FOR LIGHT, ONLY A LIMITED NUMBER OF STUDIES HAVE ACTUALLY QUANTIFIED LIGHT INTERCEPTION AND USE OF COMPETING INDIVIDUALS IN NATURAL POPULATIONS. FURTHERMORE, MOST OF THESE STUDIES FOCUSED ON HERBACEOUS COMMUNITIES AND NOT ON FORESTS.


THE SECOND PROCESS – LIGHT USE EFFICIENCY (LUE), WHICH CAN BE DEFINED AS THE RATIO OF BIOMASS PRODUCTION PER UNIT LIGHT INTERCEPTION, HAS BEEN RARELY QUANTIFIED AMONG COMPETING INDIVIDUALS IN NATURAL VEGETATION. HIKOAMAKA, SUDOH & HIROSE (1999) MODELLED CARBON ASSIMILATION RATE OF INDIVIDUALS IN A MONO-SPECIES HERBACEOUS STAND AND THEN ESTIMATED PHOTOSYNTHETIC LUE (LUEP) (HEREAFTER), LUEP WAS HIGHEST IN MEDIUM-SIZE INDIVIDUALS AND LOWER IN BOTH TALL AND SMALL INDIVIDUALS. THE LOWER LUEP IN TALLER INDIVIDUALS WAS PARTLY DUE TO THE SATURATING NATURE OF LIGHT-PHOTOSYNTHESIS RELATIONSHIP; PHOTOSYNTHETIC RATES OFTEN SATURATE AT 500–1000 μMOL M⁻² S⁻¹ PPFD, WHILE THE TOP CANOPY LEAVES RECEIVE LIGHT LEVELS THAT WERE HIGHER THAN THIS SATURATION POINT. SIMILAR STUDIES COMPARING LUEP AMONG SPECIES IN VERY YOUNG SECONDARY TROPICAL FORESTS OBTAINED VARYING RESULTS WITH LUEP EITHER HIGHER IN TALLER THAN SHORTER SPECIES (SELAAYA & ANTEN 2010), OR NOT RELATED TO STATURE (VAN KUIJK ET AL. 2008). ALL THESE STUDIES, HOWEVER, SHARE TWO IMPORTANT SHORT-COMINGS. FIRST, LUE WAS CONSISTENTLY EXPRESSED IN TERMS OF PHOTOSYNTHESIS RATHER THAN GROWTH. AT THE WHOLE-PLANT LEVEL, 20–80% OF ASSIMILATED CARBON IS LOST DUE TO RESPIRATION, AND THE FRACTION INCREASES WITH PLANT SIZE AND WITH ALLOCATION TO NONPHOTOSYNTHETIC ORGANS (DELUCIA ET AL. 2007). SECOND, THEY WERE BASED ON MODEL CALCULATIONS RATHER THAN REAL GROWTH MEASUREMENTS, AND THEIR ARE UNCERTAIN WHETHER ESTIMATED VALUES DIRECTLY LINK TO INTERSPECIFIC DIFFERENCES IN PLANT GROWTH.

WE ARE NOT AWARE OF ANY STUDY THAT ANALYSED LIGHT COMPETITION OF TREES IN RELATION TO LIGHT INTERCEPTION AND USE IN MATURE FORESTS PROBABLY DUE TO THE TECHNICAL DIFFICULTIES ASSOCIATED WITH MEASURING LIGHT AND BIOMASS IN MATURE TREES. LIGHT COMPETITION IN MATURE FOREST STANDS COULD DIFFER FROM THAT IN HERBACEOUS COMMUNITIES FOR SEVERAL REASONS. FIRST, TREE SPECIES ACCUMULATE BIOMASS OVER YEARS AND FOREST STANDS HAVE LARGE, COMPLEX STRUCTURES, WHILE HERBACEOUS COMMUNITIES HAVE LIMITED AMOUNTS OF BIOMASS AND THEIR ABOVE-GROUND STRUCTURE NORMALLY RESISTS TO ZERO ONCE THE GROWING SEASON ENDS (WINTER OR DRY SEASON) OR UNDER DISTURBANCE (E.G. FLOODING OR MOWING). SECOND, STRATIFIED STRUCTURE (I.E. CANOPY, SUBCANOPY AND UNDERSTOREY LAYERS) IS OFTEN SEEN ACROSS SPECIES IN FORESTS (KOHYAMA 1993; AIBA & KOHYAMA 1996; POURTER ET AL. 2005) BUT IS USUALLY MUCH LESS APPARENT IN HERBACEOUS STANDS. THIRD, LIGHT ATTENUATION IN THE CANOPY TENDS TO BE STRONGER IN FOREST STANDS THAN IN HERBACEOUS COMMUNITY, WHICH MAY INFLUENCE PERFORMANCE OF UNDERSTOREY SPECIES. FOR EXAMPLE, LIGHT LEVELS AT THE FOREST FLOOR IN MATURE TROPICAL FORESTS ARE TYPICALLY 1–2% OF NATURAL DAY LIGHT (CHAZDON & FETCHER 1984), WHICH IS WELL BELOW THE VALUES FOUND IN HERBACEOUS STANDS (5–20%, LARCHER 2003; HIROSE & WERGER 1995; ANTHOR 2010).

THIS STUDY AIMS TO UNDERSTAND LIGHT ACQUISITION AND USE STRATEGIES OF CO-OCCLUDING SPECIES IN A MATURE FOREST COMMUNITY TO FURTHER OUR UNDERSTANDING OF THE MECHANISMS UNDERLYING SPECIES COEXISTENCE UNDER ONE-SIDED LIGHT COMPETITION. THREE-DIMENSIONAL LEAF DISTRIBUTION AND 3D LIGHT ENVIRONMENT IN A MATURE WARM-TEMPERATE RAIN FOREST WERE DETERMINED, RESPECTIVELY, BY EMPLOYING A PORTABLE LIGHT DETECTION AND RANGING (LIDAR) SYSTEM (PARKER, HARDING & BERGER 2004) AND LIGHT SENSOR ATTACHED TO A TELESCOPIC CARBON POLE. TOGETHER WITH INDIVIDUAL CANOPY CROWN GEOMETRY AND STEM GROWTH DATA, WE SUCCESSFULLY CALCULATED LIGHT INTERCEPTION AND LIGHT USE FOR GROWTH OF INDIVIDUAL TREES. SPECIFICALLY, WE ADDRESS THE FOLLOWING QUESTIONS: (I) HOW DO SPECIES DIFFER IN THEIR GROWTH RATE IN RELATION TO THEIR HEIGHT? (II) HOW DO SPECIES DIFFER IN VERTICAL LEAF DISTRIBUTION AND LIGHT INTERCEPTION? (III) IS LIGHT INTERCEPTION SYMMETRIC IN RELATION TO BIOMASS? (IV) IS LIGHT USE EFFICIENCY RELATED TO TREE HEIGHT? THE RESULTS OBTAINED IN THIS FRAMEWORK ARE DISCUSSED IN RELATION TO SPECIES COEXISTENCE IN FORESTS.

MATERIALS AND METHODS

LIGHT INTERCEPTION AND USE EFFICIENCY

TO CLARIFY HOW CO-OCCURRING SPECIES OR INDIVIDUALS OF DIFFERENT HEIGHTS INTERCEPT AND USE THE LIGHT ENERGY FOR GROWTH, THE GROWTH RATE OF INDIVIDUALS WAS ANALYSED AS THE PRODUCT OF LIGHT INTERCEPTION EFFICIENCY (LIE) AND LIGHT USE EFFICIENCY (LUE).

\[ ΔM = ΔM/Φ × Φ/M \times M = LUE \times LIE_M \times M \]

EQUATION 1

WHERE ΔM IS BIOMASS INCREMENT PER PLANT PER UNIT TIME, Φ IS THE AMOUNT OF LIGHT INTERCEPTED PER PLANT PER UNIT TIME AND M IS PLANT ABOVE-GROUND BIOMASS. ΔM/Φ IS BIOMASS GAIN PER UNIT ABSORBED LIGHT.
denoted here as the light use efficiency (LUE). \( \Phi/M \) is light interception per unit above-ground biomass, denoted as the light interception efficiency (LIE\(_{\text{LA}}\)), which is equivalent to \( \Phi_{\text{max}} \) defined in Hirose & Werger (1995). Equation 1 can be converted into RGR = LUE \times LIE\(_{\text{LA}}\) by dividing the term M on each side of the equation, where RGR means relative growth rate.

Light interception efficiency (LIE\(_{\text{LA}}\)) can be further analysed as the product of light interception efficiency per unit leaf area (LIE\(_{\text{LA}}\), also called \( \Phi_{\text{area}} \) in Hirose & Werger 1995) and leaf area ratio (LAR, total leaf area per unit total mass);

\[
\Phi/M = \Phi/\text{LA} \times \text{LA}/M = \text{LIE}_{\text{LA}} \times \text{LAR} \tag{eqn 2}
\]

If light interception or utilization is size-asymmetric, we would expect these parameters (LIE\(_{\text{LA}}\), LIE\(_{\text{LA}}\), or LUE) to be correlated with size measures such as height or biomass.

**STUDY SITE**

A mature warm-temperate evergreen forest in Yakushima island, the southern part of Japan, was studied (latitude 30.380 N, longitude 130.627 E, elevation 150 m). This forest is located on Yakushima National Park as well as National Monumental Area of Japan. The forest plot is located on a virtually flat hill and had minimal human disturbance for at least 150 years. Annual precipitation is 4477 mm, and mean annual temperature is 19.4 degree (average over 1981–2010) at the Yakushima meteorological station (elevation 37 m) which is ca. 3 km away from the study site.

The study site was part of a long-term monitored 0.5-ha forest plot established in 1998. Diameter at breast height (DBH) of all individuals (DBH > 5 cm) in this plot was measured every 2–5 years. Within the plot, 33 different woody species (DBH > 5 cm) were recorded with *Distylium racemosum* (Hamamelidaceae) being the most abundant species. In the present study, we focused on a 1200 m\(^2\) (60 \( \times \) 20 m), subsection of the plot, in which 24 species were found (Table 1).

**LEAF AREA DISTRIBUTION AND LIGHT INTENSITY**

We used a ground-based, portable lidar system (LD-90, Riegel Laser Measurement Systems, Horn, Austria) customized according to Parker, Harding & Berger (2004) to quantify above-ground forest structure. This system measures the vertical distance to a given plant surface (leaves, branches and trunks) for 1000 times per second (1000 Hz). At every 1.25 \( \times \) 1.25 m in our studied area (= 768 places), we made a vertical profile measurement by moving the lidar system horizontally around the body of the measuring person (Aku- tsu, Khen & Toda 2007). Each measurement obtained ca. 1000 height profile data. By applying the method of MacArthur & Horn (1969), the density of foliage along height can be calculated.

\[
D(h) = -\left(\frac{d(\ln q(h))}{dh}\right) \tag{eqn 3}
\]

where \( D(h) \) is the density of foliage at height \( h \), \( q(h) \) is the probability of no laser interception within a vertical column up to \( h \) above the position of the lidar (lidar height was 1 m above the ground). By integration of \( D(h) \) for each height class, we can calculate foliage profiles along the height in the canopy. In this study, the vertical foliage profile was calculated at 1 m intervals.

As there is a trade-off between vertical accuracy and horizontal resolution (as clarified in Appendix S1, Fukushima, Hiura & Tanabe 1998), we chose 2.5 \( \times \) 2.5 m land area as a minimum size in which to determine the vertical profile of foliage, based on our preliminary trial. Accordingly, four sets of height profile data (i.e. 1.25 m \( \times \) 1.25 m \( \times \) 4 sets = 2.5 \( \times \) 2.5 m) were combined for subsequent analysis.

While the MacArthur and Horn method does not yield the absolute leaf area index (LAI), it provides relative LAI at given height intervals (Aber 1979), which was well matched with the actual measurement of leaf area distribution (Fukushima, Hiura & Tanabe 1998). As noted below, leaf area calculated by lidar matched well with that calculated using allometric equations (LAallo = 1.273 LAtri, \( \text{eqn 2} \), \( R^2 = 0.576 \)) and converged around the 1 : 1 relationship (Fig. S1), that is, the 95% confidence interval of the slope of log-log plot was 0.88–1.09. Furthermore, leaf area calculated by lidar, rather than that calculated by allometric equation, was better correlated with the amount of light interception per individual (see below for calculation) (\( R^2 = 0.662 \) vs. 0.568, Fig. S2). These results indicate that 3D leaf area distribution was well reproduced by the lidar method, and thus, we used the vertical leaf density profiles calculated with eqn (3) as a measure of leaf area distribution without further adjustment.

Three-dimensional profiles of photosynthetic photon flux density (PPFD, 400–700 nm) were measured with a PPFD sensor (LI-190SA, Li-Cor, Lincoln NE, USA) attached to a 15-m telescopic carbon rod (Taketani Trading Co., Osaka, Tokyo). The measurement was taken under an overcast sky, to represent the average light environment without confounding influence of direct sun light. Vertical light profiles were measured from 1 to 17 m (15 m + 2 m holding by person) above the ground at 1 m intervals at the centre of each grid. For each height, average PPFD over 10 seconds was logged in a data logger (LI-1400, Li-Cor). Light intensity above the canopy was used as reference, and relative light intensity along the height was calculated for each grid. In a few cases, 17 m height was not enough to reach above the canopy. In those cases, the light above the canopy measured simultaneously in a neighbouring grid was used as a reference.

**DETERMINATION OF CANOPY STRUCTURE, BIOMASS AND GROWTH**

For each individual tree, the top and bottom height of its crown, the major and minor horizontal axes of the crown (approximated as ellipse) and their orientation were recorded using an ultrasonic range finder (Vertex IV, Haglöf, Längsele, Sweden).

Diameter at breast height was measured for each individual in April 2008 and May 2011. Based on tree height, DBH and wood density data, we calculated above-ground biomass using an allometric equation, which was based on the destructive harvest data of the similar set of species found in lowland forest in Yakushima (Kitazawa et al. 1960; Kawambe 1977; See Table S1 for further information). Wood density data for most species were obtained from Aiba & Ko- hyama (1997), supplemented by additional measurement for species without existing data (Table 1). These data covered DBH from 1.5 to 72 cm, and the coefficient of determination (\( R^2 \)) of this allometric equation was 0.986 (\( n = 20 \)). The leaf area ratio (LAR) was calculated as the leaf area, calculated by the lidar measurement, per unit above-ground biomass calculated by the above-mentioned allometric equation.

Growth rate was calculated as the above-ground biomass increment per year which was based on the DBH growth collected in April 2008 and May 2011, and relative growth rate (RGR) was calculated as \( \ln(M_{2011}) - \ln(M_{2008})/T \). Where \( T \) is the time being 3 year in our case. Below-ground biomass was not considered in this study as we did not have information on this. As shown later, as LIE and
LUE varied more than an order of magnitude, variation in below-ground allocation (normally 10–20% of total biomass) may have a marginal effect on our result.

Leaf mass per area (LMA, inverse of specific leaf area (SLA)) was measured for top crown leaves from three mature individuals for each species nearby the study site. LMA and leaf area data based on lidar measurement were used to calculate total leaf mass for each individual. Leaf mass thus calculated matched well with values calculated by the allometric relationship \( \text{LMA}_{\text{all}} = 1.14 \times \text{LMA}_{\text{lidar}}^{0.70}, \quad R^2 = 0.535 \). Variation of LMA within canopy was not considered in this study, but this effect in our results should be marginal as 79% of above-ground biomass was accounted by stems rather than leaves. Furthermore, as shown later, LIEg varied more than an order of magnitude across tree heights, which overrode effects of variation of LMA.

### Table 1. Species information and characteristics of 24 species found in the study site.

<table>
<thead>
<tr>
<th>Abb</th>
<th>Species</th>
<th>Family</th>
<th>N</th>
<th>H\text{max}</th>
<th>H\text{med}</th>
<th>DBH\text{max}</th>
<th>CanoSL</th>
<th>WD</th>
<th>LMA</th>
<th>Relative light</th>
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<td>22.73</td>
<td>1.542</td>
<td>0.624</td>
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<td>187</td>
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<td>152</td>
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</tr>
<tr>
<td>Tt</td>
<td>Turginia terna</td>
<td>Staphyleaceae</td>
<td>2</td>
<td>10.4</td>
<td>8.9</td>
<td>25.31</td>
<td>0.787</td>
<td>0.48</td>
<td>101</td>
<td>4.2 (1.2–13.7)</td>
</tr>
<tr>
<td>Za</td>
<td>Zanthoxyllyum ailanthoides</td>
<td>Rutaceae</td>
<td>1</td>
<td>16.1</td>
<td>16.1</td>
<td>32.15</td>
<td>0.189</td>
<td>0.432</td>
<td>99</td>
<td>84.7 (81.5–100)</td>
</tr>
</tbody>
</table>

**CALCULATION OF LEAF AREA AND LIGHT INTERCEPTION OF EACH INDIVIDUAL**

Attenuation of light intensity within canopy crowns was considered as interception of light by plants. Delta RL (relative light) was calculated as the difference in RL between each pair of vertically aligned height classes for each grid. Leaf area density and the amount of intercepted light were thus calculated for each height class at each grid (2.5 m width × 2.5 m width × 1 m height, which we called ‘voxel’ in this study). For each individual tree, we identified the voxels that were located within its crown. By summing leaf area density and light interception over these voxels, respectively, whole-plant leaf area density and the amount of intercepted light were calculated.

When more than two individuals occupied the same voxel (overlapping crown), leaf area density and intercepted light in the voxel was equally split among the sharing individuals. It was difficult to evaluate leaf area and light interception of very small individuals due to the given resolution (2.5 × 2.5 m), and thus, individuals that occupied less than three voxels were not included in our analysis.

To calculate the daily light interception, relative light intensity was multiplied by daily average PPFD (57.47 mol m⁻² day⁻¹) which was calculated from typical insolation in Yakushima Island (12.575 MJ m⁻² day⁻¹, average across 1961–1967 Japan meteorological agency) and a conversion constant (4.57 mol PPFD MJ⁻¹ under natural light; McCree 1972; Amthor 2010). It was assumed that the forest structure remained the same throughout the year, which we believe was reasonable as the forest at our site was mature and mostly evergreen (198 of 205 individuals were evergreen) and did not exhibit large changes in canopy structure over a single season.

Further discussion about pros and cons of our method is available in Appendix S1.

**STATISTICAL ANALYSIS**

All data were log₁₀ transformed before statistical analysis. Pearson’s test was used to test significance levels of correlation among parameters. Simple regression (ordinary least square) was used to model relationships between light competition parameters and plant height. Standardized major axis slope was used to fit relationship between LIE and LUE (Warton et al. 2006). Data were analysed using R statistical package (version 2.15.0; R Foundation for Statistical Computing, Vienna, Austria).
Results

LIGHT AND LEAF DISTRIBUTION

An example transverse section of 3D light (PPFD) and foliage distribution in our study forest are shown in Fig. 1. Most of the foliage was concentrated at around 10–15 m above the ground. Lower amounts of foliage were located at the middle and lower heights and mostly pertained to subcanopy and understorey species. Light attenuated strongly within the canopy, and at 1 m above the ground, relative PPFD intensity was on average 1.25% (95% CI = 0.25–3.5) of the PPFD above the canopy. Both light intensity and foliage density were strongly heterogeneous not only vertically but also horizontally. Location of crowns measured by the rangefinder coincided well with leaf distribution measured by lidar and with attenuation of PPFD (Fig. 1b). In a few cases, lidar seemed not to capture leaves at very high positions where the PPFD measurement indicated light interception, but in general, the two measures corresponded very well to each other. More detailed transverse sections of light and foliage distribution of our studied forest are available in Figs S3 and S4.

Vertical distributions of foliage density were summarized for each species including all individuals found in the study site (Fig. 2), and their corresponding light environment was summarized in Table 1 (median and 95% CI of foliage light environment). The most abundant species, Distylium racemosum, is a late-successional evergreen species and had leaves from the top canopy to lower storey (Fig. 2). This is partly due to the fact that there are many small individuals as well as large individuals in the studied area. Quercus salicina and Machilus thunbergii are also late-successional evergreen species, but Q. salicina may be more light-demanding as indicated by their relatively high median foliage light environment (37.4% for Q. salicina and 9.1% for M. thunbergii, Table 1). Stewartia monadelpha is the only deciduous species among the 15 major species shown in Fig. 2 and is considered to be a long-lived pioneer species. There were several shade-tolerant subcanopy species, which rarely reach to the top canopy but have leaves from the subcanopy layer to the understorey layer. These included Camellia sasanqua, C. japonica, Ardisia sieboldii, Neolitsea aciculata, Myrsine sequinii, Cinnamomum tenifolium and Cleveria japonica. Their median foliage light environment was mostly <10% of full light (Table 1).

GROWTH RATES

Across individuals, the above-ground growth rate was strongly determined by tree height (56%) that linked to vertical light gradient, and horizontal heterogeneity of light had a minor influence on the tree growth rate (7%) in our studied site (see Fig. S5). These results confirmed that trees in our studied forest were subject to one-sided competition.

Figure 3a shows significant positive correlations between tree height and the above-ground growth rate both across and within species (black and grey lines are drawn for cross-species and within species, respectively). When size was normalized, species’ relative growth rate (RGR, growth expressed per unit mass) was independent of species mean height (Fig. 3b, \( P > 0.05 \)). Patterns within species were rather variable, and there was no general pattern in relationship between RGR and height.
Fig. 2. Vertical profile of foliage of the study site and of the major 15 tree species (by abundance) co-occurring in a warm-temperate rain forest. See Table 1 for species names. The scale of X-axis is the same for all figures (log₁₀-scale).

Fig. 3. (a) Growth rate, (b) relative growth rate (RGR), (c) light interception efficiency per unit above-ground biomass (LIE₃ₐ), (d) light interception efficiency per unit leaf area (LIE₃ₐ), (e) leaf area ratio (LAR, = leaf area per unit above-ground biomass) and (f) light use efficiency (LUE) of co-occurring tree species versus tree height. Each point represents species mean value. See Table 1 for species names. Black lines denote simple regression (ordinary least square, OLS) \( P < 0.05 \) solid line; \( P > 0.05 \) dotted line) for species means. Simple regressions were also drawn for individual data within species (grey line) to visualize patterns of within-species variation irrespective of levels of significances.
LIGHT INTERCEPTION AND USE STRATEGY

Light interception per unit above-ground biomass (light interception efficiency, LIE_M) was positively correlated with tree height across species and, in many cases, also within species (Fig. 3c). Taller trees intercepted disproportionately larger amounts of light relative to their mass than smaller trees did, supporting the view of asymmetric competition for light interception. As shown in eqn 2, LIE_M can be analysed as the product of light interception per unit leaf area (LIE_LA) and leaf area ratio (LAR, leaf area per above-ground mass). The correlation between LIE_LA and height was much stronger, and its slope was steeper than that of LIE_M/height relationship (Fig. 3d). Taller trees intercepted disproportionately larger amounts of light for their leaf area. On the other hand, LAR decreased with tree height both across and within species (Fig. 3e). Taller trees had relatively large fractions of stem biomass which reduced LAR.

Light use efficiency (LUE), which was calculated as biomass increment per unit intercepted light, was often negatively correlated with tree height across individuals within species (Fig. 3f), meaning that taller trees were less efficient in converting light energy to produce biomass than shorter trees. Across species, a similar negative correlation was found but not significant.

Light use efficiency and LIE_M were negatively correlated both within and across species (Fig. 4). As RGR is the product of LIE_M and LUE (eqn 1), the negative correlation between LIE_M and LUE resulted in RGR being rather similar between trees of different height. This can be recognized from the RGR values converging along the RGR = 0.01 isoline in Fig. 4. All these patterns remain similar when minor species are excluded from the analysis.

**Discussion**

SIZE-ASYMMETRIC COMPETITION FOR LIGHT INTERCEPTION

Taller individuals intercepted disproportionately large amounts of light relative to their size compared to smaller individuals both within and among species (Fig. 3c,d). This was consistent for different measures of size; above-ground biomass (Fig. 3c), total leaf area (Fig. 3d) and total leaf mass (data not shown). It seems a general pattern whether in herbaceous community or forests that taller plants intercept proportionally larger amounts of light relative to their leaf area (e.g. Hirose & Werger 1995; Anten et al. 1998; Bertness & Wayne 2000). However, in terms of light interception per unit above-ground biomass, our result contradicts the majority of herbaceous community studies, that is, taller trees intercepted proportionally larger amounts of light relative to their biomass (size asymmetric), while in herbaceous communities different sized species intercepted proportionally similar amounts of light relative to their biomass (e.g. Hirose & Werger 1995; Anten & Hirose 1999; Werger et al. 2002; Aan et al. 2006). This discrepancy may be attributed to differences in canopy structure between mature evergreen forests and herbaceous communities. First, light extinction in the canopy was much stronger in the mature forest than in herbaceous communities. In our study, on average 1.25% of day light reached the forest floor, which is typical for mature evergreen forests (Chazdon & Fetcher 1984). In herbaceous communities, this value is usually higher (i.e. 5–20% Larcher 2003), thus understory individuals in mature forests are often more strongly shaded than those in herbaceous communities. Second, understory individuals in mature evergreen forests often have long leaf life spans compared with canopy species (Kitajima & Poorter 2010; Onoda et al. 2011) that can compensate for their suppressed efficiency of light interception. Actually, in a tropical forest, it was found that shade-tolerant species had longer leaf longevity and higher lifetime light interception per unit mass than the taller pioneer species even if their instantaneous LIE_M was lower (Selaya et al. 2008).

LIGHT USE EFFICIENCY

We found that taller plants were less efficient in terms of light use than shorter plants (Fig. 3f), both within and across species. Lower LUE in taller plants was also observed in a herbaceous community (Hikosaka, Sudoh & Hirose 1999), although they modelled carbon gain rather than direct measurement of growth as was taken here. The higher LUE of small plants could be attributed to at least three factors. First, top canopy leaves cannot utilize strong light (c. 2000 µmol m⁻² s⁻¹ at midday sunny condition) efficiently for photosynthesis because leaf photosynthetic rates saturate at high PPFD (i.e. 500–1000 µmol m⁻² s⁻¹). Leaves of small plants, on the other hand, generally receive PPFD well below the saturation point, and thus, their leaf-level light use efficiency for photosynthesis can be higher. Second, diffuse
light, which is more abundant than direct light in the understorey of the forest, can be used more efficiently for photosynthesis (Gu et al. 2003). Additionally, penumbra effects (partial shadow) that tend to increase the proportion of light useful for photosynthesis in lower canopy layers, should be more pronounced in forest stands than in short herbaceous communities (Pearcy 1990). Third, small plants may have proportionally lower respiration costs. Larger plants allocate a larger fraction of biomass to supporting organs (e.g. stem and root) with size (King 1991), which was reflected in LAR reduction with stature observed here (Fig. 3c). Larger plants therefore probably use a larger fraction of their assimilated carbon for maintenance and less for growth than smaller individuals (DeLucia et al. 2007). This effect may be particularly important in forests because biomass and allocation to supporting tissues are usually much larger in trees than in herbaceous plants and also because there is a larger variation in plant size in forest communities than in herbaceous communities. Finally, taller trees may experience stronger hydraulic constraints (e.g. Ryan & Yoder 1997), photo-inhibition (e.g. Werner et al. 2001) and greater wind loading (e.g. Yasumura et al. 2002) which could also suppress their LUE.

TRADE-OFF BETWEEN LIGHT INTERCEPTION AND USE EFFICIENCY – IMPLICATION FOR SPECIES COEXISTENCE

Taller plants were more efficient in terms of light interception but tended to be less efficient in terms of light use than smaller plants (Fig. 4). As a result of this apparent trade-off between LIE and LUE, relative growth rates were less variable and independent from tree height (RGR = LUE × LIEIR)."
Species coexistence in one-sided competition


McCree, K.J. (1972) Test of current definitions of photosynthetically active radiation against leaf photosynthesis data. Agricultural Meteorology, 10, 443–453.


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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Pros and cons of our method.

Figure S1. Comparison of leaf area estimated by lidar and by allometric equation.

Figure S2. The amount of intercepted light per plant is plotted against leaf area.

Figure S3. Light profile of our studied forest.

Figure S4. Foliage profile of our studied forest.

Figure S5. Effects of vertical and horizontal heterogeneity of light on tree growth.

Table S1. Allometric equations and their original data.