Retrieval of vertical LAI profiles over tropical rain forests using waveform lidar at La Selva, Costa Rica

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Abstract

This study explores the potential of waveform lidar in mapping the vertical and spatial distributions of leaf area index (LAI) over the tropical rainforest of La Selva Biological Station in Costa Rica. Vertical profiles of LAI were derived at 0.3 m height intervals from the Laser Vegetation Imaging Sensor (LVIS) data using the Geometric Optical and Radiative Transfer (GORT) model. Cumulative LAI profiles obtained from LVIS were validated with data from 55 ground to canopy vertical transects using a modular field tower to destructively sample all vegetation. Our results showed moderate agreement between lidar and field derived LAI ($r^2=0.42$, RMSE=1.91, bias=−0.32), which further improved when differences between lidar and tower footprint scales ($r^2=0.50$, RMSE=1.79, bias=0.27) and distance of field tower from lidar footprint center ($r^2=0.63$, RMSE=1.36, bias=0.0) were accounted for. Next, we mapped the spatial distribution of total LAI across the landscape and analyzed LAI variations over different land cover types. Mean values of total LAI were 1.74, 5.20, 5.41 and 5.62 over open pasture, secondary forests, regeneration forests after disturbances, and tropical rain forest, respectively. We found for both, that the effects were not significant for moderate LAI values (about 4). However, our model derivations of LAI might be inaccurate in areas of high-slope and high LAI (about 8) if ground return energies are low. This research suggests that large footprint waveform lidar can provide accurate vertical LAI profile estimates that do not saturate even at the high LAI levels in tropical rain forests and may be a useful tool for understanding the light transmission within these canopies.

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1. Introduction

Tropical forests store 13% of the global carbon and play an important role in terrestrial carbon dynamics and other ecosystem processes (Clark & Clark, 2000). Leaf area index (LAI), commonly defined as the maximum projected leaf area per unit ground surface (Chen et al., 1997), is an important ecosystem model parameter strongly linked to plant respiration and photosynthesis (Gower & Norman, 1991). In addition, LAI is often used to parameterize surface energy balance and hydrological models for effects such as radiation attenuation and precipitation interception.

The vertical variation in LAI is related to foliage-height profiles (Aber, 1979) which have been shown to be important determinants of energy, water and nutrient flows (Parker et al., 2001). Because foliage at different height intervals contributes differently towards total photosynthesis and canopy carbon storage (Ellsworth & Reich, 1993), the vertical distribution of leaf material may also play a role in determining habitat suitability and species abundance and diversity (Swatantran et al., 2011).

The importance of LAI has thus led to considerable efforts by the remote sensing community to map its distribution over a variety of spatial and temporal scales. Passive remote sensing data have been used to derive LAI using empirical relationships between reflectance and field measured LAI (Chen & Cihlar, 1995; Chen et al., 1997; Cohen et al., 2003; Morissette et al., 2006), and using physically-based radiative transfer modeling (Koetz et al., 2005). However, results from different sensors are not consistent. Their accuracies vary considerably (Abuelgasim et al., 2006) and drop significantly in dense tropical forests where LAI is high. In addition, passive remote sensing systems do not adequately capture vertical variation in LAI. In contrast, lidar (light detection and ranging) potentially provides this vertical dimension information.

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Lidar has been successfully used to derive forest structural characteristics such as canopy height, forest structure and aboveground biomass in different forest types (Drake, 2002a; Hyde et al., 2005; Lefsky, 1999). Recent studies have used lidar data to derive LAI (Farid et al., 2008; Jensen et al., 2008; Morsdorf et al., 2006; Richardson et al., 2009; Solberg et al., 2009). Predictor variables (often called "lidar metrics") are generally derived from discrete return or waveform-based small footprint lidar data (e.g. canopy height) to perform regression analysis in these studies. Zhao and Popescu (2009) combined lidar data and other optical remote sensing metrics (e.g. NDVI) but found adding such metrics did not improve LAI estimates significantly. Riano (2004) compared LAI values from both airborne lidar and hemispherical photography in central Spain, and found that LAI was better estimated using a radius size of lidar sampling scale from 7.5 to 12.5 m. Their results suggested LAI could be better predicted using a medium footprint lidar. However, there has been little research using lidar data to estimate LAI in tropical rain forests, where the saturation problem for passive remote sensing is significant (Abuelgasim et al., 2006). Furthermore, the use of medium to large footprint waveforms to derive LAI, such as those from the airborne Laser Vegetation Imaging Sensor (LVIS) has not been explored.

Our research goal is to study the spatial and vertical distributions of LAI over the La Selva Biological Station in Costa Rica using the airborne scanning waveform lidar from LVIS. We first derive vertical LAI profiles from LVIS waveforms using the physically-based Geometric Optical and Radiative Transfer (GORT) model (Ni-Meister et al., 2001). Next, we validate the vertical LAI profiles derived from lidar with field-based measurements of destructively sampled LAI at towers and then map LAI spatially across the landscape. Finally, we assess the accuracies and sensitivity of LAI retrieval from lidar waveforms and discuss their implications for large-scale mapping.

2. Study area and data

2.1. Study area

La Selva Biological Station is located in the Atlantic lowlands of Costa Rica. It is one of the most extensively studied field sites in tropical forests, with a well-documented history of its biological data sets. The area receives an annual rainfall of 4000 mm and has a mean temperature of 26 °C. The topography of this study site is relatively low (<150 m), but there are some areas with slopes exceeding 30°. The station has a mixture of old growth and secondary lowland tropical wet forests along with remnant plantations and various agroforestry treatments. Most canopy trees here are evergreen or only briefly deciduous. Detailed site characteristics can be found in Clark et al. (2008) and Dubayah et al. (2010).

2.2. Field data

LAI was measured in a 515 ha section of upland tropical wet forest at the La Selva Biological Station by Clark et al. (2008). A modular walk-up tower was built to harvest all leaves and branches in 55 vertical transects from ground to canopy top (Fig. 1). The tower footprint was 1.30 m × 1.86 m for the first four transects (June-August 2003) and it was expanded to 2.45 m × 1.86 m for the next 51 transects (August 2003–March 2005). Because data from the two configurations did not differ significantly in LAI or forest height, they were processed together. The tower locations were selected by strict stratified random sampling. The landscape was divided in 9 classes of cells based on high, medium and low GIS-predicted phosphorus and high, medium and low GIS-predicted slope. 10 × 10 m cells were selected at random (with predetermined constraints such as no streams) with each of the 9 classes. An additional 10 low canopy sites were selected with a different semi-random protocol. Tower sites were geolocated using differential GPS and the La Selva base station. Nominal geolocation accuracy with differential correction was <1 m. Tower sites were separated by an average of 153 m from their nearest neighbor, so they represented independent samples of forest conditions within a given forest type. Leaf areas of all species were measured at each height section (1.86 m per section) in laboratory after destructive sampling (discussed below).

2.3. Lidar data

LVIS is a medium footprint (~25 m), waveform digitizing, scanning laser altimeter focusing on the study of surface topography and vegetation structure (Blair, 1999). LVIS digitizes the entire outgoing and return signal to provide a waveform from which attributes such as ground elevation, canopy height, canopy cover and canopy height profiles can be derived. Standard products from LVIS include both fully digitized waveforms as well as height metrics at different waveform energy returns (Holton, 2002; Holton et al., 2006). Many studies have shown the ability of LVIS in mapping forest structure and habitat characteristics in tropical and temperate forests (Drake, 2002b; Hyde et al., 2005), but direct derivation of LAI from LVIS waveforms has not been attempted. The LVIS instrument was flown over the entire La Selva in both 1998 and 2005. The swath width in 2005 was 2 km and nominal footprint diameter was 25 m. In this study, we used only the 2005 LVIS waveform data to derive LAI contemporaneous with the field data collection. We did not consider the temporal lags or seasonal discrepancy between field and lidar data because wet tropical forests are evergreen or only briefly deciduous and LAI values at tall sites (>21 m) did not differ between sites sampled in the dry season (January–May) or in the wet season (P>0.51, n = 10, 28) for the 2003–2005 sample period (Clark et al., 2008).

3. Methods

We derived cumulative LAI profiles from both destructive sampling and LVIS data and then compared them at the same vertical and spatial scales. Areas of collected leaves from the ground to a particular height were integrated to ascertain tower-cumulative LAI, which could then be compared to LVIS-cumulative LAI derived from GORT model. The derived LVIS LAI profiles were adjusted to better match the scale of the LAI tower measurements, as the latter has a far smaller area than an LVIS footprint. Lastly we filtered tower locations as a function of their distance from the center of the nearest LVIS footprint to explore the degree to which their non-coincidence affects LAI retrieval accuracy.

3.1. Cumulative LAI from tower measurements

Leaves harvested at each section of tower height were measured in the laboratory according to different plant functional groups: Pentaclethra (dominant trees), other trees, palms, lianas, herbaceous climbers, herbs, ferns, non-woody epiphytes and woody epiphytes (Clark et al., 2008). A LI-COR-3100 leaf area meter was used to measure the one-sided leaf area. LAI for a certain height section was quantified in the laboratory according to different plant functional groups. The LAI was calculated per height section from the ground to a particular height section. There were a total of 546 tower-cumulative LAI values at different heights from all 55 towers (i.e. each tower provided multiple cumulative LAI estimates, one every 1.86 m from the ground to the top of the canopy). However, because not all towers were sufficiently co-located with LVIS footprints, some were removed from the validation data set (discussed below).
3.2. Cumulative LAI profiles from LVIS waveforms

In this section, we derive cumulative LAI profiles from lidar waveforms using gap theory (Chen & Cihlar, 1995; Chen et al., 1997; Gower & Norman, 1991; Miller, 1967; Nilson, 1971, 1999) which quantifies the relationship between LAI and the gap frequency for horizontally homogenous canopy layers according to the general formula:

$$ P(\theta) = e^{-G(\theta)/\cos(\theta)} $$  \hspace{1cm} (1)

where $P(\theta)$ is the gap probability within canopy with a view zenith angle of $\theta$ and $G(\theta)$ is the projection coefficient representing unit leaf area on the canopy layer perpendicular to the view direction. For LVIS we assume the viewing zenith angle is constant at 0, and hence we only need information of gap probability and projection coefficient to obtain LAI.

Ni-Meister et al. (2001) developed a method to derive gap probability and canopy cover from lidar waveforms. The basic assumption of the model is that gap probability is the reverse of the vertical canopy profile as laser energy can only penetrate into the lower canopy layer or ground through gaps (including both within-crown gaps and between-crown gaps). Using this relationship, canopy closure is calculated using the cumulative laser energy return for a known ratio of canopy and ground reflectance as follows:

$$ P(z) = 1 - cover(z) = 1 - \frac{R_c(z)}{R(0)} \cdot \frac{1}{1 + \rho_v/\rho_g} $$  \hspace{1cm} (2)

where $P(z)$ and cover($z$) represent the gap probability and canopy cover percentage above a particular height $z$ within canopy respectively. The terms $R_c(z)$, $R_v(0)$ and $R_g$ are the integrated laser energy returns from the canopy top to height $z$, from canopy top to canopy bottom, and from the ground return individually. The canopy and ground reflectance are $\rho_v$, $\rho_g$ respectively. This model in general measures plant area index, not leaf area index, since branches and trunks also reflect laser energy. But we did not explicitly consider the difference between the two in this research as the large majority of energy (93%) reflected back towards the sensor comes from the leaves with only 7% from other areas of the plant (Note: both leaf and plant area data were destructively sampled to determine this ratio, but the plant area data are not published and are unavailable).

We applied a similar approach to the LVIS data to get gap probability and canopy cover at La Selva. Mean signal noise level was first subtracted from raw waveforms to reduce noise. We then applied Gaussian decomposition of waveforms to separate $R_v$ and $R_g$ (Hofton et al., 2000). This method may not accurately provide a separation if topographic slopes are present and we examine this effect using a sensitivity analysis as described in the discussion section. The quantity $\rho_v/\rho_g$ was calculated from ASD FieldSpec spectrometer (Analytical Spectral Devices, Boulder, CO, USA) measurement of soil and leaves in our study area by Clark et al. (2005). The ground reflectance $\rho_g$ was calculated as an average value of 0.14 (s.d. = 0.03) for 19 soil reflectance samples at 1064 nm. For $\rho_v$, we only considered the dominant species, Pentaclethra. Only 4 ASD measurements of Pentaclethra were available (0.31, 0.34, 0.38 and 0.51 at 1064 nm). The 0.51 value was too large for single leaf reflectance and hence was not accurate, possibly because of multiple scattering (Clark et al., 2005). As a result, we calculated the average (0.34) of the first three values. Then we obtained the $\rho_v/\rho_g$ value of 2.5 at 1064 nm and used it as the mean value for the whole study area. With the relevant information regarding canopy and ground energy separation as well as $\rho_v/\rho_g$, the cumulative gap probability and canopy cover was then calculated using Eq. (2).

Fig. 1. Land use map of La Selva Biological Station, Costa Rica. 55 LAI measurement towers were constructed across different forest areas, but mainly focused on old-growth forest.
Finally, we calculated the apparent foliage profiles and cumulative LAI profiles based on the derived gap probability. The apparent foliage profile was defined by the following equation:

$$F_{app}(z) = \frac{d \log P(z)}{dz}$$ (3)

The log transformation of gap probability follows MacArthur and Horn (1969); the density of foliage can be estimated from the distribution of first leaf distance. Note that it is actually a transformation of Eq. (1). The cumulative LAI profile was then calculated through the actual foliage profile (or foliage area volume density), which is a projection adjustment of $F_{app}(z)$ (Ni-Meister et al., 2001) using the following equation:

$$LAI_{cum}(z) = C \times \int_{z_0}^{z} F_{app}(z)dz = C \times \int_{z_0}^{z} \frac{d \log P(z)}{dz} \cdot \frac{1}{G}dz$$ (4)

where $LAI_{cum}(z)$ is the cumulative LAI as a function of height $z$ and $z_0$ is the height location of the canopy bottom. The term $F_{app}(z)$ is the foliage area volume density with units of $m^2/m^3$ and $G$ is the projection coefficient used to adjust the apparent foliage profile $F_{app}(z)$ to $F_{app}(z)$. Assuming a random foliage distribution within the canopy, we set the projection coefficient $G$ to be 0.5 (Ni-Meister et al., 2001). Clumping index $C$ is another important parameter which adjusts the linear relationship between effective LAI and true LAI (Chen et al., 1997). Chen et al. (2005) derived global foliage clumping indices from multi-angular satellite POLDER data and we chose the mean clumping index value of 1.58 for broadleaf and evergreen forest.

3.3. Scale adjusted cumulative LAI from LVIS waveform

LAI estimates from lidar and measurements from field towers have different footprint areas (~500 m² for LVIS vs. less than 5 m² for tower). A direct comparison between these two datasets may be problematic, especially in areas with low canopy cover or high canopy cover variability. For example, the LAI value from LVIS would be smaller than from a tower because tower footprints include only trees whereas LVIS footprints cover both trees and gaps. Therefore, it is necessary to convert cumulative LAI derived from LVIS to the same scale of tower measurement by adjusting for these footprint discrepancies.

We performed a scale adjustment from LVIS LAI to tower using LVIS canopy cover (Eq. 5).

$$LAI_{scale}(z) = \frac{LAI_{cum}(z)}{f_{cover}(0)} = \left(1 + \frac{\rho_z}{\rho_k} \frac{R_z}{R_k(0)}\right) \cdot C \times \int_{z_0}^{z} \frac{d \log P(z)}{dz} \cdot \frac{1}{G}dz$$ (5)

The adjustment is based on the assumption that foliage distribution within the tower is the same as all other canopy-covered areas within an LVIS footprint. We divided LVIS LAI by the canopy cover to approximate the same foliage distribution as the tower LAI. This has the effect of excluding between-tree gap areas in the calculation of LAI in an LVIS footprint. Total canopy cover ($f_{cover}$) was calculated using Eq. (2).

Note that canopy cover derived here is only an approximation because we cannot separate within-crown gaps and between-crown gaps directly. LVIS LAI has also been integrated from original vertical resolution (about 0.3 m) to tower section height (1.86 m).

Total LAI for an LVIS footprint was directly calculated by setting the height variable $z$ to the maximum canopy height in $LAI_{cum}(z)$. It can also be calculated in Eq. (6) after solving the differential lidar equations of Eqs. (3) and (4).

$$LAI_{total} = \frac{C}{G} \times \ln \left(1 + \frac{R_k(0)}{\rho_k} \frac{R_z}{\rho_z}\right)$$ (6)

This total LAI value is at LVIS footprint scale and is unadjusted for scale differences with the towers (i.e. not divided by total canopy cover). Landscape scale LAI was then mapped using the total LAI derived in Eq. (6).

3.4. Distance of tower from lidar footprint center

Not all towers may be suitable for validating LVIS LAI because they may be too far away from the centers of the laser footprints (i.e. not coincident). The distance between LAI towers and laser shot center may also have a significant effect on canopy height measurement and the accuracy of LAI retrieval. The canopy height retrieval accuracy may drop significantly when the distance between field measurement and laser pointing center is greater than about 5 m (Blair & Hofton, 1999; Frazer et al., 2010; Hyde et al., 2005). We thus examined results after filtering out those towers farther than 5 m. This resulted in the removal of 16 towers and reduced the total validation points from N= 546 to 185.

4. Results

4.1. Comparison of lidar and tower LAI

Representative examples of cumulative LAI are shown in Fig. 2. The vertical resolution of cumulative profiles from LVIS is 1.86 m to match that of the towers. Cumulative LAI profiles from towers and LVIS generally showed the same trend for all types of LAI distributions (e.g. in Fig. 2 with low LAI ≈ 3, medium LAI ≈ 6 and high LAI ≈ 10). Cumulative LAI values generally increase as canopy height increase within a profile, but there can be a large difference of total LAI values for the same canopy height level (as it is the case for medium LAI ≈ 6 and high LAI ≈ 10 in Fig. 2).

Both original GORT derived cumulative LAI and scale-adjusted cumulative LAI were plotted against the tower measured cumulative LAI (Fig. 3). The original GORT model explains about 42% of the total variance with a bias of −0.32 and root mean square error (RMSE) of 1.91. The scale-adjusted model slightly improves this result explaining about 50% of total variance with a bias of 0.27 and RMSE of 1.79. Results further improved upon filtering out towers more than 5 m away from laser pointing center (Fig. 4). After adjustment for both scale and coincidence, our model explained about 63% of the total variance with a bias of 0.00 and RMSE of 1.36.

Fig. 2. Examples of cumulative LAI profiles from tower measurements and derived from LVIS.
were underpredicted by LVIS rise. Bins used to collect leaves. Note that after scale adjustment, many of the value that ment towers. The total sampling number is 546, which is the number of total tower bins used to collect leaves. We mapped spatial variations of total LAI (Fig. 5), as well as vertical LAI integrations from 0 to 5 m, 5–10 m, 10–20 m and 20 m–top canopy (Fig. 6) over the entire landscape. LAI values show great spatial variability both within and between land cover types at the scale of LVIS footprints (25 m). Total LAI distributions over different land cover and land use areas are summarized in Table 1 and Fig. 7. We found that the lowest LAI values were over open pastures (mean = 1.74, s.d. = 2.72). LAI of successional plots were somewhat higher (mean = 2.31, s.d. = 3.29). Regeneration forests from selective-logging had much higher LAI values (mean = 5.41, s.d. = 2.82). Secondary forests showed variability in LAI as a function of forest age (ranging from 6 years to 39 years), but also considerable variability of LAI within successional stages (Fig. 7). In general, LAI increases rapidly at early successional stages from about 6 years to 22 years, reaching a maximum at about 30 to 34 years before tapering off as stands mature. This is consistent with the concept of gap development as forests age (Kellner et al., 2011). The mean LAI value of all secondary forests was 5.20, close to the mean LAI value of old-growth forests (5.62). A t-test performed between the total LAI of old-growth and that of all the secondary forests combined resulted in a p-value < 0.05, indicating the difference was significant. Vertical LAI distributions also exhibit differences across different land cover types (Fig. 6). For example, integrated layer LAI for the top-most layer (20 m and above) tended to be much smaller for secondary forest than for old-growth forests (panel 4, Fig. 6).

5. Discussion

Both vertical LAI and total LAI were derived from LVIS waveforms with the GORT model (Ni-Meister et al., 2001). Our results demonstrate that vertical LAI distributions may be derived from lidar waveforms, in addition to total LAI. We stress here that these results are entirely based on physical derivation of LAI, not statistically based regression methods, as is commonly done. Our methodology thus provides a potential pathway for measuring LAI profiles without the need for field-measured LAI values to develop model relationships, though ancillary data (or assumptions) are required to parameterize our model (e.g. the ratio of vegetation to ground reflectance).

There were differences between the LVIS-derived cumulative LAI profiles and field measurements with about 37% of the total variance unexplained by our model. Even so, our results are comparable to results found in temperate and boreal needle forests using small footprint lidar (Jensen et al., 2008; Morsdorf et al., 2006). These results are encouraging considering the spatial and vertical heterogeneity of tropical rainforests and their high LAI values.

One source of unexplained variance in our model may be the large differences of footprint sizes between the towers and LVIS data. Even though we attempted to adjust for these differences, our method was only an approximation and thus could lead to errors in validation. Another source of error compounded with the difference in footprint size may be related to the non-coincidence of LVIS footprint centers with tower centers. While we tried to minimize this effect by including only those towers within 5 m of an LVIS footprint, errors may still be present. Consider shifting a 2 m × 2 m column a few meters in a tropical forest, the forest structure captured in the column may change considerably even under a small shift. Note that geolocation of either the towers or the footprint was done with high accuracies (<1 m) and is not considered as a significant source of error.

Another source of error may be the use of incorrect input parameters in our model (i.e. model error in contrast to the errors just discussed). To assess this, we analyzed model sensitivity to variations in one key parameter in the model known to affect canopy cover retrieval and LAI: leaf/soil reflectance ratio. The spatial variation of leaf/soil reflectance ratio $\rho_v/\rho_g$ could have a large impact on the model performance. The $\rho_v/\rho_g$ value often varies for different sites or even within sites due to different environmental conditions. It may also vary temporally as well: foliage has different spectral responses and structural distribution in different growing periods, and the ground reflectance also varies according to the water content and ground cover. We applied a mean value of 2.5 to the whole study area, and this may have introduced errors into the model. The high soil moisture in La Selva decreases the soil reflectance and gives a relatively high leaf/soil reflectance ratio (Monteith & Unsworth, 2008; Stoner & Baumgardner, 1981). Ni-Meister et al. (2001) found that a smaller ratio value would lead to a smaller gap probability. Morsdorf et al. (2006) did not take the variation of leaf reflectance into consideration because their study area was considered to be homogenous for both canopy and understory.

We varied $\rho_v/\rho_g$ from about 1 to 3 to evaluate its effect on LAI (Fig. 8). We found that for a moderate LAI (about 4) the range
would be about less than 1 (varying from 3.3 to 4.2). Recall our model results had RMSE values that ranged from about 1–2; thus, it is possible much of our average error may be explained by spatial variation in \( \rho_v/\rho_g \). Unfortunately, without detailed measurements of this value it is impossible to further assess its impact relative to other sources of error.

The ratio of ground return energy in total reflected energy (\( R_g/(R_g+R_v(0)) \)), is another key element in the LAI retrieval model. This ratio is not a parameter, per se, because it is derived from the waveform itself. However, it is highly sensitive to signal noise in certain situations. A high ratio of ground return energy is caused by low vegetation cover and a low total LAI value. But the relationship is nonlinear, and theoretically retrieved LAI does not saturate with decreasing ground energy ratio. However the LAI value becomes quite sensitive to the fluctuation of ground energy ratio when the ground energy ratio becomes small. A small change in \( R_g/R_v(0) \) will change the derived LAI value significantly. As canopy cover (and LAI) increases the ground energy necessarily becomes smaller. If noise values increase, or if topographic slopes are present (reducing returned ground energy) (Harding, 2005; Lefsky et al., 2007; Pang et al., 2006) then errors may occur.

We applied different levels of noise into the ground portion of waveforms to analyze the sensitivity of LAI to \( R_g/R_v(0) \). We found that for moderate and lower LAI (about 4) there was little sensitivity to noise (Fig. 9a). In contrast, for high LAI (about 8) (Fig. 9b) LAI values could be reduced by about 1.5 when the same level of noise was introduced. This is then another possible source for the scatter in Figs. 3 and 4. One implication of this sensitivity is that our LAI retrieval method may be less accurate over densely vegetated areas on steep slopes (and these occur at La Selva). There is no easy solution to this problem. If laser energy is increased to enable canopy penetration for dense forests, there is a subsequent risk of saturation for less dense areas, either from the canopy portion of the waveform or the ground return. Next generation waveform lidars may use dual channels (one low gain and one high gain) to avoid this issue.

Considering again Fig. 4, based on our discussion above, we would expect errors to increase starting around LAI values of 4 or so. There is no clear relationship between error and LAI however in this figure, although some heteroskedasticity appears around LAI values greater than 2. The great decrease in scatter from Figs. 3 to 4 is based on removing non-coincident comparisons, and the decreased bias and RMSE show how strong this effect is. The remainder of the scatter in Fig. 4 is thus a combination of any remaining non-coincidence (which may be as large as 5 m), variations in the ground to canopy reflectance ratio, and signal noise induced by topography and/or high canopy cover. Without knowing the true variability of these factors it is difficult to partition errors between these remaining sources. We note only that the resulting RMSE value of 1.36 m is consistent with and bounded by our sensitivity analyses.

Landscape level mapping of LAI may help to distinguish between some successional forest types and degraded forests. Differentiating among these over tropical areas has been difficult using optical remote sensing (Asner, 2005). While total LAI shows some ability to classify successional states (Fig. 7), it ignores the vertical distribution of LAI which may help better distinguish between classes. For example, consider Fig. 6 which shows the vertical LAI distribution of La Selva that incorporates all land cover types. LAI integration values at different height stratification layers suggest that the vertical structure of the canopy varies by land cover types and successional states: it is a function not just of total LAI, but of how the LAI is arranged vertically.

![Total LAI mapped across La Selva as derived from LVIS. Regenerating pastures have the lowest LAI values. Old growth forests have the highest mean LAI value and secondary forests are somewhat lower.](image-url)
In particular, distinguishing between older secondary forests and old-growth forests, while difficult using canopy height alone, may be possible using vertical canopy information from lidar. The efficacy of such an approach remains to be tested and is beyond our scope here, but has significance for efforts to map and monitor successional forests and degraded areas (for example, as part of REDD+ activities (Edwards et al., 2010)).

6. Conclusion

The vertical distribution of foliar material, as represented by LAI, has been hypothesized to be a critical variable for many biophysical processes, yet it has been largely unattainable at landscape scales.

Table 1
Total LAI from different land cover and land use areas.

<table>
<thead>
<tr>
<th>Land cover</th>
<th>LVIS shots</th>
<th>Mean (m²/m²)</th>
<th>S.D. (m²/m²)</th>
</tr>
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<tr>
<td>Open pasture</td>
<td>3228</td>
<td>1.74</td>
<td>2.72</td>
</tr>
<tr>
<td>Secondary forests</td>
<td>13,919</td>
<td>5.20</td>
<td>3.20</td>
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<tr>
<td>Successional plots</td>
<td>77</td>
<td>2.31</td>
<td>3.29</td>
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<tr>
<td>Selectively-logged forests</td>
<td>7068</td>
<td>5.41</td>
<td>2.82</td>
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<tr>
<td>Old-growth forests</td>
<td>35,842</td>
<td>5.62</td>
<td>2.99</td>
</tr>
<tr>
<td>Abandoned agroforestry</td>
<td>1415</td>
<td>4.13</td>
<td>2.81</td>
</tr>
</tbody>
</table>

Fig. 6. Vertical LAI integration maps from 0 to 5 m, 5 to 10 m, 10 to 20 m and above 20 m.

Fig. 7. Box plot of total LAI distribution over different forest successional types. The median LAI value is lowest for earlier succession stages and a reaches maximum value for 30–34 year-old secondary forests. Central lines give the median and boxes above and below the line give the interquartile range. Dashed lines give the 5% and 95% ranges. Non-overlapping median notches indicate significant differences between those medians at roughly a 95% confidence interval.
As a result, our ability to understand vertical canopy organization and assess its importance in a variety of theoretical and applied domains has been severely limited at all but the most local scales. Our research is one of the few attempts to derive LAI profiles using lidar data based on physical model retrieval rather than through empirical methods. Our study has shown that large footprint waveform lidar can provide estimates of vertical LAI distribution in a tropical rainforest, even under conditions of high canopy cover. Further research is required to assess the efficacy of our methods across varying landscapes and biomes. The validation of our approach was greatly aided by having actual, destructively sampled LAI measurements. Such data sets are rare indeed but their value is well worth the effort involved in obtaining them as they allow for direct comparison of models with reality. Ground-based lidar holds great promise for providing detailed LAI observations and may be an attractive alternative to destructive sampling (Strahler et al., 2008). The increased use of airborne lidar for forestry and carbon surveys, as well as the potential of retrieving these observations from space, underscores the urgency of continued model development. If successful this may lead to vastly improved data sets of LAI profiles across large areas and provide inputs for a variety of ecological, hydrological and climatological models that currently often use indirect and inaccurate parameterizations of this important attribute.

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