Estimating Vertical Distribution of Vegetation Cover in Temperate Heterogeneous Forests Using Airborne Laser Scanning Data

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Vertical structure is important for understanding forest environment, yet difficult to characterize, especially in temperate heterogeneous forests where the structure is complex. This study used data from a small-footprint airborne laser scanning (ALS) to estimate vegetation coverage in four stratum ranges in a warm temperate forest in Japan: >12 m, 8 - 12 m, 4 - 8 m, and 0 - 4 m in height. Field data were collected in 17 broad-leaved and 12 coniferous sample plots, consisting of the proportion of vegetation cover in each stratum range. The field and ALS measurements were conducted in summer, during leaf-on conditions. Using echo attributes (first, last, intermediate, and only), we calculated the vegetation coverage index (VCI) at 1-m height intervals. The cumulative sum of the VCI (CUMVCI) was then computed and compared with field observations. Linear regression analysis showed that the ALS data gave reasonable estimates of vegetation coverage in the upper two or three stratum ranges in broad-leaved stands, and in the upper two stratum ranges in coniferous stands. The model gave reproducible estimates until approximately 95% of the total returns had been applied. We conclude that ALS data can provide useful information on natural habitats in the management of warm temperate forest.

Keywords: Forest Structure; Remote Sensing; Airborne Laser Scanning

Introduction

Remote sensing is an effective tool for obtaining spatial information overlarge areas, which enables the development and assessment of management plans for forests and other ecosystems.It can be an attractive alternative to conventional field survey because it has the ability to obtain the measurements from the areas that are limited by accessibility and because the data collection/processing are efficient. Airborne laser scanner (ALS) offers distinct advantages in the representation of three-dimensional spatial structures (Lefsky et al., 2002), and numerous studies have successfully used this technique to estimate the characteristics of forest stands (e.g., Nilsson, 1996; Magnussen & Boudewyn, 1998; Lefsky et al., 1999; Næsset, 2002; Næsset & Økland, 2002).

Traditionally, researchers have described forest structure in terms of stand attributes such as tree height, stem density, diameter at breast height (DBH), and basal area (BA). These attributes are especially useful when applied to homogeneous forests (e.g., boreal coniferous forests); however, they may not fully describe the complex spatial patterns in heterogeneous forests in the warm temperate zone. Vertical distribution of foliage and woody materials is one of the attributes most commonly used to represent forest stand structure(Brokaw and Lent 1999) and the first in which a quantitative relationship was established between an element of structure and a measure of faunal diversity (McElhinny et al., 2005). In a landmark study on forest birds, MacArthur and MacArthur (1961) established a linear relationship between foliage height diversity (FHD), which describes the distribution of foliage within different stratum ranges, and bird species diversity. In warm temperate forests, vertical distribution of foliage and woody materials could be a good attribute for assessing forest wildlife habitat.

Several studies have attempted to characterize the vertical structure of forests using ALS (Zimble et al., 2003; Clark et al., 2004; Maltamo et al., 2005; Hill & Broughton, 2009). These studies aimed at distinguishing single-storied and multi-storied stand structures, or characterizing the understory in terms of tree height and density. Few studies have used ALS data to estimate the stand structure including the vertical distribution of foliage. Coops et al. (2007) found that ALS-based models of vertical foliage distribution are robust when compared with field observations in Canadian coniferous forests, and Hashimoto et al. (2004) investigated the use of leaf-off ALS data to derive indices describing forest habitat for birds in a deciduous forest in Japan. Miura and Jones (2010) demonstrated the ability to characterize ecological structure in a dry Eucalypt forest in Australia. These studies indicate the possibility of estimating the vertical distribution of forest foliage using ALS data; however, a potential of using leaf-on ALS data in a warm temperate broad-leaved forest has yet to be investigated.

More recently, high-resolution full-waveform recording ALS system became commercially available. Using this system, a digitized echo waveform of the sensor reveals all the informa-
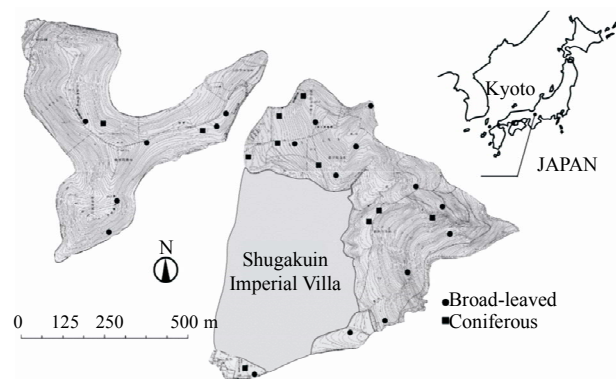
tion the laser pulse collected during its trip to the surface (Hug et al., 2004). Persson et al. (2005) compared the point clouds from the conventional discrete-return sensor and the point clouds extracted from the waveform sensor in several forest stands. They demonstrated that additionally extracted points from waveform were obtained from reflections in the tree crowns or in the understory. Thus, the vertical point distribution from waveform returns is expected to provide more detailed three-dimensional information of stands.

The objective of the present study was to investigate the use of leaf-on ALS data acquired by full-waveform sensor in predicting the vertical distribution of vegetation cover within different strata of a warm temperate forest. Vegetation coverage in this study, defined as the proportion of the area covered with vegetation consisting of foliage or other woody materials, was estimated at four vertical stratum ranges (>12 m, 8 - 12 m, 4 - 8 m, and 0 - 4 m) from the proportions of pulse returns in each height range. The technique presented in this study, which we call the Attribute Based Weighting (ABW) method, is based on the attributes of laser returns and each of the developed indices is weighted according to the numbers of returns. This method was used to create indices of vegetation cover applicable to heterogeneous broad-leaved and coniferous forests.

Materials and Methods

Study Area

The study site is located in the mountains of Shugakuin Imperial Villa, Kyoto city, in western Japan (35˚03′N, 135˚48′E), covering an area of 53 ha (**Figure 1**). The area is characterized by mountainous forests and a complex topography, which varies in elevation from 100 to 343 m above sea level (a.s.l). The landscape of the forest consists of a mosaic of relatively small stands of various tree species. The forest types within the study area include coniferous plantation, broad-leaved, and mixed stands with diverse vegetation structures. The dominant coniferous species are Japanese cedar (*Cryptomeria japonica* D. Don), Japanese cypress (*Chamaecyparis obtuse* Sieb. et Zucc.), and Japanese fir (*Abies firma* Sieb. et Zucc.). More than 30 species of broad-leaved trees are present, including *Quercus* spp. (*Quercus serrata* Murray, *Quercus variabilis* Bl., and *Quercus-glauca* Thunb.) and Japanese maple (*Acer palmatum* Thunb.). The composition of broad-leaved stands is typical of forests of the warm-temperate zone in Japan, comprising a mixed community of many broad-leaved evergreen species in the upper canopy, succeeded by a complex vertical profile containing several distinct tree layers. In general, two or three tree layers can be identified in addition to the shrub layer (Shidei, 1974).

Ground Reference Data

Vegetation coverage was assessed in collected in 17 broad-leaved and 12 coniferous sample plots (each 10 × 10 m) during the summer of 2008. The most widely known of the measuring approaches is that of Braun-Blanquet scale (1932) which defines the coverage and abundance of plant communities. It is often applied with four vegetation layers, trees (B), shrubs (S), herbs (K), and mosses (M). Based on this concept, the proportion of vegetation cover was determined at six stratum ranges within each plot (>12 m, 8 - 12 m, 4 - 8 m, 2 - 4 m, 1 - 2 m, and 0 - 1 m). The field measurements for the 0 - 1 m, 1 - 2 m, and 2 - 4 m strata were subsequently combined and reported as one stratum (0 - 4 m). The locations of all the plots were determined by the differential global positioning system (DGPS) (GPS Pathfinder ProX; Trimble Navigation Ltd., USA) and by compass survey (Tracon LS-25 surveying compass; Ushitaka Mfg. Co., Ltd., Japan).

ALS Data Collection

ALS data were acquired from a helicopter (Nakanihon Air Service Co., Ltd.) on 23 July 2008 using a Riegl LMS-Q560 laser scanner. Average flying altitude was 300 m a.g.l., resulting in a footprint diameter of approximately 15 cm. Specifications of the ALS data are listed in **Table 1**.

The ALS survey provided digitized echo signals, which were then converted into laser point clouds using RiAnalyze software (RieglLMS GmbH, Austria). RiAnalyze applies a full waveform analysis to digitized echo signals and transforms geometric data (i.e., range and scan angles) into Cartesian coordinates (RieglLMS GmbH, 2009). Using RiAnalyze software, only local maxima with absolute amplitudes exceeding threshold values are taken into account; by applying Gaussian pulse estimation, point clouds with four different threshold values were available. Average echo densities were between 72 returns/m^2 at the highest threshold value and 85 returns/m^2 at the lowest threshold value. Although we analyzed the dataset using different threshold values, the results of the different trials were not significantly different (as determined by Tukey's HSD test); therefore, the dataset obtained with the highest threshold value which is routinely used in practical operations was selected for this study, because less noise was present in the data.

Table 1.
Specifications of the ALS data.

Parameter	Value
Laser wavelength	1550 nm
Flight altitude	300 m
Flight speed	80 km/h
Laser pulse frequency	150 kHz
Scan frequency	80 Hz
Divergence	0.5 mrad
Footprint	0.15 m
Swath distance	346 m
Scan angle	±30˚

Figure 1.
Study area and distribution of sample plots.

Each return was classified into one of four echo attributes: 1) first—the first return of a multiple return; 2) last—the last return of a multiple return; 3) intermediate—intermediate returns between the first return and the last return of a multiple return; and 4) only—a single return. **Figure 2** shows examples of each type of vegetation return.

Data Analysis

To generate a DTM, first, ALS data consisting of all returns were classified by Terrascan software (Terrasolid Inc., Finland) to distinguish between "ground" and "vegetation" returns. The procedure was performed by an embedded triangulated irregular network (TIN) algorithm developed by Axelsson (2000). **Table 2** shows parameter settings of the ground classification. Second, a DTM raster with a 50 cm grid was created, also using the TIN algorithm. The remaining data were classified using the DTM, and the points above the DTM were classified as vegetation returns. Finally, the height above the ground of each vege-

tation return was calculated by subtracting the altitude of the DTM from the altitude of the vegetation return. Returns below 0.5 m were excluded from further analysis to eliminate the effects of misclassifications of vegetation and ground returns.

Model Development

Our approach, ABW method is based on echo attributes of laser returns. First, using the points classified as vegetation returns and their echo attributes (first, last, intermediate, and only), we calculated two parameters for each 1 m stratum (**Figure 3**): 1) The first parameter (FO) is related to the first and singular echo attributes; for the stratum $i = 1$, FO is

$$\text{FO}_1 = \frac{n_{F1} + n_{O1}}{\sum\limits_{k=1}^{m} \left(n_{Fk} + n_{Ok} \right)} \quad (1)$$

and for other strata ($i \geq 2$), FO is
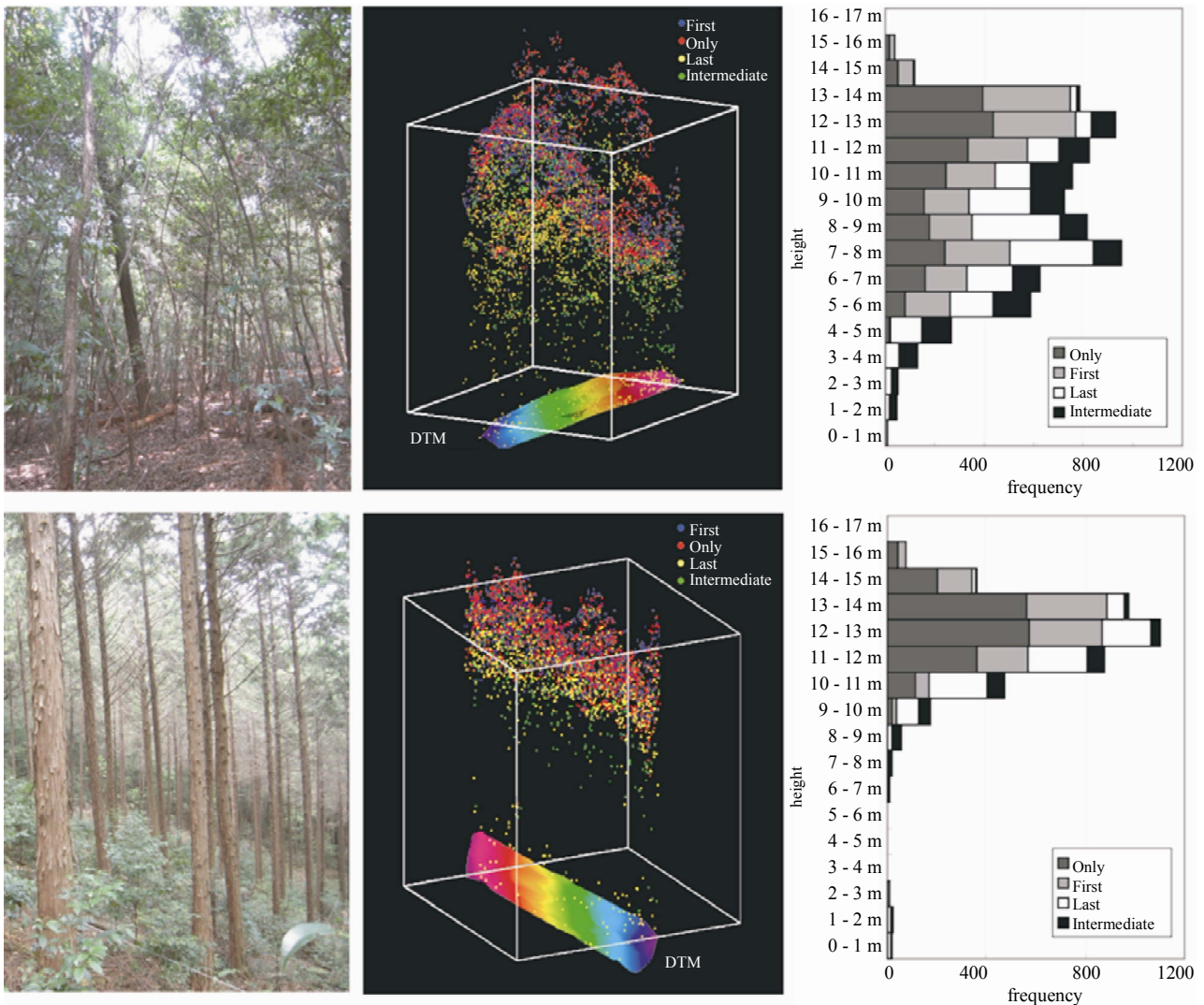
Figure 2.
Examples of broad-leaved (top) and coniferous (bottom) vegetation plots. Each row shows a photograph of the plot, a 3-D profile of classified echo attributes of vegetation returns, and a histogram of ALS-derived vegetation return frequencies based on height above the ground.

Table 2.
Parameter settings used for the classification of ground returns.

Ground Classification Parameter	Setting
Max Building Size	60 m
Iteration Angle	12°
Iteration Distance	1.5 m
Terrain Angle	88°
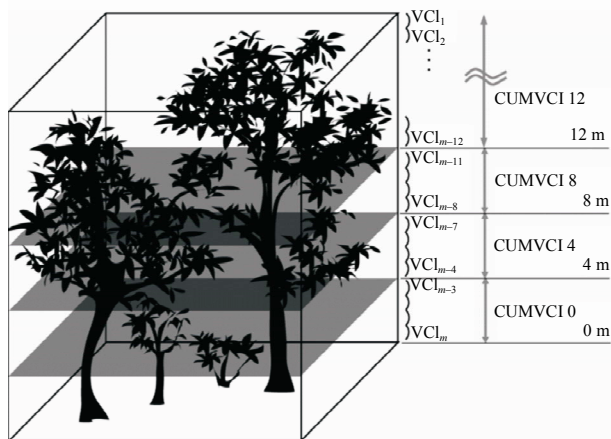
Figure 3.
Schematic showing the calculation of the cumulative vegetation coverage index (CUMVCI) for different stratum ranges. VCI: vegetation coverage index.

$$FO_i = \frac{n_{Fi} + n_{Oi}}{\sum_{k=1}^{m}(n_{Fk} + n_{Ok}) - \sum_{k=1}^{i-1}(n_{Fk} + n_{Ok})}, \qquad (2)$$

where n_F is the number of first echoes, n_O, is the number of only echoes, i is the number of the target stratum (counted at 1-m intervals from the top stratum), and m is the total number of strata. As both the first and singular echo attributes are the first objects detected, we assumed that FO is related to the overstory canopy density; 2) The second parameter (IL) is related to the intermediate and last echo attributes; when $i \geq 2$, IL is

$$IL_i = \frac{n_{Ii} + n_{Li}}{\sum_{k=1}^{i-1} n_{Fk}}, \qquad (3)$$

where n_I is the number of intermediate echoes and n_L is the number of last echoes. In the model, the intermediate and last echo attributes for the first stratum were ignored, because IL represents the proportion of the intermediate and last echoes relative to the total number of first echoes obtained from the previous stratum. The intermediate and last echoes are subsequent detections that follow the first detection of objects. Therefore, we assumed that IL is related to the density of the sub-canopy or understory.

Second, the vegetation coverage index (VCI) of each stratum was calculated as the average of FO and IL, weighted according to the magnitude of the denominator of each parameter. For $i \geq 2$, we have

$$VCI_i = FO \times \frac{\sum_{k=1}^{i-1}(n_{Fk} + n_{Ok}) - \sum_{k=1}^{i-1}(n_{Fk} + n_{Ok})}{\left\{\sum_{k=1}^{m}(n_{Fk} + n_{Ok}) - \sum_{k=1}^{i-1}(n_{Fk} + n_{Ok})\right\} + \sum_{k=1}^{i-1} n_{Fk}}$$

$$+ IL \times \frac{\sum_{k=1}^{i-1} n_{Fk}}{\left\{\sum_{k=1}^{m} n_{Fk} + n_{Ok} - \sum_{k=1}^{i-1}(n_{Fk} + n_{Ok})\right\} + \sum_{k=1}^{i-1} n_{Fk}} \qquad (4)$$

and for $i = 1$, we have

$$VCI_1 = FO_1. \qquad (5)$$

The cumulative sum of the vegetation coverage index (CUMVCI) from the hth to the ith stratum (for $h < i$) was calculated as

$$_h CUMVCI_i = VCI_h + \sum_{j=h+1}^{i}\left\{VCI_j \prod_{k=1}^{j-1}(1 - VCI_k)\right\}. \qquad (6)$$

This formula is analogous to the cumulative effects of semi-transparent sheets of light.

Finally, CUMVCI for each stratum was obtained for comparison with field measurements. Above 12 m,

$$CUMVCI\ 12 = {}_1CUMVCI_{m-12}; \qquad (7)$$

from 8 to 12 m,

$$CUMVCI\ 8 = {}_{m-11}CUMVCI_{m-8}; \qquad (8)$$

from 4 to 8 m,

$$CUMVCI\ 4 = {}_{m-7}CUMVCI_{m-4}; \qquad (9)$$

and from 0 to 4 m,

$$CUMVCI\ 0 = {}_{m-3}CUMVCI_{m}. \qquad (10)$$

Statistical Analysis

Calculated CUMVCI 12, CUMVCI 8, CUMVCI 4, and CUMVCI 0 by the ABW method were compared with field measurements of the corresponding stratum ranges. For each stratum range, we performed a linear regression (yielding the slope, the intercept, and their 95% confidence intervals (CI)) and calculated the root mean square error (RMSE). The prediction error was calculated as the difference between field measurements and values predicted from ALS data. All analyses were performed with R software, v. 2.12.0 (R Development Core Team, Austria).

Results

The CUMVCI of all stratum ranges were compared with field measurements. Results of the linear regression analyses are summarized in **Tables 3** and **4** and **Figures 4** and **5**. In broad-leaved stands, for the stratum range >12 m, the RMSE was 0.164, corresponding to 37% of the mean observed value. For the stratum range, 8 - 12 m, the RMSE was 0.230, corresponding to 41% of the mean observed value. For the stratum range, 4 - 8 m, the RMSE was 0.393, corresponding to 56% of the mean observed value. The lowest stratum range, 0 - 4 m, showed the highest RMSE (0.562), corresponding to 85% of the mean observed value.

ALS model underestimation of the vegetation index was observed in cases where points plotted below the 1:1 relationship line (**Figure 4**). The slopes of regression lines were close to 1

Table 3.
Results of linear regression analyses for each stratum range in broad-leaved stands. Regressions are shown in **Figure 4**.

		Estimate	*p*-value	Lower 95%	Upper 95%
Above 12 m	Slope	1.043	1.12×10^{-6}***	0.771	1.315
	Intercept	0.049	4.94×10^{-1}	−0.099	0.197
8 - 12 m	Slope	0.606	6.78×10^{-3}**	0.196	1.015
	Intercept	0.172	1.73×10^{-1}	−0.083	0.427
4 - 8 m	Slope	0.631	2.97×10^{-1}	−0.607	1.870
	Intercept	−0.017	9.68×10^{-1}	−0.901	0.866
0 - 4 m	Slope	0.127	5.87×10^{-1}	−0.357	0.611
	Intercept	0.038	8.10×10^{-1}	−0.289	0.364

*p*-value: ***< 0.001, **< 0.01, *< 0.05.

Table 4.
Results of linear regression analyses for each stratum range in coniferous stands. Regressions are shown in **Figure 5**.

		Estimate	*p*-value	Lower 95%	Upper 95%
Above 12 m	Slope	0.713	4.07×10^{-3}**	0.290	1.137
	Intercept	0.307	6.37×10^{-2}	−0.017	0.632
8 - 12 m	Slope	0.982	2.19×10^{-5}***	0.692	1.272
	Intercept	−0.043	5.15×10^{-1}	−0.184	0.098
4 - 8 m	Slope	0.195	2.94×10^{-2}*	0.026	0.364
	Intercept	0.024	4.63×10^{-1}	−0.047	0.095
0 - 4 m	Slope	0.045	3.96×10^{-1}	−0.067	0.158
	Intercept	0.018	4.58×10^{-1}	−0.033	0.069

p-value: ***< 0.001, **< 0.01, *< 0.05.
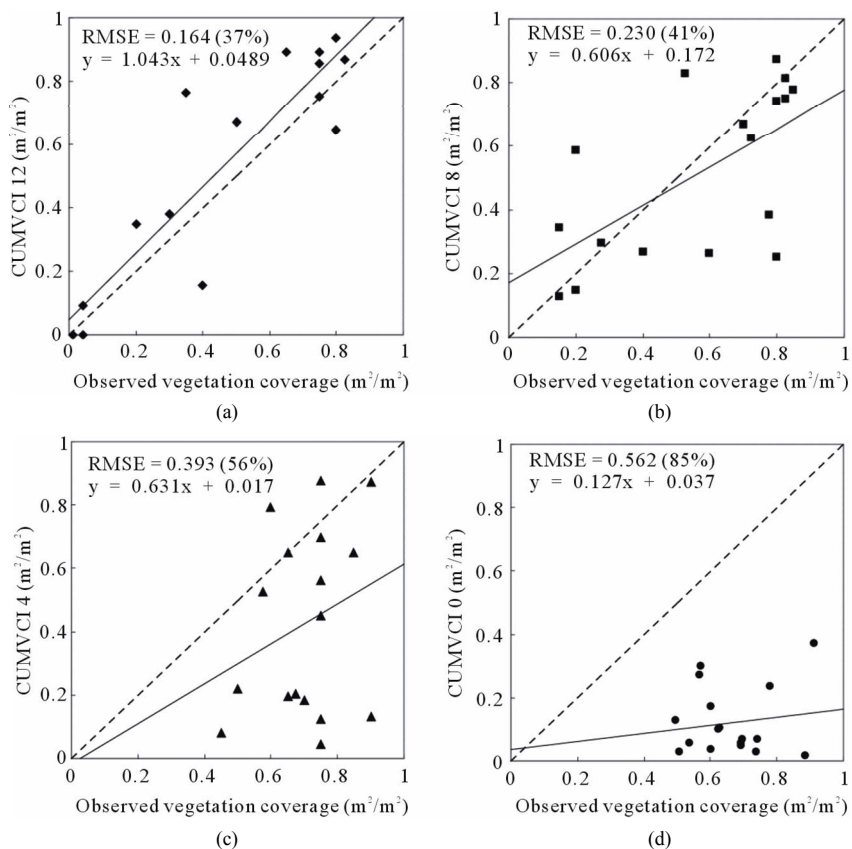
Figure 4.
Observed vegetation coverage versus predicted values of the cumulative vegetation coverage index (CUMVCI) for stratum ranges in broad-leaved plots: (a) above 12 m; (b) 8 - 12 m; (c) 4 - 8 m; and (d) 0 - 4 m. Regression lines are solid; dashed lines show 1:1 relationships.
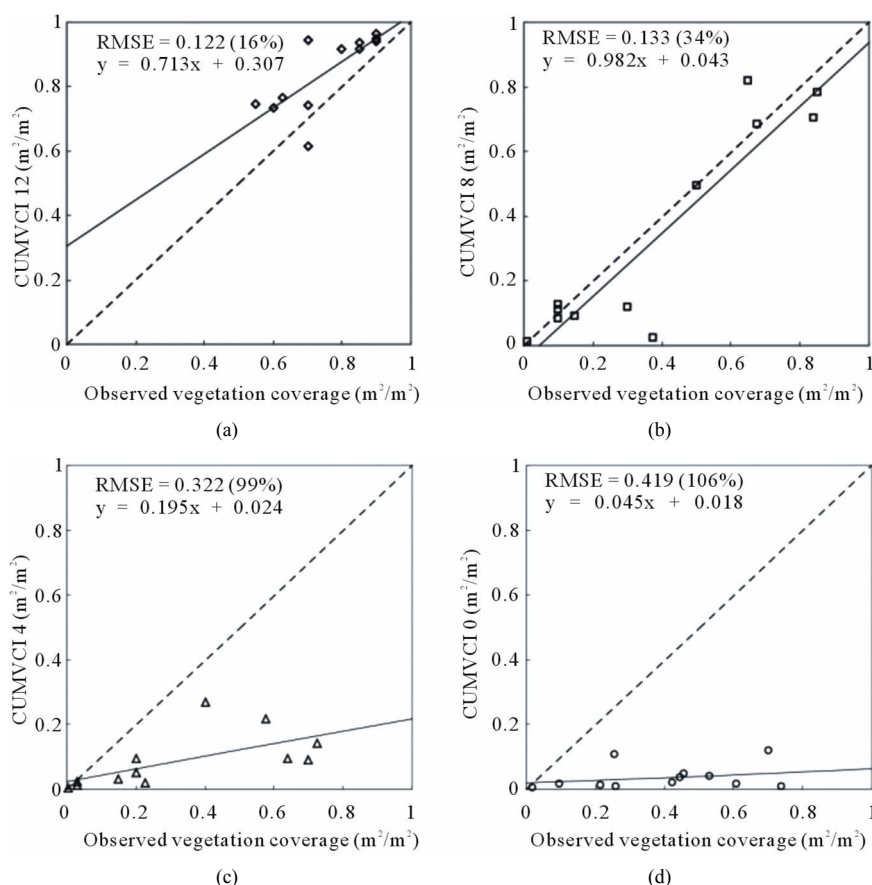
Figure 5.
Observed vegetation coverage versus predicted values of the cumulative vegetation coverage index (CUMVCI) for stratum ranges in coniferous plots: (a) above 12 m; (b) 8 - 12 m; (c) 4 - 8 m; and (d) 0 - 4 m. Regression lines are solid; dashed lines show 1:1 relationships.

in upper stratum ranges, but decreased for stratum ranges closer to the ground. The slopes (±95% CI) for the stratum ranges >12 m, 8 - 12 m, and 4 - 8 m were, respectively, 1.043 ± 0.148, 0.606 ± 0.409, and 0.631 ± 1.238; intercepts (±95% CI) for these stratum ranges were, respectively, 0.049 ± 0.148, 0.172 ± 0.255, and −0.017 ± 0.884. There were no significant differences between observed and predicted values of the vegetation index, as the 95% CIs included slopes of 1 and intercepts of 0. However, for the stratum range 0 - 4 m, the 95% CI for the slope did not contain the value 1 (**Table 3**).

In coniferous stands, for the stratum range >12 m, the RMSE was 0.122, corresponding to 16% of the mean observed value. For the 8 - 12 m stratum range, the RMSE was 0.133, corresponding to 34% of the mean observed value. RMSE values in the stratum ranges 4 - 8 m and 0 - 4 m were particularly high, 0.322 and 0.419, respectively, corresponding to 99% and 106% of the mean observed values, respectively (**Figure 5**). The slopes (±95% CI) for the stratum ranges >12 m and 8 - 12 m were, contain the slope of 1; intercepts (±95% CI) for these stratum ranges were, respectively, −0.043 ± 0.141 and 0.024 ± 0.070, both of which contained the intercept of 0. However, for the remaining stratum ranges (4 - 8 m and 0 - 4 m), slopes of the regression lines were significantly different than 1.

Figure 6 shows the mean percentage of available vegetation returns and the RMSE for each stratum range. In coniferous

stands, available vegetation returns decrease dramatically from the stratum range >12 m to the 4 - 8 m range; thus, only a small percentage of available returns are available for the lower two stratum ranges. In broad-leaved stands, the percentage of available vegetation returns decreases more gradually than in coniferous stands.

Discussion

We investigated the use of ALS data (proportion of returns distinguished by attributes: first, last, intermediate, and singular) for estimating stratified vegetation cover. The model was applied to broad-leaved and coniferous forest stands. In the case of broad-leaved stands, the model gave reproducible estimates of vegetation coverage within the upper stratum ranges (>12 m and 8 - 12 m); in these ranges, RMSE values were 0.164 and 0.230, respectively, corresponding percentage of mean observed values remaining less than 50%. For the stratum range 4 - 8 m, although about half the points plotted close to the 1:1 line, a number of points clustered below this line, indicating that the ALS model under estimated vegetation coverage (**Figure 4(c)**). In coniferous stands, the estimation accuracy was acceptable in the first and second stratum ranges (>12 m and 8 - 12 m); however, it dropped severely in the lower stratum ranges. RMSE values increased from 0.133 in the stratum range 8 - 12 m (corresponding to 34% of the mean observed value) to 0.322 in the
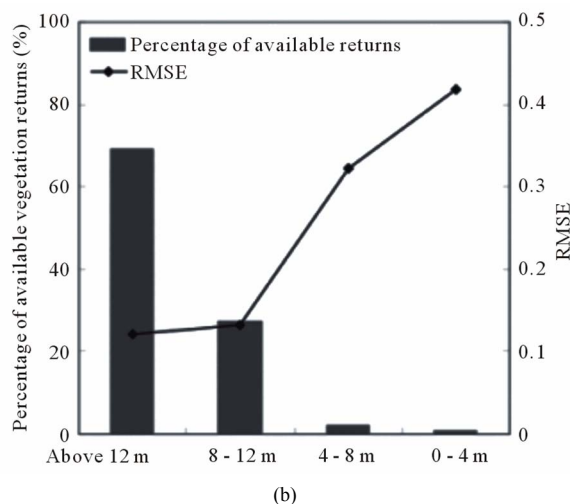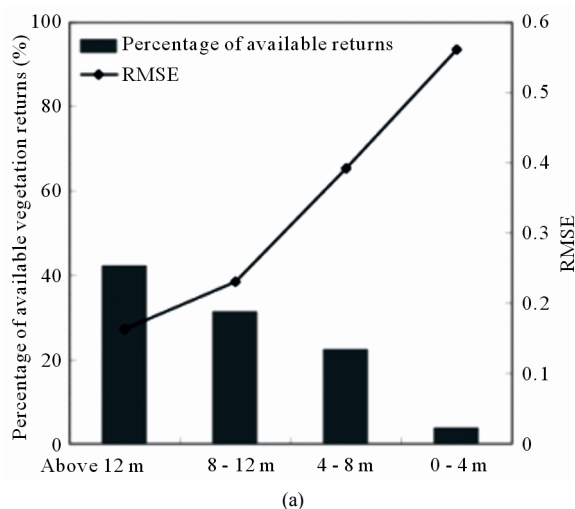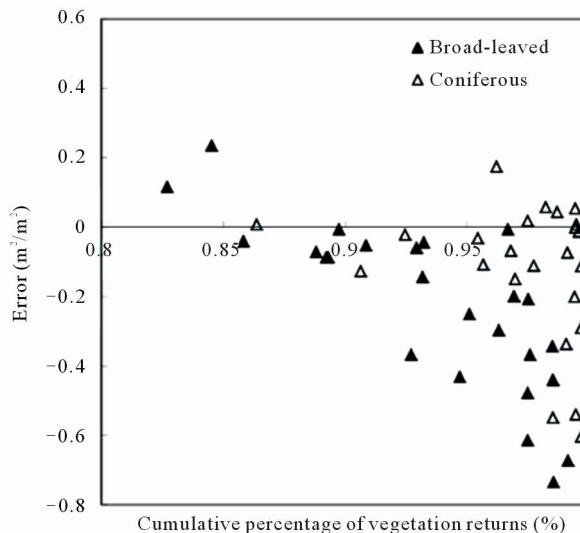
Figure 6.
Mean percentage of available vegetation returns and the root mean square error (RMSE) in each stratum range, for (a) broad-leaved stands and (b) coniferous stands.

Figure 7.
Errors in the 8 - 12 m and 4 - 8 m stratum range plotted against cumulative percentage of vegetation returns above 4 m in height.

stratum range 4 - 8 m (corresponding to 99% of the mean observed value). In the regression analysis, the CIs for the slope and the intercept did not contain the values of 1 and 0, respectively, in the lower stratum ranges (4 - 8 m and 0 - 4 m); this implies that the number of available returns was insufficient to accurately estimate vegetation coverage in lower stratum ranges (**Figure 7**).

It is likely that the underestimation was caused by a deficiency of return pulses. **Figure 7** shows the relationship between errors and the ratio of the cumulative sum of the vegetation returns to all vegetation returns for the second (8 - 12 m) and the third (4 - 8 m) stratum ranges. The errors were distributed rather evenly until approximately 90% of the total return had been incorporated into the model in both broad-leaved and coniferous stands. However, results show consistent underestimation after approximately 95% of the total returns had been used. This indicates that there are not sufficient available returns for the model, which resulted in the failure of the estimation.

The difference in pulse return distributions between broad-

leaved and coniferous stands observed in this study can be explained by the canopy shape and foliage distribution. Previous studies pointed out that crown shape may affect the height distributions of ALS data (Nelson, 1997; Næsset, 1997, 2004; Holmgren & Persson, 2004; Moffiet et al., 2005) and pulse penetration of the upper canopy depends on density, reflectivity and orientation of leaves and canopy closure (Gaveau & Hill, 2003, Clark et al., 2004). Moffiet et al. (2005) described differences in laser penetration between species of the broad-leaved poplar box and the coniferous cypress pine; while poplar box exhibits larger gaps in crown foliage, the needle density of cypress pine provides less opportunity for a significant second reflection. In this study, vegetation coverage in the highest strata of coniferous stands is relatively dense; this pattern is a result of plantation without thinning, so that stands developed dense foliage canopy surfaces. This was probably a reason why there were less pulse returns for the lower layers in the coniferous stands. Furthermore, Persson et al. (2005) compared the point clouds that are extracted using the waveform signal with the point clouds recorded from the conventional discrete-return ALS system in pine, spruce and deciduous stands. The results revealed that the increase in number of points extracted from waveform compared to points delivered by the discrete-return system was at 57% for deciduous stand, whereas pine and spruce stands recorded at 18% and 30% respectively. This may indicate that full-waveform data can be used to give a better description of the vertical vegetation distribution in broad-leaved forests. More training data sets with more variations need to be collected in different conditions (e.g., species, age) for further analysis.

Conclusion

This paper proposed a new technique, the ABW method, for reproducing the vertical distribution of vegetation cover using leaf-on ALS data of warm temperate forests. This approach is unique in its ability to predict and quantify vegetation cover as a function of vertical stratum range. Notably, the models gave reasonable estimates of vegetation cover until approximately

95% of the total number of ALS returns had been incorporated into the model. The results in this study show that the presented method can be used for estimating the vertical distribution of vegetation cover in the upper two or three stratum ranges in broad-leaved stands, and in the upper two stratum ranges in coniferous stands.Although CUMVCI was calculated for four stratum ranges in this study, the approach can accommodate different numbers of stratum ranges.Future research should examine the applicability of the model to different forest types.

Acknowledgements

REFERENCES

Axelsson, P.E. (2000). DEM generation from laser scanner data using adaptive TIN models. *International Archives of the Photogrammetry and Remote Sensing, 33,* 110-117.

Braun-Blanquet, J. (1932). *Plant sociology: The study of plant communities* (English translation). New York: McGraw-Hill.

Brokaw, N. V. L., & Lent, R. A. (1999). Vertical structure. In I. Hunter, & L. Malcom (Eds.), *Maintaining biodiversity in forest ecosystems* (pp. 373-399). Cambridge: Cambridge University Press. doi:10.1017/CBO9780511613029.013

Clark, M. L., Clark, D. B., & Roberts, D. A. (2004). Small-footprint lidar estimation of sub-canopy elevation and tree height in a tropical rain forest landscape. *Remote Sensing of Environment, 91,* 68-89. doi:10.1016/j.rse.2004.02.008

Coops, N. C., Hilker, T., Wulder, M. A., St-Onge, B., Newnham, G., Siggins, A., & Trofymow, J. A. (2007). Estimating canopy structure of Douglas-Fir forest stands from discrete-return LiDAR. *Trees, 21,* 295-310. doi:10.1007/s00468-006-0119-6

Gaveau, D. L. A., & Hill, R. A. (2003). Quantifying canopy height underestimation by laser pulse penetration in small-footprint airborne laser scanning data. *Canadian Journal of Remote Sensing, 29,* 650-657. doi:10.5589/m03-023

Lefsky, M. A., Cohen, W. B., Acker, S. A., Parker, G. G., Spies, T. A., & Harding, D. (1999). Lidar remote sensing of the canopy structure and biophysical properties of Douglas-Fir Western Hemlock Forests. *Remote Sensing of Environment, 70,* 339-361. doi:10.1016/S0034-4257(99)00052-8

Hashimoto, H., Imanishi, J., Hagiwara, A., Morimoto, Y., & Kitada, K. (2004). Estimating forest structure indices for evaluation of forest bird habitats by an airborne laser scanner. In M. Thies, B. Koch, H. Spiecker, & H. Weinacker (Eds.), *Laser scanners for forest and land- scape assessment: Proceedings of the ISPRS Working Group VIII/2,* Freiburg, 3-6 October 2004, 254-258.

Hill, R. A., & Broughton, R. K. (2009). Mapping the understory of deciduous woodland from leaf-on and leaf-off airborne LiDAR data: A case study in lowland Britain. *ISPRS Journal of Photogrammetry and Remote Sensing, 64,* 223-233. doi:10.1016/j.isprsjprs.2008.12.004

Holmgren, J., & Persson, Å. (2004). Identifying species of individual trees using airborne laser scanner. *Remote Sensing of Environment, 90,* 415-423. doi:10.1016/S0034-4257(03)00140-8

Hug, C., Ullrich, A., & Grimm, A. (2004). LITEMAPPER-5600: A waveform-digitizinglidar terrain and vegetation mapping system. *Remote Sensing and Spatial Information Sciences, 36,* 24-29.

MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology, 42,* 594-598. doi:10.2307/1932254

Magnussen, S., & Boudewyn, P. (1998). Derivations of stand heights from airborne laser scanner data with canopy-based quantile estimators. *Canadian Journal of Forest Research, 28,* 1016-1031. doi:10.1139/x98-078

Maltamo, M., Packalén, P., Yu, X., Eerikäinen, K., Hyyppä, J., & Pitkänen, J. (2005). Identifying and quantifying structural characteristics of heterogeneous boreal forests using laser scanner data. *Forest Ecology and Management, 216,* 41-50. doi:10.1016/j.foreco.2005.05.034

McElhinny, C., Gibbons, P., Brack, C., & Bauhus, J. (2005). Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management, 218,* 1-24. doi:10.1016/j.foreco.2005.08.034

Miura, N., & Jones, S. D. (2010). Characterizing forest ecological structure using pulse types and heights of airborne laser scanning. *Remote Sensing of Environment, 114,* 1069-1076. doi:10.1016/j.rse.2009.12.017

Moffiet, T., Mengersen, K., Witte, C., King, R., & Denham, R. (2005). Airborne laser scanning: Exploratory data analysis indicates potential variables for classification of individual trees or forest stands according to species. *ISPRS Journal of Photogrammetry and Remote Sensing, 59,* 289-309. doi:10.1016/j.isprsjprs.2005.05.002

Nelson, R. (1997). Modelingforest canopy heights: The effects of canopy shape. *Remote Sensing of Environment, 60,* 327-334. doi:10.1016/S0034-4257(96)00214-3

Nilsson, M. (1996). Estimation of tree weights and stand volume using anairborne lidar system. *Remote Sensing of Environment, 56,* 1-7. doi:10.1016/0034-4257(95)00224-3

Næsset, E. (2002). Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. *Remote Sensing of Environment, 80,* 88-99. doi:10.1016/S0034-4257(01)00290-5

Næsset, E. (2004). Practical large-scale forest stand inventory using a small-footprint airborne scanning laser. *Scandinavian Journal of Forest Research, 19,* 164-179. doi:10.1080/02827580310019257

Næsset, E., & Økland, T. (2002). Estimating tree height and tree crown-properties using airborne scanning laser in a boreal nature reserve. *Remote Sensing of Environment, 79,* 105-115. doi:10.1016/S0034-4257(01)00243-7

Persson, Å., Söderman, U., Töpel, J., & Ahiberg, S. (2005). Visualization and analysis of full-waveform airborne laser scanner data. *Proceedings of ISPRS Workshop on Laser Scanning 2005,* Enschede, 12-14 September 2005, 103-108.

R Development Core Team (2010). *R: A language and environment forstatistical computing.* Vienna: R Foundation for Statistical Computing.

RIEGL LMS GmbH (2009). *Full Waveform Analysis Software RiANALYZE for RIEGL Airborne Laser Scanners LMS-Q560 and LMS-Q680.*

Shidei, T. (1974). Forest vegetation zones. In M. Numata (Eds.), *The flora and vegetation of Japan* (pp. 87-124). Tokyo/Amsterdam: Kodansha/Elsevier Scientific Publishing Company.

Soininen, A. (2003). *Terra Scan User's Guide.*

Zimble, D. A., Evans, D. L., Carlson, G. C., Parker, R. C., Grado, S. C., & Gerard, P. D. (2003). Characterizing vertical forest structure using small-footprint airborne LIDAR. *Remote Sensing of Environment, 87,* 171-182. doi:10.1016/S0034-4257(03)00139-1