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Detecting seasonal change of broad-leaved woody canopy leaf area density profile using 3D portable LIDAR imaging

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Abstract. Seasonal change of vertical leaf area density (LAD) profiles of woody canopy broad-leaved trees (*Zelkova serrata* [Thunberg] Makino) was estimated using 3D portable scanning light detection and ranging (LIDAR) imaging. First, 3D point cloud data for the canopy were collected using a portable LIDAR in spring, summer, autumn and winter. For data collection, the canopy was evenly scanned by the LIDAR from three positions 10 m above the ground. Next, the vertical LAD profile in each season was computed from the LIDAR data using the voxel-based canopy profiling (VCP) method. For the computation, non-photosynthetic tissues were eliminated using the LIDAR data obtained during winter. Influence of leaf inclination angle (LIA) on LAD estimation was corrected by LIA data measured by a high-resolution portable scanning LIDAR. The resultant profiles showed that LAD values tended to increase at the upper canopy from spring to summer and decrease at the middle and lower canopy from summer to autumn. Moreover, LIDAR-derived LIA distributions were compared among different seasons. LIA showed an even distribution in spring but changed to a planophile distribution in summer. In autumn, the angles in the <30° class decreased and those between the 30 and 40° classes increased.

Additional keywords: Japanese zelkova, leaf area index (LAI), leaf inclination angle (LIA), voxel-based canopy profiling (VCP).

Introduction

The plant canopy plays important functional roles in cycling materials and energy through photosynthesis and transpiration, maintaining plant microclimates and providing habitats for various species (Monteith 1973; Jones 1992; Ehleringer and Field 1993; Larcher 2001). Determining the vertical structure of the canopy is very important because the 3D composition of the canopy helps to sustain these functional roles (Graetz 1990; Lefsky *et al*. 2002; Schurr *et al*. 2006; Omasa *et al*. 2007). Moreover, it is important to measure change in the vertical structure accompanied by canopy growth over time in order to understand plant phenological phenomena and long-time scale plant dynamics.

The vertical canopy structure is often represented by the leaf area density (LAD) in each horizontal layer, which is defined as one-sided leaf area per unit of horizontal layer volume (Weiss *et al*. 2004). The leaf area index (LAI) is then calculated by vertically integrating the LAD profile data. To obtain LAD, stratified clipping of leaves has been used as a direct method (Monsi and Saeki 1953). Although this direct method offers accurate results, it is labour intensive and its destructive nature does not permit intact and repeated measurements of canopy structure as plants change over time with growth. 3D digitising by ultrasonic or electromagnetic devices has been used as another direct method where a pointer is located at the position of each plant component and geometric information is recorded as 3D spatial coordinates (Sinoquet *et al*. 1991, 1998, 2007; Thanisawanyangkura *et al*. 1997; Drouet *et al*. 1999). Although this technique allows non-destructive measurement of the detailed 3D structure of plants, it is labour intensive and is therefore unfavourable to take repeated measurements to capture the temporal changes of the canopy structure. As an indirect method, the gap-fraction method has been widely applied to measure canopies (e.g. Li-Cor LAI-2000 plant canopy analyser; Lang and Yueqin 1986; Neumann *et al*. 1989; Norman and Campbell 1989; Chason *et al*. 1991; Welles and Norman 1991; Chen and Cihlar 1995). This method allows automatic data collection and non-destructive measurement of the canopy structure by using light transmittance through the canopy. However, the accuracy of the measurement is affected by the spatial distribution of leaves and by sunlight conditions (Chason *et al*. 1991; Jonckheere *et al*. 2004). As described above, measuring temporal changes of vertical canopy structures remains difficult.

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Recently, light detection and ranging (LIDAR) imaging, which is an active remote-sensing technique that uses a laser scanner, has been used for canopy measurements (Omasa *et al*. 2000, 2002, 2003, 2007, 2008; Harding *et al*. 2001; Hyyppä *et al*. 2001; Lefsky *et al*. 2002; Brandtberg *et al*. 2003; Riaño *et al*. 2003; Holmgren and Persson 2004; Næsset *et al*. 2004; Hosoi *et al*. 2005, 2008; Hosoi and Omasa 2006, 2007, 2009*a*; Nakai *et al*. 2009). LIDAR imaging can measure the distance between the sensor and a target based on the elapsed time between the emission and return of laser pulses (the time-of-flight method) or based on trigonometry (the optical-probe or light-section methods), so that 3D information of the target can be obtained. Several researchers have attempted to measure vertical foliage profiles using portable ground-based non-scanning and scanning LIDAR (Radtke and Bolstad 2001; Lovell *et al*. 2003; Parker *et al*. 2004; Tanaka *et al*. 2004; Takeda *et al*. 2005, 2008; Henning and Radtke 2006; Hosoi and Omasa 2006, 2007, 2009*a*; Van der Zande *et al*. 2006; Omasa *et al*. 2007). A portable ground-based scanning LIDAR has several beneficial features that overcome weak points in conventional ways of measuring temporal changes of vertical canopy structures. First, the non-destructiveness allows intact canopy measurement over time. Second, it is an active sensor, which means that measurements are not affected by the light condition in the field. Third, the ability to scan horizontally and vertically allows efficient data collection, where many 3D data of the canopy can be recorded quickly and automatically as 3D point-cloud data. Fourth, the high-ranging accuracy and resolution provide faithful 3D information of the canopy. Finally, its portability facilitates repeated measurements over time. Recently, we utilised the above described benefits of the portable scanning LIDAR and demonstrated that the vertical LAD profile of a broad-leaved woody canopy can be measured accurately by optimising the measurement settings (Hosoi and Omasa 2007). Although the measurement was conducted only during summer, temporal changes in the vertical LAD profile could be captured by repeating the measurement over time. In the study by Hosoi and Omasa (2007), leaf inclination angle (LIA) distribution was also measured using a high-resolution portable scanning LIDAR and correcting the influence of LIA on the LAD estimation. Besides such use, LIA distribution itself can be considered as one of the measures to express 3D canopy structures and thus the temporal change offers useful information about plant activities (Comstock and Mahall 1985; Imai *et al*. 1994; Gratani and Bombelli 2000; Barchuk and Valiente-Banuet 2006). Temporal measurement has been difficult using conventional ways, e.g. use of clinometers or 3D digitisers (Norman and Campbell 1989; Sinoquet *et al*. 1998; Gratani and Ghia 2002) because of the labour-intensiveness. By repeatedly applying the LIDAR-based method over time, temporal changes of LIA distribution could also be captured more easily and accurately.

In the present study, vertical LAD profiles of the broad-leaved canopy of *Zelkova serrata* [Thunberg] Makino were estimated over three different seasons using a portable scanning LIDAR. By comparing the LAD estimation between each season, the ability of the portable scanning LIDAR to detect seasonal changes of the vertical LAD profile was evaluated. In addition, LIA distributions were measured during each season using a high-resolution portable scanning LIDAR. While they were used for correcting the influence of LIA on LAD estimation, their tendencies were compared between three different seasons. The usefulness of the LIDAR-based seasonal measurements of LIA distributions was then evaluated.

Materials and methods

Study site

The study was carried out in a mixed plantation with nearly flat topography in Ibaraki Prefecture, 40 km north-east of central Metropolitan Tokyo, Japan (35°59′N, 140°02′E). The dominant tree species were Japanese cedar (*Cryptomeria japonica* [L.f.] D. Don), Japanese red pine (*Pinus densiflora* Siebold and Zuccarini), ginkgo (*Ginkgo biloba* Linnaeus) and Japanese zelkova (*Zelkova serrata* [Thunberg] Makino). The understory included grasses, forbs and young evergreen trees such as *Camellia japonica* Linnaeus, *Ilex integra* Thunberg and *Ternstroemia gymnanthera* Sprague. A Japanese zelkova canopy was chosen for measurement and a 4×4 m measurement plot was established beneath the canopy (Fig. 1*a*).

Direct measurement of leaf area density (LAD)

The actual LAD of the canopy was measured directly by stratified clipping in September 2005, the month following the light detection and ranging (LIDAR) measurements of the leafy canopy. The measurement plot was divided into four 2×2 m quadrats (Fig. 1*b*) and the region above the plot was divided into 64 cells (each $2 \times 2 \times 0.5$ m high) between the heights of 5 and 13 m (Fig. 1*c*). Each cell was distinguished by a reference number (l, m, n) (Fig. 1*c*), where l, m and n correspond to the x, y and z coordinate values, respectively. All leaves of the zelkova canopy in the measurement plot were clipped manually using a cherry picker and labelled according to the cell from which they came. It took approximately 1 month to finish the clipping. Only leaves were clipped and attention was paid not to cut the branches or shoots. To obtain the leaf area, part of the clipped leaves was scanned as JPEG images using a desktop scanner (FB636U, Canon Inc., Tokyo, Japan) and dried in an oven at 80°C for 3 days. The leaf area and corresponding dry weight were used to calculate the area : dry weight ratio (i.e. the specific leaf area, SLA). All other leaves were also dried under the same conditions to obtain the dry weight of each of the cells. The leaf area in each cell was then determined by multiplying the dry weight of a cell by the SLA, and the LAD of each cell was calculated by dividing the leaf area by the cell volume (2 m^3). By integrating the LAD values vertically, the actual LAI values were obtained for each quadrat and for the whole canopy. Descriptive variables for the Japanese zelkova canopy were: height, 12.5 m; LAI, 4.59 $m^2 m^{-2}$; mean LAD, 0.57 $m^2 m^{-3}$; and mean SLA, 11.9 $m^2 kg^{-1}$. More details about the direct measurement can be found in Hosoi and Omasa (2007).

Measurements using two types of portable scanning LIDARs

A portable scanning instrument for LIDAR imaging (LPM-25HA, RIEGL, Horn, Austria) was used for LAD measurement. This instrument was able to obtain the distance to the surface of any object between 2 and 60 m from the sensor by measuring the elapsed time between the emitted and returned laser pulses (the time-of-flight method) with an accuracy of

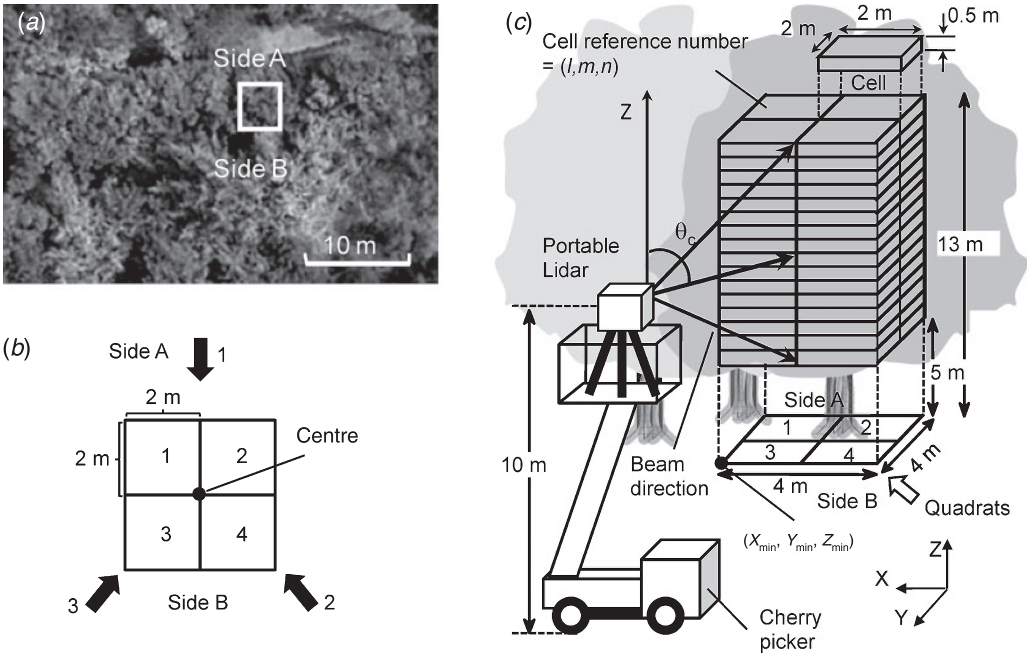

Fig. 1. A 4 × 4 m plot established at the study site. (*a*) An aerial photograph of the study site. The white rectangle shows the location of the measurement plot that includes a Japanese zelkova canopy. (*b*) Quadrats established on the ground in the measurement plot. Each quadrat is 2 × 2 m. Black arrows show the directions in which LIDAR scanning were performed. (*c*) Illustration of cells established within the measurement plot and LIDAR measurement using a cherry picker. Each cell was distinguished by a reference number (*l*, *m*, *n*), where *l*, *m* and *n* correspond to the *x*, *y* and *z* coordinate values, respectively. θ_c represents the central zenith angle.

±8 mm. A rotating mount driven by built-in stepper motors with 0.009° of accuracy panned and tilted the LIDAR head. The Japanese zelkova canopy within the measurement plot was scanned from three positions 10 m above the ground (position 1 on side A and positions 2 and 3 on side B; Fig. 1*b*) using the cherry picker in August 2005 and May, August and November 2006 (Fig. 1*c*). On each date, it took several hours to measure the canopy from the three positions. For all four measurements, the central angle of zenith laser scan (= the central zenith angle, θ_c; Fig. 1*c*) was 90.0° (i.e. horizontal direction) and the corresponding scan zenith angle was ±33.1°. The azimuth scan angle ranged from ±18° to ±28°. The average distance between the three LIDAR positions 10 m above the ground and a point 10 m above the centre of the measurement plot was 12.8 m. Those measurement settings were determined based on the results in Hosoi and Omasa (2007), which offered the most accurate LAD estimation. In addition to the measurements of the leafy canopy, the same canopy was measured from the six ground positions in February 2006, when it was leafless. The central zenith angle and the scan zenith angle were 57.8° and ±28°. More details about the measurement can be found in Hosoi and Omasa (2007).

Another portable fine-resolution scanning LIDAR that calculates distances based on trigonometry (a modified TDS-130 L 3D laser scanner; Pulstec Industrial Co. Ltd, Hamamatsu, Japan; in which the laser beam wavelength for ranging was changed from 656 to 785 nm) was used to measure LIA (Hosoi and Omasa 2007, 2009*b*). The LIDAR's measurable range is 3.5 to 10 m. The range and scan resolutions are ~1 and 2 mm, respectively, at a measurement range of ~5 m. A rotating mount with a stepper motor and a galvano mirror within the LIDAR head automated the horizontal and vertical scanning. Leaves within quadrats 1 and 2 (see Fig. 1*b*) were scanned by the LIDAR from a position on the ground at side A, ~5 m from the centre of the measurement plot, in August 2005. The measurement took up to 1 hour so windless conditions were chosen to avoid disturbance of the canopy. The same scanning was repeated in May, August and November 2006, which corresponded to 17, 118 and 194 days after bud break. In the LIDAR-derived 3D point cloud images, each leaf was distinguishable because of the fine resolution. After randomly and interactively selecting 250 leaves in each of the images, each leaf was approximated as a plane and normals to the planes were estimated. LIAs were derived from the angles of these normals with respect to the zenith and the distributions were obtained for each of the measurement dates. In the present zelkova tree, approximation of the leaf surfaces as planes was valid during the three seasons.

Voxel-based computation of LAD

LAD computation followed the voxel-based canopy profiling (VCP) method (Hosoi and Omasa 2006). LIDAR-derived datasets for each measurement date were composed of three point-cloud data obtained from each of the three measurement positions. The individual coordinate systems for these data were registered into a single point-cloud dataset with a common 3D coordinate system for each measurement date using the iterative closest-point algorithm (Besl and McKay 1992). The data measured from the ground when the trees were leafless in February 2006 were also registered using this algorithm. Non-photosynthetic tissues such as trunks, branches and understory were excluded by subtracting points corresponding to data obtained in the leafless canopy from the data obtained in the leafy canopy. All points in the registered dataset were converted into voxel coordinates for each measurement date using the following equations:

$$i = \mathrm{Int}\left(\frac{X - X_{\min}}{\Delta i}\right) + 1 \qquad (1)$$

$$j = \mathrm{Int}\left(\frac{Y - Y_{\min}}{\Delta j}\right) + 1 \qquad (2)$$

$$k = \mathrm{Int}\left(\frac{Z - Z_{\min}}{\Delta k}\right) + 1 \qquad (3)$$

where (i, j, k) represents a voxel's coordinates within the voxel array, Int is a function that rounds off the result of the calculation to the nearest integer, (X, Y, Z) represents the point coordinates of the registered LIDAR data, $(X_{\min}, Y_{\min}, Z_{\min})$ represent the minimum values of (X, Y, Z) (see Fig. 1*c*) and $(\Delta i, \Delta j, \Delta k)$ represent the voxel element size. The voxel element size was determined according to the range and scan resolution of the portable ground-based LIDAR and was thus set to $5 \times 5 \times 5$ mm. Voxels converted from points within the LIDAR dataset were assigned an attribute value of 1. Next, all laser beams emitted from the LIDAR positions were traced within the voxel array in accordance with the actual laser beam angles. Voxels through which one or more laser beams passed without touching the canopy were assigned the attribute value of 2. LAD was computed for each of the cells within the measurement plot using these attribute values and the following equation:

$$\mathrm{LAD}_{lmn} = \frac{\cos\theta_{lmn}}{G(\theta_{lmn})} \cdot \frac{1}{\Delta H} \sum_{k=m_h}^{m_h+\Delta H} \frac{n_{\mathrm{I}}(k)}{n_{\mathrm{I}}(k) + n_{\mathrm{P}}(k)}. \qquad (4)$$

where (l, m, n) represents the cell reference number, θ_{lmn} is the mean zenith angle for all laser beam incidences within a cell, and $n_{\mathrm{I}}(k)$ and $n_{\mathrm{P}}(k)$ are the numbers of voxels with attribute values of 1 and 2, respectively, in the kth layer of a cell. ΔH is the vertical thickness of a cell (0.5 m), and m_h and $m_{h+\Delta H}$ are the voxel coordinates on the vertical axis and are equivalent to the height of the bottom of cell h and the top $h + \Delta H$ in orthogonal coordinates ($h = m_h\ \Delta k$). $G(\theta_{lmn})$ is the mean projection of a unit leaf area on a plane perpendicular to the direction of the laser beam at θ_{lmn} (Norman and Campbell 1989; Welles and Norman 1991; Jonckheere *et al.* 2004; Weiss *et al.* 2004). $\cos(\theta_{lmn})\ [G(\theta_{lmn})\ ]^{-1}$ is a factor that corrects for the influence of the LIA and laser beam direction. $\cos(\theta_{lmn})[G(\theta_{lmn})]^{-1}$ was determined for each of the measurement dates using the LIA distributions acquired by the fine-resolution portable LIDAR, as described in the section 'Measurements using two types of portable scanning LIDARs'.

The LAD estimates computed for each of the cells were averaged horizontally and the LAD profile for the whole measurement plot (including four quadrats) was obtained in each of the measurement dates. The vertical integration offered LAI estimates for the measurement plot in each of the dates.

Results

Figure 2 shows seasonal change of 3D LIDAR images of the Japanese zelkova canopy in 2006 after registration of LIDAR images measured from three 10 m above ground positions (or six ground positions in the case of February). The areas enclosed by the broken white line correspond to the measurement plot. Each type of tissue is distinguishable within the images due to the fine resolution. In February, defoliation had completed and thus leaves were not observed in Fig. 2*a* except in the undergrowth. In May, leaf growth progressed as shown in Fig. 2*b*. In August, leaf growth progressed even further and densely distributed leaves were observed in Fig. 2*c*. In November, defoliation had already begun and a reduction of leaves was observed in Fig. 2*d*.

Figure 3 shows LIA distributions of the zelkova canopy in May, August and November 2006 obtained by a high-resolution portable scanning LIDAR. In May 2006, the angles evenly distributed and ranged through almost all angle classes. Ninety percent of the angles were included in classes <65°. The mean value and the standard deviation were 34.1° and 20.0°, respectively. In August 2006, the inclination angles shifted to smaller classes compared with the ones in May 2006 and a peak was observed at the smallest class (including those <5°) so that planophile distribution was obtained. The distribution ranged from the 0 to 60° class and 88% of the angles were included in the <40° class. The mean value and the standard deviation were 18.0° and 12.9°. In November 2006, the angles in the <30° class decreased and those between the 30 and 40° classes increased compared with those in August 2006, so that the angle classes <45° became more even. The range extended up to the 85° class but 88% of the angles were included in classes <45°. A peak was observed at the 10° class and the mean value and the standard deviation were 22.8° and 15.4°, respectively.

To evaluate the accuracy of the LAD estimates, the LIDAR-derived LAD profile for the measurement plot in August 2005 was compared with the corresponding actual stratified clipping values (Fig. 4*a*). Although the LAD was a little underestimated at around 11 m and overestimated at below 10 m and around 12 m, overall the LIDAR-derived LAD agreed with the actual profile. The root mean square error (RMSE) was 0.26 $m^2\ m^{-3}$. The LIDAR-derived LAI in August 2005 was 4.24 with an absolute percent error of 11.8%.

Figure 4*b* shows the LAD profiles for the measurement plot in May to November 2006. In May 2006, a peak was observed at a height of 11.0 m with a value of 1.09 $m^2\ m^{-3}$ and mean LAD of 0.29 $m^2\ m^{-3}$. In August 2006, LAD values increased at almost all heights. The peak was at a height of 11.5 m with a value of 1.39 $m^2\ m^{-3}$ and mean LAD of 0.52 $m^2\ m^{-3}$. In November 2006, LAD values decreased at heights mainly between 8.5 and 12.5 m. The peak was at a height of 11.5 m with a value of 1.18 $m^2\ m^{-3}$ and mean LAD of 0.31 $m^2\ m^{-3}$. Over the three seasons, the LAD profiles were tailed towards a lower height.

Based on the LAD profiles in Fig. 4*b*, the changes in LAD over the seasonal course in 2006 were examined (Fig. 5). The positive

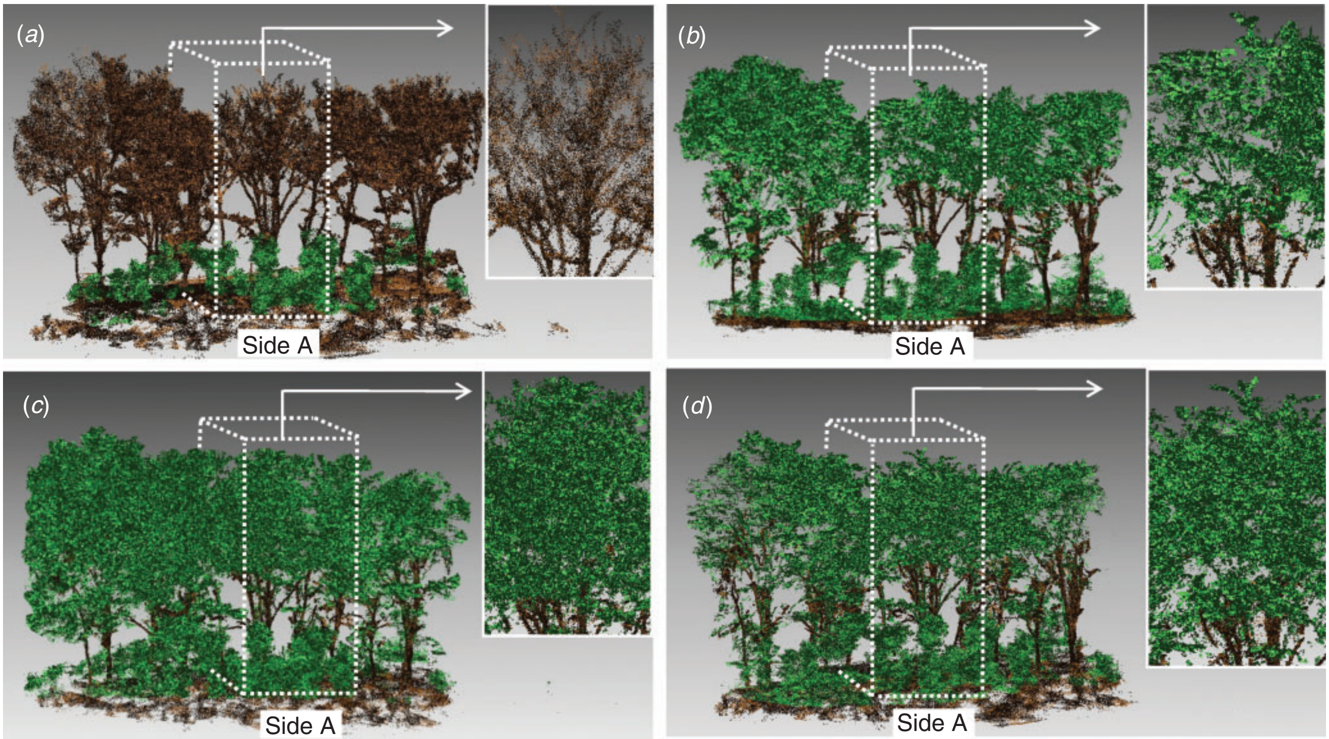

Fig. 2. Seasonal change of 3D LIDAR images of the Japanese zelkova canopy in the study site. Each image shows the result after registration of LIDAR images obtained from several measurement positions in each measurement date: (*a*) February, (*b*) May, (*c*) August and (*d*) November 2006. The areas enclosed by the broken white lines correspond to the measurement plot. Close-up views of a potion of the canopy are on the right side in each figure (leaves are coloured green and the other plant parts and soil are coloured brown in the online version of this manuscript).

and negative signs of the change in Fig. 5 correspond to the increase and decrease of leaves, respectively. From May to August 2006, the leaves increased at almost all heights and three peaks were observed at 9.0, 10.5 and 12.0 m heights. The maximum change was observed at 12.0 m. At 11.0 and 11.5 m, which correspond to each peak of the LAD profiles in May and August 2006, respectively (Fig. 4*b*), a small increase of LAD was observed (Fig. 5). From August to November 2006, the leaves decreased at almost all heights due to defoliation. The peaks observed were similar to the heights from May to August 2006, but the maximum peak height was 10.5 m, which was lower than the period from May to August 2006. The heights at 11.0 and 11.5 m showed a small decrease of LAD where the height of 11.5 m corresponded to peaks in the LAD profiles of August and November 2006 (Fig. 4*b*).

Discussion

LIDAR-derived LIA distributions clearly showed distinctive features in each measurement date. In August 2006, leaves had already matured and the planophile LIA distribution appeared, where low LIA leaves are most frequent. In contrast, it is commonly observed that leaves of Japanese zelkova trees incline with high LIA at the early leaf growth stage just after bud break. According to the tendencies of LIA at the two growth stages, the LIA distribution in May 2006, which includes both low and high values, would show the transition of LIA from early to mature leaf growth stages. Such changes in LIA from growth can be translated as adaptation to the environment as reported in previous studies on different species and environments (Comstock and Mahall 1985; Imai *et al*. 1994; Gratani and Bombelli 2000; Barchuk and Valient-Banuet 2006). In November 2006, the distribution shifted to higher angle classes compared with those in August 2006. In November 2006, defoliation had already started, so the increase of higher angle classes would have been due to leaf senescence. The present study has shown that a high-resolution portable scanning LIDAR can make effective and accurate measurements of seasonal LIA change. In future studies, it would be useful if more regions of the canopy are measured using this method to obtain spatial variations of LIA distributions.

Comparing LIDAR-derived LAD profiles between August 2005 and August 2006 (Fig. 4), the shapes of the profiles were somewhat different from each other. This may resulted from the annual change of foliage distribution accompanied by the environmental change in each year. In addition, stratified clipping in 2005 may have affected the foliage distribution in 2006. Although only leaves were clipped, leaving branches or shoots in 2005, the sudden removal of leaves in the growing season may have affected the tree activity; i.e. the reduced amount of assimilates stored in the artificially defoliated canopy may have affected the dynamics of foliation in the following spring. In the seasonal comparison of the profiles, it was shown that a portable scanning LIDAR can detect the difference in LAD profiles in each season (Fig. 4*b*). This enables us to discuss the changes in LAD accompanied by seasonal course (Fig. 5). From May to August,

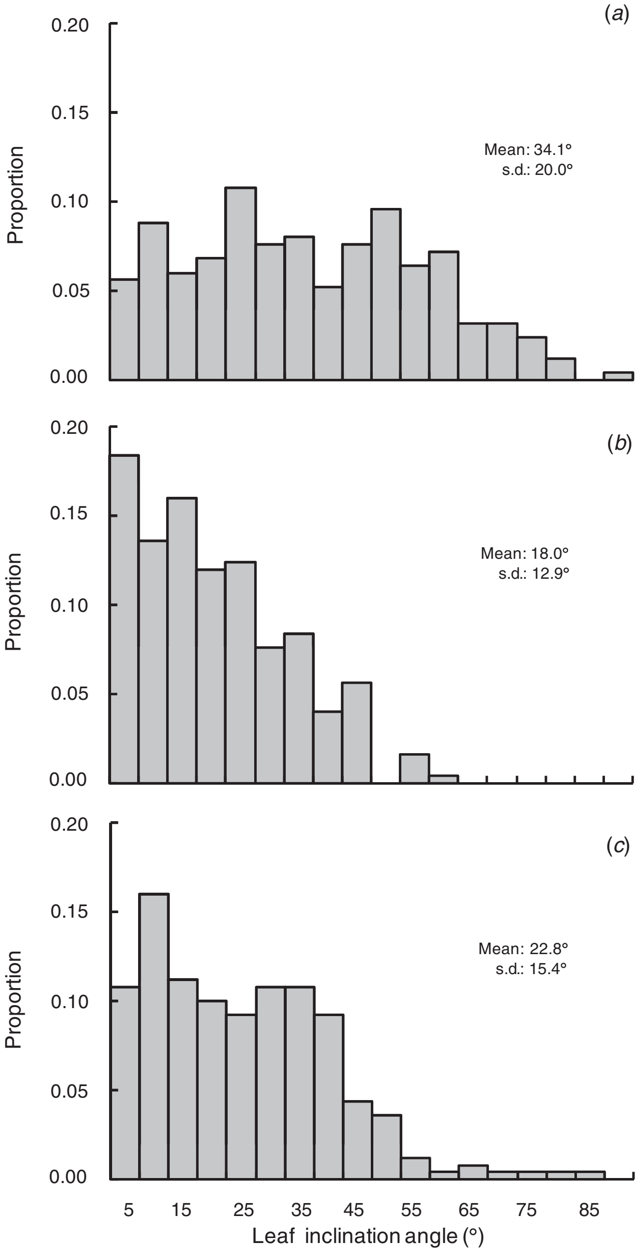

Fig. 3. Leaf inclination angle distributions of the zelkova canopy obtained by a high resolution portable scanning LIDAR. (*a*) May, (*b*) August and (*c*) November 2006. s.d., standard deviation.

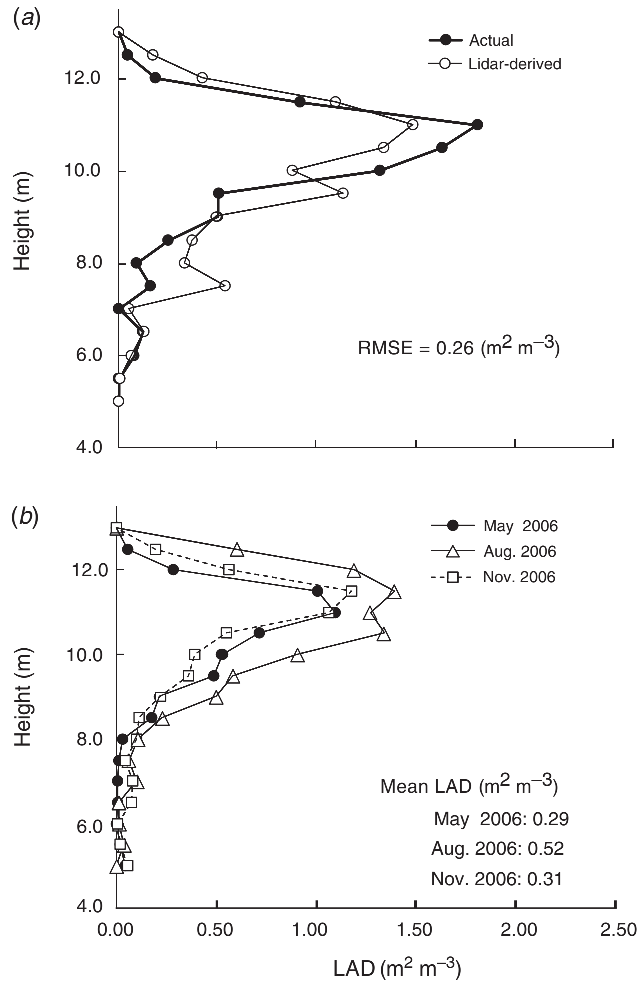

Fig. 4. LAD profiles for the measurement plot. (*a*) Comparison of LAD profiles in August 2005 between LIDAR-derived estimates and the actual stratified clipping values. (*b*) Comparison of LIDAR-derived LAD profiles among three different dates in 2006. RMSE, root mean square error of the LAD estimates.

leaves grew steadily at the upper canopy above 11 m. Leaves are able to capture more light at the upper canopy than the middle or lower canopy; thus more leaves would have grown there. In contrast, the period from August to November showed that defoliation progressed at the canopy below 10.5 m compared with the upper canopy. This may suggest that leaves that can capture more light remain longer on the tree at defoliation. In previous work, such differences in the progress of defoliation dependent on leaf position was also observed in an alder (*Alnus glutinosa* (L.) Gaertn.) canopy where defoliation started earlier in leaves within a shaded region (Eschenbach and Kappen 1996). Fewer changes in LAD at around 11.0 m in the periods May–August and August–November may be attributed to the underestimation of LAD in August 2006 because the LAD profile in August 2005 showed a little underestimation at around the same height (Fig. 4*a*). Similar underestimation also possibly occurred in August 2006. Recently, we showed that the underestimation around the peak was improved by interpolating the underestimated part using fitting functions (Nakai *et al*. 2009). Although study of this method is still in progress with regard to the applicability to various situations, it may contribute to a more reliable estimation around the peak of the LAD profile. Overall, it has been shown that seasonal trends of LAD change can be captured clearly by our proposed method of using a portable scanning LIDAR. In future studies, the applicability of the method to be expanded to other fields and species using not only ground-based portable scanning LIDAR, but also airborne scanning LIDAR, needs to be investigated.

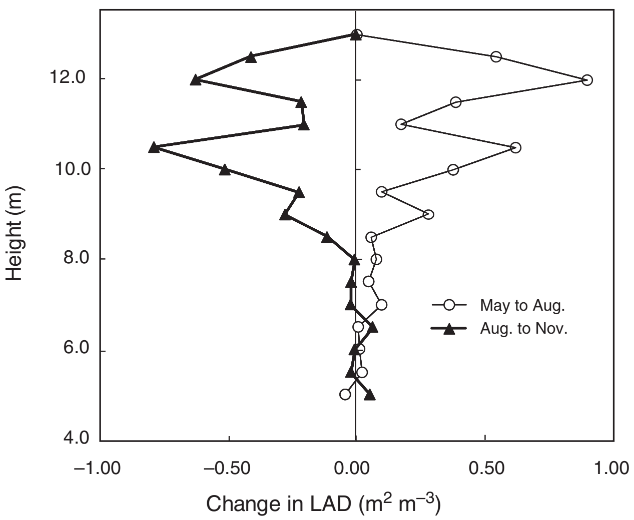

Fig. 5. Changes in LIDAR-derived LAD profiles over the seasonal course in 2006. The positive and negative signs of the change correspond to increase and decrease of leaves, respectively.

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