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Ground-Based Estimation of Leaf Area Index and Vertical Distribution of Leaf Area Density in a *Betula ermanii* Forest

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We developed a ground-based method for estimating leaf area index (LAI) and vertical distribution of leaf area density (LAD) for two *Betula ermanii* plots, combining an allometric method for tree leaf area with the MacArthur–Horn (MH) method using a portable laser rangefinder, including a correction for changes in leaf inclination angle along the vertical gradient measured with a portable digital protractor from a canopy access tower in each plot. Vertical distribution of projected leaf area density obtained by the MH method (LAD_{MH}) was transformed to relative distribution for allotting fixed LAI to different heights. Hence, we first developed an allometric method for estimating tree leaf area for LAI determination. Trunk cross-sectional area at branching height (AB) was accurately estimated ($r^2 = 0.97$) from ground-based measurements of tree dimensions. We used this method to apply pipe model allometry between tree leaf area and AB, and estimated LAI (4.56 and 4.57 $m^2\ m^{-2}$). We then examined how leaf inclination angle affected estimation of the vertical distribution of actual LAD. Leaf inclination angle measurements revealed that actual LAD in the upper canopy was 1.5–1.8-times higher than LAD_{MH}, because of steep leaf inclination, while the correction factor was 1.15–1.25 in the lower canopy. Due to the difference among heights, vertical distribution of LAD estimated with correction for vertical change in leaf inclination was more skewed to the upper canopy than that without correction. We also showed that error in LAD distribution can result if horizontal canopy heterogeneity is neglected when applying the MH method.

Keywords leaf area density, LAI, leaf inclination angle, MacArthur–Horn method, pipe model, allometry, *Betula ermanii*

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1 Introduction

The estimation of leaf area index (LAI, $m^2\ m^{-2}$) and leaf area density (LAD, $m^2\ m^{-3}$) profiles (vertical distribution of LAD) of forest stands using a non-destructive method is important for stand-scale studies. Such studies include those on ecosystem management (Mas and Dietsch 2003), estimation of biomass and forest productivity (Ryan et al. 2004, Lefsky et al. 2005), habitat structure of organisms in the forest canopy (Nadkarni and Sumera 2004, Prusinski et al. 2006), flux exchange of forests (Tanaka et al. 2004), and modeling of stand dynamics (Watanabe et al. 2004, Toda et al. 2007).

The MacArthur and Horn (1969) method, hereafter termed the MH method, is one of the most promising non-destructive methods for estimating LAD profiles, especially since portable laser rangefinders have become available for measuring leaf heights (e.g., Radtke and Bolstad 2001, Parker et al. 2004). In the MH method, heights of individual leaves directly above a site on the forest floor are measured using a rangefinder. With some assumptions, it is possible to convert height data for individual leaves observable from the forest floor to an LAD profile, including layers hidden by lower leaves. The MH method using a portable laser rangefinder does not always require a very fast, accurate (but expensive) measurement system or data processing program as in, for example, Hosoi and Omasa (2007). However, LAD obtained by the MH method (hereafter LAD_{MH}) is an underestimate. Clumping of leaves leads to underestimations of LAD, especially in conifers (Oker-Blom and Kellomäki 1983, Oker-Blom et al. 1991, Welles and Cohen 1996). Leaf inclination was also predicted to contribute to this underestimation (Radtke and Bolstad 2001, Parker et al. 2004), because the MH method is based on measurements of the vertical projection of inclined leaves, and so LAD_{MH} at a given height should be smaller than actual LAD. The LAI estimated by the MH method (hereafter LAI_{MH}), which is equivalent to the integrated value of LAD_{MH} from the ground to the top of the canopy, is also underestimated. Although vertical distribution of leaf inclination angle has long been studied (e.g., Ford and Newbould 1971, Hollinger 1989, Kull et al. 1999, Utsugi et al. 2006, Hosoi and Omasa 2007), information on leaf inclination for various tree species is still limited, compared with that for leaf clumping. While some previous studies assumed that leaf inclination was constant throughout the canopy (e.g., Lefsky et al. 1999), greater inclinations of leaves of broadleaf species are generally found at the top than in the lower canopy (Warren-Wilson 1963, Ford and Newbould 1971). LAD_{MH} and LAI_{MH} should therefore be corrected by taking into account the various leaf inclination angles at different heights within the canopy.

Another source of underestimation in the MH method is the sample size; if the number of range-finding measurements is small, both LAD and LAI are underestimated (Aber 1997b). Therefore, recent studies using the MH method have employed a measurement system with a very high range-finding rate of the laser in order to obtain a sufficient sample size in a short time (e.g., Parker et al. 2004). However, such high-speed laser rangefinders have a disadvantage in that they cannot distinguish between leaves and other woody organs (trunks and branches), so that further correction is necessary when estimating LAD profiles. Because LAD estimation by the MH method assumes that leaves are randomly distributed in a given horizontal layer, the non-randomness of leaf distribution in a horizontal layer may also lead to errors in LAD estimation (Welles and Cohen 1996). For example, Radtke and Bolstad (2001) used the MH method with numerous measurements of single leaf heights from regularly chosen sites on the forest floor, spread over the entire study plot, but this measurement scheme involves the assumption that the entire canopy of the study plot is horizontally homogeneous. However, the canopy surface of a forest generally undulates spatially (e.g., Sumida 1993, 1995), which would result in non-random leaf distribution in a given horizontal layer, but no study has considered the effects of canopy undulation on LAD estimation by the MH method.

The MH method does, however, provide a satisfactory estimate of the vertical distribution of relative LAD, i.e., actual LAD of each height relative to actual LAI such that the sum of (LAD Δh)'s for the entire canopy equals unity (Δh, unit height interval), is similar to the vertical distribution of relative LAD obtained by the MH method

(Aber 1979a, 1979b, Fukushima et al. 1998), even if the absolute value of actual LAD is underestimated by the MH method when the number of range-finding measurements is small. This is because the relative LAD profile is independent of the number of leaf height measurements (Aber 1979b). Hence, if LAI is estimated by another reliable method, it can be used to convert the relative LAD estimated by the MH method to an actual LAD profile as the product of LAI and relative LAD.

The allometric method is thought to give a reliable estimate of stand LAI (Madgwick and Satoo 1975, Ogawa and Kira 1977). Unfortunately, the allometric relationship for estimating leaf area or leaf weight for one stand is not always applicable to another stand as long as trunk diameter at 1.3-m height ($D_{1.3}$) and/or tree height (H) are used for estimation of tree leaf area (Kira and Shidei 1967, Zianis et al. 2005). In contrast, the allometric relationship between the amount of leaves on a tree and the trunk diameter at branching height (the height just below the lowest branch of a tree; DB) for one stand is applicable to other stands of the same species (the pipe model; Shinozaki et al. 1964a, b, Kira and Shidei 1967). The difficulty in using pipe model allometry is that measurement of DB, which involves climbing to branching height, is very labor intensive and time consuming compared with $D_{1.3}$ and H measurement, which can be carried out from the forest floor. This is one reason why obtaining a ground-truth estimate of LAI for a given stand remains difficult, even though data for allometric relationships are available for many types of forest (e.g., Shidei and Kira 1977). To use existing allometry data for tree leaf area estimation, we need a practical method for measuring or estimating DB that does not require tree climbing. If the estimated DB is comparable to measured DB, previously published pipe model allometry data will be applicable to a given stand.

The objective of the present paper is to propose a simple, low-cost method of estimating LAI and LAD profiles for a broadleaf forest using ground-based measurements. Our strategy was to use the MH method only to obtain the relative LAD profile for conversion to the LAD profile using the LAI obtained with the allometric method. Our aims were 1) to explore a ground-based measurement method for estimating DB for estimating tree leaf area using pipe model allometry, 2) to utilize a portable laser rangefinder to exclusively measure heights to leaves using the MH method, 3) to correct the obtained relative LAD profile by taking into account leaf inclination, and 4) to consider the effect of the measurement/data-processing scheme of the MH method on the LAD profile in relation to the undulating structure of the canopy.

2 Materials and Methods

2.1 Study Sites

Measurements were conducted in two study plots of a naturally regenerated *Betula ermanii* Cham. stand (44°23´03˝N, 142°19´07˝E) within the Hokkaido University Uryu Experimental Forest, Japan. Characteristics of the plots are summarized in Table 1. One of the plots had dense undergrowth of a dwarf bamboo, *Sasa kurilensis* (Rupr.) Makino et Shibata, whereas all aboveground parts of *S. kurilensis* had been continually removed from the other plot since 1998. The two plots, within the same continuous stand of *B. ermanii*, are referred to as SI (*Sasa*-intact) and SR (*Sasa*-removed), respectively. These plots were established to study interactions between *B. ermanii* trees and *S. kurilensis* undergrowth (Takahashi et al. 2002, 2003, Tripathi et al. 2005, 2006a, 2006b, Ishii et al. 2008). As our focus was on the foliage profile of *B. ermanii* trees, the *S. kurilensis* leaves were excluded from measurement.

2.2 Leaf Inclination Measurement System and Field Measurements

To measure leaf inclination, we used a portable digital protractor (Pro3600, Macklanburg-Duncan, USA) weighing 330 g and with an inclination measurement accuracy of 0.05°. The protractor was connected to a pocket PC (HP iPAQ hx2490b, Hewlett-Packard, USA) with a 2-m electronic cable connecting to a RS232C interface. The cable branched at the RS232C interface of the protractor, and had an electrical remote switch

Table 1. Characteristics of *Betula ermanii* trees in the study plots (SI (*Sasa*-intact) and SR (*Sasa*-removed) in 2004 (the time of MacArthur-Horn (MH) method measurements, mean tree heights and mean branching heights of trees are based on measurements taken in 2005). Parentheses indicate values for all tree species. Other tree species are *Phellodendron amurense* Ruprecht, *Sorbus commixta* Hedlund, and *Salix bakko* Kimura. Plots were 20 m × 30 m, and stands were 29 years old in both plots.

Plot	Tree density (ha^{-1})	Total basal area (m^2 ha^{-1})	Mean tree height (m)	Mean branching height (m)
SR	9650 (11800)	16.09 (19.63)	11.2 (10.4)	6.5 (5.8)
SI	11300 (12700)	18.87 (21.11)	10.3 (9.4)	6.4 (5.7)

attached at one end. When the remote switch was pressed, inclination data were automatically logged in the pocket PC. A small level was attached to the protractor so that the body stood upright when positioned to measure inclination angle, to prevent underestimation of inclination. The connection cable, electrical remote switch, and data-storing software were produced by Timbertech (Japan), and the total cost of the system (including protractor and pocket PC) was approximately ¥160 000 in 2007.

Leaf inclination (angle to the horizontal) was measured from the canopy-access scaffolding tower (about 14 m in height) at each plot. In each 1-m deep height class, several twigs within reach (about 1 m from the tower) were randomly chosen from two to four *B. ermanii* trees. Leaf inclination angle was measured for all the leaves on these twigs using the digital protractor. More than 100 leaves were measured for each height class. If there were less than about 100 leaves in the height class, the leaf inclination data were pooled with those from a higher or lower height class. More than 1000 leaves in each plot were measured in a day. Measurements were conducted on 13 and 14 September 2007.

2.3 Laser Rangefinder System and Field Measurements

For the MH method, we used a DISTOpro4a laser rangefinder (Leica Geosystems, Switzerland). The DISTOpro4a's laser spot has a 6-mm diameter at a distance of 10 m, and 18 mm at 30 m (Leica Geosystems 2001). Its typical distance measuring accuracy is 1.5 mm, and the possible range of measurement without a target plate is 0.3 to 30.0 m. As the laser uses a visible wavelength (635 nm), we were able to ascertain the location of the laser spot in the field.

In the measurement system used in the present study, the DISTOpro4a was connected to an electrical release switch (REL-02, AROCK Industry Co. Ltd., Japan) via a release connection cable (CB3M, AROCK Industry Co. Ltd., Japan), which connects to the DISTOpro4a interface. A vertical telescopic viewfinder (Leica731719, Leica Geosystems, Switzerland) was set on the DISTOpro4a, enabling us to see the laser spot on a distant target. The DISTOpro4a was mounted on a commercial camera tripod to ensure that the laser beam was emitted directly upwards. Each component of this system was commercially available, and the total cost of the system (including the DISTOpro4a) was approximately ¥200 000 in 2004. The total weight of the system, including the tripod, was approximately 1.6 kg. Production of DISTOpro4a has ceased, but a new version of the laser rangefinder with the functions and interfaces necessary for the present method became available in 2009, with a measurement range of ~100 m (DISTO D8; Leica Geosystems, http://www.leica-geosystems.com/corporate/en/lgs_78069.htm).

Laser dot diameter is considered to be a significant source of error in laser measurements (Denison 1997). We tested the target-size sensitivity of DISTOpro4a (hereafter DISTO) and its capacity to range through openings using the method of Parker et al. (2004). Circular targets (1 and 2 cm in diameter) and a target board with square openings (1 and 2 cm diagonally) were positioned approximately 2 m in front of a wall and 10, 15, 20, and 30 m from the DISTO. Ten replicate measurements were made, and an index of relative error for the target diameter was then calculated (Parker et al. 2004): [(measurement distance – actual distance to target) / (distance between target and wall)]. For both target diameters, the relative errors were always smaller than 0.005 for these distances, except for the 1-cm target at a 30-m distance, for which the error was 0.33. The relative error for the capacity to range through openings was calculated as follows: [(actual distance to wall – measurement distance) / (distance between target and wall)]. Relative errors were smaller than 0.0005 and 0.006 for opening sizes of 2 cm and 1 cm, respectively, at all distances, except for the 1-cm target at a 30-m distance, where the relative errors were much smaller (< 0.01) than those of the range-finding system of Parker et al. (2004) (Riegl LD90-3100HS, Riegl Laser Measurement Systems, Austria). In these tests, within distances ≤ 20 m, absolute errors of measurement distances were within 1 cm for both a target of 1-cm diameter and a 1 cm opening size.

In preliminary trials we found that the most time-consuming task in the field was stabilizing the position of the laser spot emitted from the DISTO; using a monopod (instead of a tripod) resulted in measurement errors. As described below, we checked the location of the laser spot on the plant with a viewfinder; thus, we could not check both the verticality of the monopod and the laser spot location simultaneously. The use of a release switch, tripod, and platform largely solved these problems. The system was positioned on a 0.8 m × 0.8 m wooden platform placed on a folding camping table. The area of the platform was smaller than the average crown projection area of a tree, so that the space sampled had minimal horizontal heterogeneity of leaf distribution; a larger area may include both spaces with and spaces without leaves due to the convex outer surface of a tree crown. Extendable leg attachments were fixed on the lower sections of each of the four legs of the camping table to enable us to level the surface of the wooden platform. The height to the target was shown on the release switch display a few seconds after pressing the button on the release switch of the DISTO, allowing us to maintain the direction of the laser beam. Small movements of leaves in gentle winds did not affect the measurements. We manually recorded the displayed distances and several measurement conditions (error messages from the DISTO, etc.) for reference during data analyses in the lab. When measuring leaf heights with the DISTO, we confirmed that the laser spot was located on a leaf by looking through the telescopic viewfinder. If the laser spot fell on a stem or branch, we ignored the reading and adjusted the position of the tripod. We excluded height data of stems and branches, recording only distances to leaves. When the laser beam failed to intercept any plant surface, an error message indicating that the laser reflection signal was too weak was shown on the monitor. We recorded this as a "sky hit". These cases were verified visually through the viewfinder, as error messages can occur for reasons other than sky hits. Sky hits were sometimes erroneously recorded as the distance to a non-target leaf or twig if the leaf or twig was blown across the path of the laser beam by the wind. To avoid such false measurements, measurements were only made under calm conditions.

A line transect approximately 30-m long was established close to the center of each plot. The platform was moved at approximately 3-m intervals along the transect to cover 10 "measurement sites" on the forest floor in each plot. We recorded 25 height measurements with the laser at each measurement site. For each laser measurement, the tripod was moved ≥15 cm along the level board to avoid measuring the same leaf repeatedly. The level board maintained the vertical orientation of the laser beam. Multiple laser measurements on the platform enabled more rapid measurement than measuring once at a site and repeating it over the plot area. At five measurement sites, five additional measurements (i.e., a total of 30 measurements) were recorded, because no sky hits were recorded in the first 25 laser measurements. When sky hits were still not recorded after the 30 measurements, we assumed that a sky hit had occurred on the 31st height measurement. Measurements were conducted on 29 July 2004. Under favorable conditions, it took 2–3 h for two operators (one operating the rangefinder and the other recording heights) to complete leaf height measurements at the 10 sites within a study plot.

2.4 Calculation of Leaf Area Density in the MH Method

We calculated the $\mathrm{LAD_{MH}}$ profile from the leaf height data following MacArthur and Horn (1969). The $\mathrm{LAD_{MH}}$ of a height class between heights of h_{i-1} and h_i ($h_{i-1} < h_i$, $i = 1, 2, 3, \ldots$) at measurement site k ($k = 1, 2, \ldots, 10$), $\mathrm{LAD}_{\mathrm{MH}i,k}$ ($\mathrm{m^2\ m^{-3}}$), was calculated as follows:

$$\mathrm{LAD}_{\mathrm{MH}i,k} = \ln(N_{i-1,k} / N_{i,k}) / \Delta h \qquad (1)$$

where $N_{i-1,k}$ is the number of laser beams entering the horizontal plane at h_{i-1}, $N_{i,k}$ is the number of laser beams that passed through the horizontal plane at h_i without being intercepted by leaves in the horizontal layer, and Δh is the constant depth interval of a height class ($h_{i,k} - h_{i-1,k} = 1$ m); hence, $N_{i-1,k} \geq N_{i,k}$. The sum of ($\mathrm{LAD}_{\mathrm{MH}i,k}\ \Delta h$) values from the forest floor to the top of the canopy (i.e., for all i layers) for measurement site k is $\mathrm{LAI}_{\mathrm{MH}k}$ ($\mathrm{m^2\ m^{-2}}$) (= ln(number of laser beams emitted / number of sky hits) Aber (1979a)).

2.5 Data Processing Methods for Estimating $\mathrm{LAD_{MH}}$

As mentioned above, we conducted leaf height measurements from a small area on the forest floor and repeated the measurements at 10 sites within each plot. However, an alternative measurement scheme would have been equally feasible, involving numerous measurements of single leaf heights from randomly, or regularly, chosen sites on the forest floor spread over the entire study plot (e.g., Radtke and Bolstad 2001), by assuming that the entire canopy structure in which leaves are horizontally randomly distributed is level (= the "level" canopy) (Fig. 1a). Although we did not use this scheme in the field, calculation of $\mathrm{LAD_{MH}}$ while assuming horizontal levelness is possible. Before estimating LAD profiles using the MH method and LAI with the allometric method, we examined the effect of the choice of data processing on estimates of $\mathrm{LAD_{MH}}$ in relation to the assumption of canopy structure. Here, it was assumed that the $\mathrm{LAD_{MH}}$ profiles obtained at the 10 measurement sites were real profiles, whereby the canopy structure of each study plot was assumed to comprise 10 component structures (= the "unlevel" canopy; Fig. 1a) and the measurements undertaken at each measuring site were assumed to represent each component. We then compared the resulting plot $\mathrm{LAD_{MH}}$ profiles ($\mathrm{LAD_{UNLEVEL}}$) with the profiles compiled under the assumption that the entire canopy structure of a plot is level. The latter $\mathrm{LAD_{MH}}$ is referred to as $\mathrm{LAD_{LEVEL}}$. Note that in this analysis the subscript "MH" is omitted, but the subscripts "LEVEL" and "UNLEVEL" represent $\mathrm{LAD_{MH}}$ calculated only from the leaf height measurements of the MH method.

$\mathrm{LAD}_{\mathrm{LEVEL}i}$, the $\mathrm{LAD_{LEVEL}}$ of the i-th layer ($= h_i - h_{i-1}$) of a plot, was calculated from Eq. 1 by pooling all leaf height data of the plot as follows:

$$\begin{aligned}
\mathrm{LAD}_{\mathrm{LEVEL}i} &= \ln\left[\left(\sum_{k=1}^{10} N_{i-1,k}\right) \Big/ \left(\sum_{k=1}^{10} N_{i,k}\right)\right] / \Delta h \\
&= \ln\left[\left(\sum_{k=1}^{10} N_{i-1,k} / 10\right) \Big/ \left(\sum_{k=1}^{10} N_{i,k} / 10\right)\right] / \Delta h \qquad (2) \\
&= \left[\ln\left(\sum_{k=1}^{10} N_{i-1,k} / 10\right) - \ln\left(\sum_{k=1}^{10} N_{i,k} / 10\right)\right] / \Delta h
\end{aligned}$$

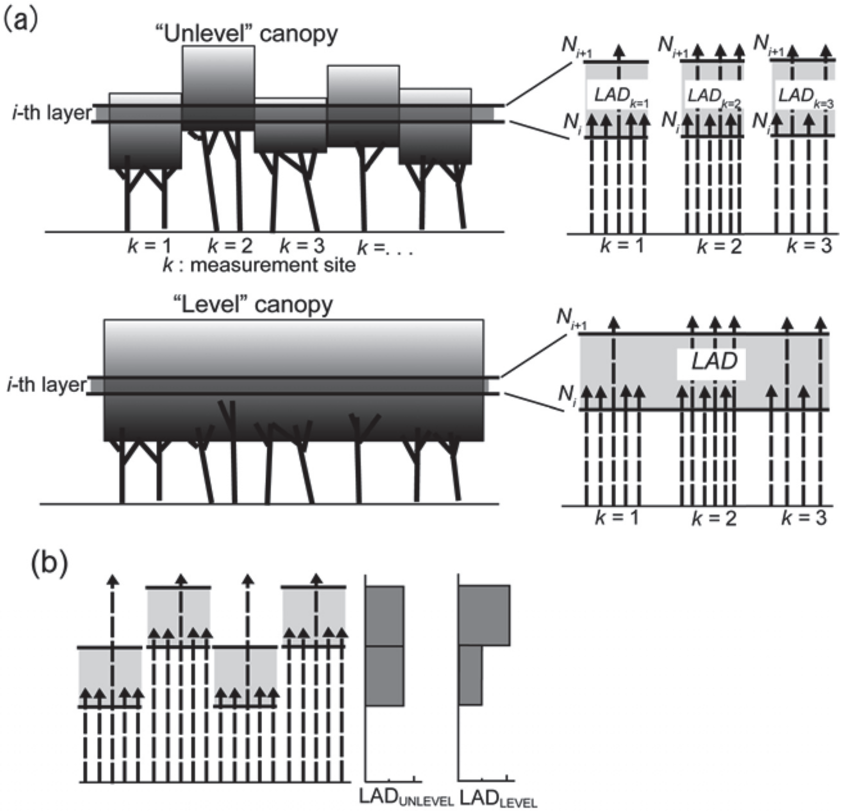

Fig. 1. Schematic of the MacArthur–Horn (MH) method measurement scheme in relation to canopy structure. Shaded part represents the canopy, and arrows indicate each leaf height measurement. (a) The level canopy model and the unlevel canopy model. (b) A possible error associated with the canopy structure assumption. The canopy above each of the four measurement sites has the same $\mathrm{LAI}_{\mathrm{MH}k}$ $(=\ln(5/1)=1.61$; Eq. 1), while the entire canopy assumes an unlevel structure. The mean $\mathrm{LAD}_{\mathrm{MH}i}$ of each horizontal layer among the four measurement sites in the unlevel canopy model ($\mathrm{LAD}_{\mathrm{UNLEVEL}i}$) is calculated as $0.81/\Delta h$ $(=(\ln(5/1)/\Delta h)\times 2/4)$, whereas the $\mathrm{LAD}_{\mathrm{MH}}$'s of the canopy assuming the level canopy model ($\mathrm{LAD}_{\mathrm{LEVEL}i}$), calculated by pooling the laser height data from the four measurement sites, are $0.51/\Delta h$ $(=\ln(20/12)/\Delta h)$ and $1.10/\Delta h$ $(=\ln(12/5)/\Delta h)$ for the lower and upper layers, respectively.

where $\Delta h = h_i - h_{i-1}$ (= 1 m). Note that each of the two terms in the square brackets in Eq. 2 represents the natural logarithm of the arithmetic mean of the number of laser beams at the ten measurement sites. For simplicity, Eq. 2 is expressed as:

$$\mathrm{LAD}_{\mathrm{LEVEL}i} = \ln(A_{i-1}/A_i)/\Delta h \tag{3}$$

where A_i represents the among-measurement site arithmetic mean of the number of laser beams for height, h_i. The $\mathrm{LAI}_{\mathrm{MH}}$ of a study plot obtained under the assumption of a level canopy is denoted by $\mathrm{LAI}_{\mathrm{LEVEL}}$, and is given by:

$$\mathrm{LAI}_{\mathrm{LEVEL}} = \sum_i \left(\mathrm{LAD}_{\mathrm{LEVEL}i}\Delta h\right) \tag{4}$$

In the unlevel canopy model, the mean $\mathrm{LAD}_{\mathrm{MH}}$ of the i-th horizontal layer ($\mathrm{LAD}_{\mathrm{UNLEVEL}i}$) in a study plot is given by the arithmetic mean of the ($\mathrm{LAD}_{\mathrm{MH}i,k}$)'s (Eq. 1) of the 10 measurement sites of the i-th layer:

$$\begin{aligned}\mathrm{LAD}_{\mathrm{UNLEVEL}i} &= \sum_{k=1}^{10} \mathrm{LAD}_{\mathrm{MH}\;i,k}/10 \\ &= \sum_{k=1}^{10}\Big[\ln(N_{i-1,k}/N_{i,k})/\Delta h\Big]/10 \\ &= \left\{\left[\sum_{k=1}^{10}\ln(N_{i-1,k})/10\right] - \left[\sum_{k=1}^{10}\ln(N_{i,k})/10\right]\right\}/\Delta h \\ &= \left[\ln\left(\prod_{k=1}^{10} N_{i-1,k}\right)^{1/10} - \ln\left(\prod_{k=1}^{10}N_{i,k}\right)^{1/10}\right]/\Delta h\ . \end{aligned} \tag{5}$$

Because each of the two terms in the square brackets in Eq. 5 represents the natural logarithm of the geometric mean of the number of laser beams emitted at the ten measurement sites, Eq. 5 is expressed as:

$$\mathrm{LAD}_{\mathrm{UNLEVEL}i} = \ln(G_{i-1}/G_i)/\Delta h \tag{6}$$

where G_i is the among-measurement site geometric mean of the number of laser beams for height h_i. The mean $\mathrm{LAI}_{\mathrm{MH}}$ of a study plot ($\mathrm{LAI}_{\mathrm{UNLEVEL}}$) is given by:

$$\mathrm{LAI}_{\mathrm{UNLEVEL}} = \sum_{i=1}\left(\mathrm{LAD}_{\mathrm{UNLEVEL}i}\Delta h\right) \tag{7}$$

2.6 Evaluation of the Difference between $\mathrm{LAD}_{\mathrm{LEVEL}}$ and $\mathrm{LAD}_{\mathrm{UNLEVEL}}$

To determine the reason for the difference between $\mathrm{LAD}_{\mathrm{LEVEL}}$ and $\mathrm{LAD}_{\mathrm{UNLEVEL}}$ results, the following analysis was conducted. From Eqs. 3 and 6, for the i-th layer, we have:

$$\begin{aligned}&\mathrm{LAD}_{\mathrm{LEVEL}i} - \mathrm{LAD}_{\mathrm{UNLEVEL}i} \\ &= \ln(A_{i-1}/A_i)/\Delta h - \ln(G_{i-1}/G_i)/\Delta h \\ &= [\ \ln(A_{i-1}/A_i) - \ln(G_{i-1}/G_i)]/\Delta h \\ &= [\ \ln(A_{i-1}/G_{i-1}) - \ln(A_i/G_i)\ ]/\Delta h \end{aligned} \tag{8}$$

Hence, if $\mathrm{LAD}_{\mathrm{LEVEL}i} - \mathrm{LAD}_{\mathrm{UNLEVEL}i} \leq 0$, it follows that:

$$(A_{i-1}/G_{i-1}) \leq (A_i/G_i) \tag{9}$$

In other words, if $(A_{i-1}/G_{i-1}) \leq (A_i/G_i)$, or if (A_i/G_i) increased from height h_{i-1} to height h_i (i.e., with increasing height), then $\mathrm{LAD}_{\mathrm{LEVEL}i} \leq \mathrm{LAD}_{\mathrm{UNLEVEL}i}$ would result between layer h_{i-1} and h_i. It is therefore relevant to question why the A_i/G_i ratio increases with height. To answer this question, we examined the values that the A_i/G_i ratio is able to take. Because the arithmetic mean of the number of laser beams ($N_{i,1}$, $N_{i,2}, \ldots, N_{i,k}, \ldots, N_{i,10}$) passing through the horizontal plane h_i among the 10 measurement sites is mathematically equal to or greater than the geometric mean:

$$A_i/G_i \geq 1 \tag{10}$$

where

$$A_i/G_i = 1 \text{ only if } N_{i,1} = N_{i,2} = \ldots = N_{i,k} = \ldots = N_{i,10} \tag{11}$$

That is, the A_i/G_i ratio is minimized (= 1) only if the number of laser beams ($N_{i,k}$ values) is the same for all measurement sites (between $k = 1$ and 10) for a given height h_i. If the number of laser beams $N_{i,k}$ for a given height differs between measurement sites, the A_i/G_i ratio is greater than 1, and may increase with increasing variation among $N_{i,k}$ values. Hence, we calculated the coefficient of variation (CV_i) of the number of laser beams $N_{i,k}$ for each height i among the 10 measurement sites as an index of the variation. $\mathrm{LAD}_{\mathrm{LEVEL}i} \leq \mathrm{LAD}_{\mathrm{UNLEVEL}i}$ or $(A_{i-1}/G_{i-1}) \leq (A_i/G_i)$ (Eq. 8) would be explained by $\mathrm{CV}_{i-1} \leq \mathrm{CV}_i$ or by more among-site variation in the number of laser beams in the upper horizontal plane h_i of the i-th layer. Hence, we examined if change in ($\mathrm{LAD}_{\mathrm{UNLEVEL}i} - \mathrm{LAD}_{\mathrm{LEVEL}i}$) with increasing height is accompanied by increasing CV_i with height h_i. Note that the number of laser beams that passed through the topmost height of the canopy at each site corresponds to the number of sky hits at that site. Because the number of laser beams emitted was similar among the measurement sites (or $CV_i \approx 0$ in the lowermost height of the canopy), if CV_i is largest at the topmost height of the canopy, this means that the LAI_{MHk} (Section 2.4) differed among the 10 sites. Otherwise, the difference between $LAD_{UNLEVELi}$ and LAD_{LEVELi} observed in a layer may be ascribed to the undulating canopy rather than to differences in LAI_{MHk} among the sites; as shown in Fig. 1b, the difference between LAD_{LEVELi} and $LAD_{UNLEVELi}$ can also occur in an unlevel canopy even if the LAI_{MHk}'s are all the same among the measurement sites. In Fig. 1b, CV_i's at the lowermost and uppermost heights of the canopy are the same ($CV_i = 0$), and it is largest at the middle height ($CV_i = 0.77$). In this case, $LAD_{LEVELi} - LAD_{UNLEVELi} < 0$ in the lower part of the canopy, but $LAD_{LEVELi} - LAD_{UNLEVELi} > 0$ in the upper part (Fig. 1b).

2.7 Correction of LAD_{MH} for Leaf Inclination in a Horizontal Layer

Let us assume that individual leaf area S is the same throughout the canopy, that the number of leaves in the unit volume of space at a given horizontal layer above a measurement site is n, and that the leaf inclination angle of each leaf is θ. The sum of the vertical projection area of the leaves, LA_p, is calculated as $LA_P = \Sigma\ [S \cos\theta]$, while the sum of total leaf area, $LA_T, = \Sigma S = nS$. It then follows that:

$$LA_T = LA_P[1/(\cos\theta)_{mean}] \quad (12)$$

where $(\cos\theta)_{mean}$ shows the average $\cos\theta$ of the n leaves (i.e., $(\Sigma\cos\theta)/n$). Note that we focused on $(\cos\theta)_{mean}$ of the leaves rather than on mean θ, as LA_T cannot be obtained with the cosine of the mean value of θ or with $[LA_P/\cos(\text{mean }\theta)]$. Because $1/(\cos\theta)_{mean} \geq 1$, Eq. 12 estimates the factor by which projected leaf area should be multiplied to convert it to actual leaf area. Hereafter, $1/(\cos\theta)_{mean\,i}$ in a horizontal layer i is referred to as FM_i (factor of multiplication for layer i).

2.8 Plot LAD Profile and Vertical Change in Leaf Inclination

Because plot LAI (LAI_{plot}, $m^2\,m^{-2}$) is determined by an allometric method, we must decide how to allot LAI_{plot} to the respective height classes when estimating the plot LAD profile. Hence, in the following four models for plot LAD, we first transformed $LAD_{UNLEVELi}$ and LAD_{LEVELi} of the i-th layer into "relative LAD_i" such that:

$$\text{relative LAI} = \sum_i (\text{relative } LAD_i \Delta h) = 1 \quad (13)$$

and

$$LAD_i = LAI_{plot}\ (\text{relative } LAD_i) \quad (14)$$

The following two models are for estimation of LAD profile without correcting for vertical change in leaf inclination angle. In the first model (M1), the relative LAD profile of a plot at a given height class i (relative LAD_i, $m^2\,m^{-2}$) is simply calculated using LAD_{LEVELi} (Eq. 2) and LAI_{LEVEL} (Eq. 4) of a level canopy model, as follows:

$$\text{M1: relative}LAD_i = LAD_{LEVELi}/LAI_{LEVEL} \quad (15)$$

Similarly, for the unlevel canopy model without leaf inclination correction (M2), the relative LAD_i profile of each plot is given using Eqs. 5 and 7 as follows:

$$\text{M2: relative}LAD_i = LAD_{UNLEVELi}/LAI_{UNLEVEL} \quad (16)$$

The following two models are for LAD profile estimation taking into account the correction for vertical change in leaf inclination angle. Here it is assumed that FM_i of a given height class i is the same irrespective of the measurement site in each plot, because the vertical change of leaf inclination was measured at only one location in each plot. In the third model (M3), relative LAD_i was calculated for the level canopy taking into account the changes of leaf inclination angle with height. The relative LAD_i of each plot is given as:

M3:

$$\text{relative } LAD_i = FM_i\ LAD_{LEVEL\,i} \Big/ \sum_i \left(FM_i\ LAD_{LEVEL\,i}\ \Delta h\right) \quad (17)$$

The last model (M4) employs the unlevel canopy model with correction for vertical change in leaf inclination. Relative LAD_i is given as:

M4:

$$\text{relative } \mathrm{LAD}_i = \mathrm{FM}_i\, \mathrm{LAD}_{\mathrm{UNLEVEL}\,i} \Big/ \sum_i \left(\mathrm{FM}_i\ \mathrm{LAD}_{\mathrm{UNLEVEL}\,i} \Delta h\right) \tag{18}$$

The denominators of Eqs. 17 and 18 correspond to leaf inclination-corrected $\mathrm{LAI}_{\mathrm{LEVEL}}$ and $\mathrm{LAI}_{\mathrm{UNLEVEL}}$, respectively, estimated only using the MH method measurements, i.e., not $\mathrm{LAI}_{\mathrm{plot}}$ determined using the allometric method. Each of the four relative LAD_i models (Eqs. 15–18) satisfies Eqs. 13 and 14. Thus, $\mathrm{LAI}_{\mathrm{plot}}$ obtained by the allometric method is allotted to each height *i* according to the relative LAD_i under the assumption of each model.

Note that $\mathrm{LAD}_{\mathrm{MH}}$ was measured by the MH method in 2004 while leaf inclination was measured in 2007. The canopy height increased by about 2 m from 2004 to 2007. Hence, we assumed that the change in mean leaf inclination with increasing depth from the top of the canopy downward was similar in 2004 and 2007. Moreover, tree height (H) and branching height (HB) measurements could not be conducted in 2004 (see the next section); thus, $\mathrm{LAI}_{\mathrm{plot}}$ was estimated based on 2005 tree inventory data, under the assumption that $\mathrm{LAI}_{\mathrm{plot}}$ in 2005 was the same as that in 2004.

2.9 Tree Surveys, Pipe Model Allometry, and Estimation of AB

To estimate tree leaf area (LA) from the allometric relationship between LA and the cross-sectional area of the trunk at branching height, AB (which is proportional to DB^2 (trunk diameter at branching height)^2), we explored a method of estimating AB, without climbing trees, based on measurements of $\mathrm{D}_{1.3}$ (trunk diameter at 1.3 m height), H, and HB. In 2005, 2006, and 2007, H and HB were measured for all trees in the plot using a height pole. $\mathrm{D}_{1.3}$ was also measured and converted into cross-sectional area, $\mathrm{A}_{1.3}$, assuming that the trunk cross-section was circular. We climbed trees using a mono-pole ladder (Rocky ladder, Tomoe Kasei Kogyo Inc., Japan), and DB was measured for 62 *B. ermanii* trees and 39 trees of other species in the SR plot in 2006, and for 79 *B. ermanii* trees and 20 trees of other species in the SI plot in 2007. DB was then converted into AB.

Pipe model allometry, i.e., the relationship between LA and AB, was investigated by felling nine trees of different sizes. Trees were taken from an area surrounding the two study plots in 2005 and 2006. For each tree, all leaves were clipped and weighed fresh. The total leaf dry weight was calculated from fresh weight–dry weight conversion samples of each tree, and total leaf area of the leaves was calculated from fresh weight–leaf area conversion samples. We also used a dataset from a different 17-year-old stand (as of 2002) of *B. ermanii*, which was taken at a naturally regenerated stand located approximately 1 km from the study site (Kujiraoka 2004). Fifteen trees were felled between June and August 2002, and were measured in the same way as those in our study plots. These data were used to explore the pipe model allometric relationship between LA and AB.

Ormerod (1973) introduced the following equation for estimating upper-stem trunk taper:

$$\mathrm{D}' = \mathrm{D}_{1.3}\ [(\mathrm{H}-\mathrm{H}')/(\mathrm{H}-1.3)]^b, \tag{19}$$

where D' is trunk diameter at a given height H', and *b* is the coefficient for stem taper. If we set H' = HB and D' = DB, and express trunk diameters using cross-sectional areas, we have:

$$\mathrm{AB} = \mathrm{A}_{1.3}\ [(\mathrm{H}-\mathrm{HB})/(\mathrm{H}-1.3)]^{2b} \tag{20}$$

To ascertain if this relationship holds, we investigated the relationship between AB and $\mathrm{A}_{1.3}[(\mathrm{H}-\mathrm{HB})/(\mathrm{H}-1.3)]$ using the measured values of H (m), HB (m), $\mathrm{A}_{1.3}$ (cm^2), and AB (cm ^{2}) for the 62 *B. ermanii* trees in the SI plot, the 79 *B. ermanii* trees in the SR plot, and also the data for the 15 *B. ermanii* trees in the 17-year-old stand.

3 Results

3.1 Pipe Model Allometry

As previously reported (Shinozaki et al. 1964b), the allometric relationship for LA differed between trees of the 17-year-old stand and those

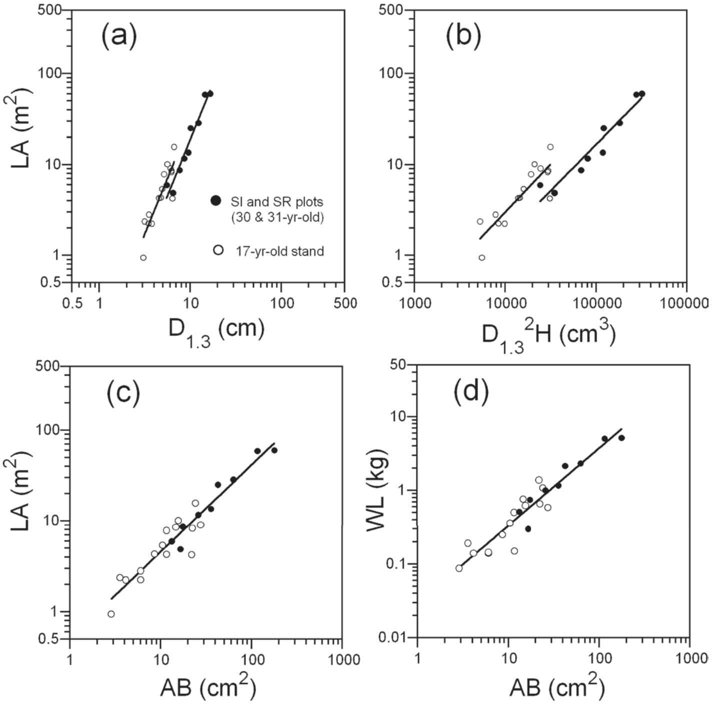

Fig. 2. Regressions for individual tree leaf area (LA) of *B. ermanii*. Closed circles represent trees around SI and SR plots; open circles represent trees of a 17-year-old stand (Kujiraoka, 2004). Relationships between (a) LA and $D_{1.3}$, (b) LA and $D_{1.3}{}^2H$, (c) LA and AB, and (d) WL and AB. For (a) and (b), regression equations are not presented. For the regressions in (c) and (d), see main text.

of the SI and SR plots when the relationship with $D_{1.3}$ (ANCOVA, for slopes, d.f. = 20, $p = 0.05$, $F = 0.000672$; for intercepts, d.f. = 21, $p < 0.05$, $F = 5.273$) or $D_{1.3}{}^2H$ (ANCOVA, for slopes, d.f. = 20, $p = 0.05$, $F = 0.0390$; for intercepts, d.f. = 21, $p < 0.05$, $F = 8.261$) was used (Fig. 2a,b), but the relationships were statistically identical in the relationship with AB (Fig. 2c) (ANCOVA, for slopes, d.f. = 20, $p = 0.05$, $F = 0.258$; for intercepts, d.f. = 21, $p = 0.05$, $F = 0.00294$). Because the log-transformed relationship between LA (m^2) and AB (cm^2) did not differ significantly between the SR and SI plot data and the 17-year-old stand data (ANCOVA, for slopes, d.f. = 20, $p = 0.05$, $F = 0.258$; for intercepts, d.f. = 21, $p = 0.05$, $F = 0.0029$), we pooled the data of the 24 trees and obtained the following relationship (Fig. 2c):

$$\log_{10}(LA) = \log_{10}(0.500) + 0.959 \log_{10}(AB) \qquad (21)$$

where $r^2 = 0.913$, $n = 24$, $p < 0.001$, $F = 232.06$, and root mean square error (RMSE) = 0.133 for $\log_{10}(LA)$.

We calculated a conversion factor (CF) of 1.048 to correct the bias associated with the log-transformation of Eq. 21 (Sprugel 1983). Hence, LA of a given tree is calculated as:

$$LA = 1.048\ (0.500\ AB^{0.959}) \qquad (22)$$

A similar result was obtained for the relationship between leaf dry weight of a tree (WL, kg) and AB (Fig. 2d). Neither slopes nor intercepts differed between the regressions for closed and open circles (ANCOVA, for slopes, d.f. = 20, $p = 0.05$, $F = 0.0001$; for intercepts, d.f. = 21, $p = 0.05$, $F = 0.0055$); thus, both datasets were pooled and the following result was obtained; $\log_{10}(WL) = \log_{10}(0.0294) + 1.050 \log_{10}(AB)$, where $r^2 = 0.893$,

$n = 24$, $p < 0.001$, $F = 185.07$ and RMSE = 0.163 for $\log_{10}$(WL). The CF for the log-transformation correction was 1.073.

3.2 Plot LAI

The following relationship was obtained between AB and [$A_{1.3}$ (H−HB)/(H−1.3)]:

$$\log_{10}(\mathrm{AB}) = \log_{10}(1.005) + 1.001 \log_{10} [\mathrm{A}_{1.3} (\mathrm{H-HB})/(\mathrm{H}-1.3)] \quad (23)$$

where $r^2 = 0.965$, $n = 156$, $p < 0.0001$, $F = 4266.86$, and RMSE = 0.0652 for $\log_{10}$(AB) (Fig. 3). Because the slope and the intercept did not differ significantly from 0 and 1, respectively (both $p > 0.05$), we adopted the following equation, which is identical to Eq. 20, with its exponent $(2b) = 1$, to estimate AB of each tree, including those for which DB was not measured by climbing the trees:

$$\mathrm{AB} = \mathrm{A}_{1.3} [(\mathrm{H-HB})/(\mathrm{H}-1.3)] \quad (24)$$

We further checked if using measured AB or the AB value estimated by Eq. 24 would change the allometric relationship between LA and AB (Eq. 21) using the data of the 24 felled trees. For a comparison with Eq. 21, we obtained $\log_{10}$(LA) = $\log_{10}$(0.461) + 0.983 $\log_{10}$(AB estimated by Eq.24) with $r^2 = 0.905$, $n = 24$, $p < 0.0001$, $F = 208.54$ and RMSE = 0.140 for $\log_{10}$(LA). Neither the slopes nor the intercepts differed between the two regressions (for both slopes, d.f. = 44, $p = 0.05$, $F = 0.067$; for intercepts, d.f. = 45, $p = 0.05$, $F = 0.023$; ANCOVA). Moreover, for these 24 trees, the averages of actual LA by leaf clipping (12.73 m^2), of LA estimated by measured AB and Eq. 21 (12.41 m^2), and of LA estimated by the calculated AB with Eqs 21 and 24 (12.12 m^2) were not significantly different (total d.f. = 71, $F = 0.009$, $p > 0.05$; ANOVA). Hence, Eq. 24 was used to estimate the AB of each *B. ermanii* tree in the two plots, then it was used to estimate their LA using the pipe model allometry between LA and AB (Eq. 22).

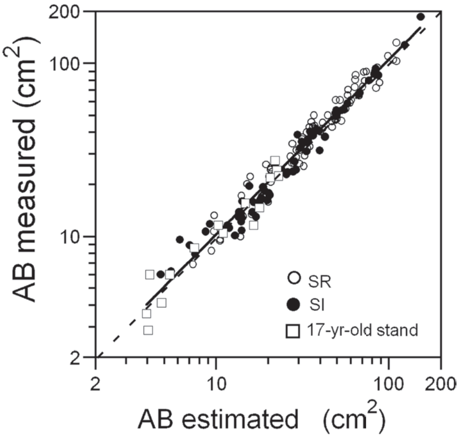

Fig. 3. Relationship between measured AB and estimated AB (=$A_{1.3}$[(H−HB)/(H−1.3)]) for *B. ermanii* trees. Data from 62 trees in the SR plot measured in 2006, 79 trees in the SI plot in 2007, and 15 trees in a 17-year-old stand in 2002 are shown. The thick regression line shows Eq. 23 (section 3.2). The diagonal broken line is a 1:1 line.

When calculating plot LAI using the allometric method (Eq. 22), leaf areas for species other than *B. ermanii* (Table 1) were assumed to be calculated with the same regression as that of *B. ermanii*. Calculated LAI values for 2004 were almost the same in both the SI plot (4.56 $m^2 m^{-2}$) and the SR plot (4.57 $m^2 m^{-2}$).

3.3 Vertical Changes in Cosine of Leaf Inclination Angle

In both plots, the relative frequency of $\cos\theta$ of an individual leaf in each depth tended to be left-tailed as the height class became lower (data not shown). Fig. 4 shows changes in the mean value of the cosine of leaf inclination of individual leaves ($(\cos\theta)_{\mathrm{mean}i}$) in the SR and SI plots along with depth from the top of the canopy of each plot. For each plot, the relationship was approximated by a non-rectangular hyperbolic equation (Johnson and Thornley 1984):

$$(\cos\theta)_{\mathrm{mean}i} = \frac{p_1 \cdot \mathrm{Depth} + p_2 - \sqrt{(p_1 \cdot \mathrm{Depth} + p_2)^2 - 4 \cdot p_1 \cdot p_2 \cdot p_3 \cdot \mathrm{Depth}}}{2 \cdot p_3} + p_4 \quad (25)$$

where Depth (m) is the depth from the canopy top, and p_1–p_4 are parameters. The equation was numerically obtained such that the residual sum of squares was minimal, and we obtained (p_1, p_2, p_3, p_4) = (0.085, 0.250, 0.987, 0.615) for the SI plot ($n = 8$, RMSE = 0.0137) and (0.132, 0.376, 0.982, 0.421) for the SR plot ($n = 8$, RMSE = 0.0424). The theoretical asymptotic value (when depth is sufficient) of $(\cos\theta)_{\mathrm{mean}i}$ is given as ($p_2 + p_4$); 0.871 for SI and 0.801 for SR. Consequently, the mean values of $\cos\theta$ in each height class ($(\cos\theta)_{\mathrm{mean}i}$) in each plot increased with increasing depth from the top of the canopy (Fig 4). The mean cosine values were smallest (0.55 and 0.67 in SR and SI, respectively) at the highest height class. This suggests that actual leaf area in the highest part of the canopy is more than 1.5 (≈ 1 / 0.67) times greater than the projected leaf area estimated by the MH method. In the lower part of the canopy, actual leaf area was 1.15 times larger than the vertically projected area for SI and 1.25 times larger for SR, as the theoretical asymptotic values indicate.

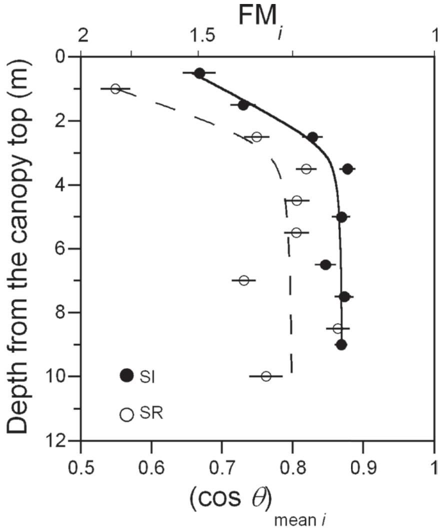

Fig. 4. Vertical changes in $(\cos\theta)_{\mathrm{mean}i}$ for SI and SR plots, plotted against depth from canopy surface. FM$_i$ values ($= 1 / (\cos\theta)_{\mathrm{mean}i}$) are shown on the upper abscissa. Horizontal bars are standard errors. For approximation curves, see Eq. 25.

3.4 LAD Profile Estimated by the Four Models

Fig. 5 shows a comparison of the LAD profiles among the four models (M1–M4). As expected from the greater FM$_i$ values at a depth < 2 m from the top of the canopy (Fig. 4), LAD in the upper layers (12–10 m) using the models with leaf inclination angle correction (M3 and M4) was greater than that without the correction (M1 and M2, respectively) in each of the unlevel and the level canopy models in both plots. In contrast, in the layer < 10 m, LADs with leaf inclination correction (M3 and M4) were smaller than those without leaf inclination correction (M1 and M2, respectively), although the FM$_i$ values were more than 1 (Fig. 4). Note that a larger value of FM$_i$ at a given height could not increase the LAD without leaf inclination correction in proportion to the FM$_i$ at that height, because LAI$_{\mathrm{plot}}$ is already fixed by the allometric method. Instead, the difference of FM$_i$ values among different heights changed the shape of the relative LAD profile. Due to a steep leaf inclination in the upper canopy, the vertical distribution of LAD with leaf inclination

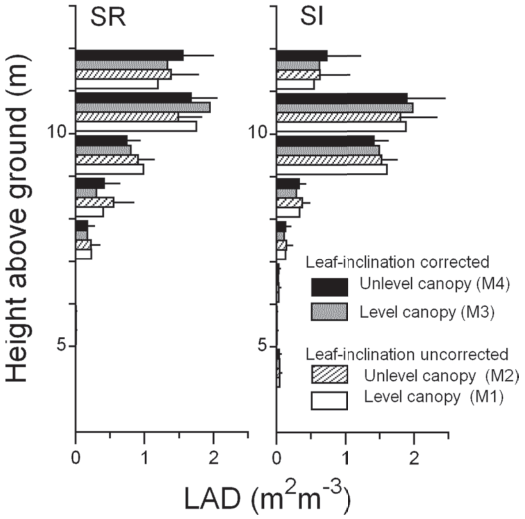

Fig. 5. LAD profiles generated by the four models (M1–M4 in Section 2.8). In the unlevel canopy models (M2 and M4), standard errors among the 10 measurement sites are given by horizontal line segments.

correction was more skewed to the upper canopy than that without. As a result, the increase in LAD at heights >10 m with leaf inclination correction relative to that without the correction was only about 1.1 times in both plots, despite the high FM_i of 1.82 in SR and 1.50 and 1.37 in SI (Fig. 4) at these heights. Even so, there was an increase in the proportion of the sum of the plot LAD_i values of the two highest height layers (>10 m) to that of the lower height classes: before leaf inclination correction (M1 and M3), the proportions were 53% in the SI plot and 63–64% in the SR plot, and after correcting for leaf inclination (M2 and M4), the proportions were 57% in the SI plot and 71–72% in the SR plot. The leaf inclination correction accounted for more of the LAD fraction in higher canopies.

When LAD estimates were compared between the unlevel and the level canopy models, the LADs from the level canopy models (M1 and M3) were 15% smaller than those from the unlevel canopy models (M2 and M4) in the highest layer (11–12 m), irrespective of correction for leaf inclination. The opposite trend occurred in the second and the third layers (9–11 m), in which the LADs from the level canopy models were 8–17% and 4–5% greater than those from the unlevel canopy models in the SR and SI plots, respectively. As shown below, these results can be explained by the assumption of the level canopy model in which the undulating canopy was treated as a level canopy.

For assessing the effects of canopy heterogeneity, changes with height in ($LAD_{UNLEVELi} - LAD_{LEVELi}$) (Eqs. 8 and 9; without leaf inclination correction) and CV_i of the number of laser beams at each height h_i were investigated (Fig. 6). CV_i was smallest at the lowest canopy height, because below the canopy the number of laser beams emitted was similar among measurement sites (Fig. 6b). In both plots, ($LAD_{UNLEVELi} - LAD_{LEVELi}$) was always >0 except for 10–11 m of the SR plot, and was largest at the highest height (Fig. 6a), indicating that the difference resulted from variation in LAI_{MHk} among measurement sites (see Section 2.6). In the SI plot, CV_i had a similar value between 10 and 11 m in height (Fig. 6b), suggesting that the difference of ($LAD_{UNLEVELi} - LAD_{LEVELi}$) cannot be explained by $CV_{1-i} < CV_i$ (Section 2.6), and that it may be related to undulation of the canopy surface as in Fig. 1b. Actually, the topmost heights of the canopy above a site were 10 m at three out of the 10 sites, 11 m at five sites, and 12 m at two sites in the SI plot, while in the SR plot it was 10 m at one site, 11 m at another site, and 12 m at the remaining eight sites (data not shown); i.e., the canopy surface height was more varied in the SI plot. In the SR plot, on the other hand, ($LAD_{UNLEVELi} - LAD_{LEVELi}$) decreased above 9 m, and the difference was nearly 0 (slightly negative) between 10–11 m. This suggests that the level canopy model might be applicable in this layer, but the continuously increasing CV_i with height suggests that among-site variation in the number of laser beams passing through a height increased with height, probably affected by variation of leaf distribution patterns within the canopy.

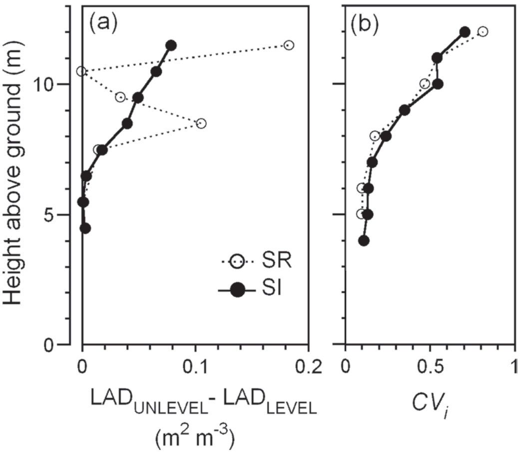

Fig. 6. Changes in (a) ($LAD_{UNLEVEL} - LAD_{LEVEL}$) with height, and (b) the coefficient of variation (CV_i) of the number of laser beams passing through the i-th height in plots SR and SI.

4 Discussion

4.1 LAI Estimation by Allometric Methods

AB estimation using H, HB, and $D_{1.3}$ measurements (Eq. 24) allows us to use pipe model allometry for estimating tree leaf area, LA, from ground-based field measurements. Although we used our own pipe model allometry between AB and LA, previously obtained data for pipe model allometric relationships (either published or unpublished, but available) exist for many types of stands in Japan (e.g., Shidei and Kira 1977), and pipe model allometry for one stand is applicable to other stands (Shinozaki et al. 1964b). Our ground-based method for AB estimation would allow us to apply data from previous studies to pipe model allometry if no measurements were made for AB.

The LAI of *B. ermanii* stands in Japan has been reported to be 4.5 $m^2\ m^{-2} \pm 1.0\ m^2\ m^{-2}$ (average ± standard deviation) (Tadaki 1977), and our results from the allometric methods (Eqs. 22 and 24) lie within this range. Moreover, we also applied these allometric relationships to another *B. ermanii* stand (a different 17-year-old stand to that where we obtained the allometric relationship of this study). For this stand, LAI was estimated to be 4.76 $m^2\ m^{-2}$ in 2003 (with tree inventory data from 2003), close to the LAI of 4.56 $m^2\ m^{-2}$ in 2002 estimated using very detailed three-dimensional light measurements of the canopy (Kubo et al. 2008). Therefore, the method of AB estimation using Eq. 24 is promising for estimating the LAI of a given stand of *B. ermanii* if pipe model allometry is available.

We have not yet examined the applicability of Eq. 24 to other tree species. For Eq. 24 to hold, the exponent (*b*) of Eqs 19 and 20 should equal 0.5. In this case, the shape of the trunk taper is a quadratic paraboloid (Ormerod 1973), although this is a deduction from thicknesses at only two points on the trunk from the tree top, $(H-HB)$ and $(H-1.3)$. Many equations approximating trunk taper have been proposed (e.g., van Laar and Akça 2007), and some theoretical studies have argued that trunk taper should satisfy the requirement for reducing mechanical stress (Morgan and Cannell 1994) and for physiological processes (Mäkelä 2002). Such equations are not always readily comparable to the trunk taper empirically expressed by Eq. 24. In future studies we will establish a theoretical basis for the validity and wider applicability of Eq. 24 to other tree species.

4.2 Importance of Leaf Inclination Correction and the Canopy Structure Assumption to the MH Method

Fig. 4 showed that leaf inclination was consistently greater in the SR plot than in the SI plot, even in the lower canopy. We did not determine why this occurs, but it may reflect a difference in water and/or nutrient status between the two plots (Takahashi et al. 2002, 2003, Tripathi et al. 2005, 2006a, 2006b, Ishii et al. 2008). As suggested by Pearcy et al. (2005), leaf inclination would be related to the mode of radiation capture for photosynthesis and leaf transpiration. Thus, the observed leaf inclination differences may have been affected by, or related to, physical and physiological differences between the two plots.

Our results for leaf inclination angle (Fig. 4) should serve as a caution against LAD estimation using high-speed laser measurement systems such as LIDAR if the LAD profile estimation is not accompanied by LAI estimated by other trustworthy methods. For example, with the unlevel canopy model, $LAI_{UNLEVEL}$ (LAI_{MH} without correction for leaf inclination, Eq. 7) was 2.27 and 2.41 in the SR and SI plots, respectively. If LAD had been estimated solely by the MH method without using LAI_{plot} from the allometric method, $LAD_{UNLEVEL\,i}$ at a height >10 m would have increased proportionally to FM_i at that height (1.82 in the SR plot and 1.50–1.37 in the SI plot; Fig. 4) because of the leaf inclination correction, and the resultant leaf inclination-corrected $LAI_{UNLEVEL}$ (= denominator of Eq. 18; see Section 2.8) would have increased about 1.6 to 1.3 times, or to 3.68 and 3.14, in the SR and SI plots, respectively, after correction for leaf inclination for the entire canopy. These leaf inclination-corrected $LAI_{UNLEVEL}$'s are still smaller than the LAI_{plot}, probably because of the small number of laser emissions at each measurement site. In contrast, we demonstrated that the increase in LAD at height >10 m due to leaf inclination correction was only about 1.1 times, despite the high FM_i values at that height, without increasing the LAD_i in proportion to the FM_i. Although leaf inclination correction resulted in a larger fraction of LAD_i in higher canopies, the increase associated with leaf inclination correction could be much smaller than the FM_i value. This may explain why LAD profiles estimated by the MH method using the relative LAD_{MH} in previous studies appeared to agree well with actual LAD profiles, despite the fact that the MH method lacks leaf inclination corrections. From this viewpoint, estimation of LAI without depending on the MH method is important.

Preliminary consideration of Fig. 1b and the results presented in Fig. 6 suggests that the assumption of the level canopy model can lead to errors in LAD estimation because of canopy heterogeneity. At several measurement sites, we encountered no sky hits because of a small number of laser measurements, and assumed one sky hit at such points. This suggests that the variation in LAI_{MHk} among the 10 sites was greater than we estimated. If among-measurement site variation in LAI_{MH} is expected to be large within a given study plot, measurements and calculations of LAD_{MH} should be undertaken in a spatially homogenous area. Thus, measuring leaf heights in small areas at different measurement sites would be an important measurement scheme for reducing error associated with canopy heterogeneity.

Our LAD estimation would have been more reliable if we had continued the measurements until we obtained at least a few sky hits. However, to obtain the relative LAD_{MH} profile, a greater number of laser measurements is not required (Aber 1979b). As our analyses employed relative LAD (Section 2.8), with LAI_{plot} being obtained separately by the allometric method, the error in LAD_i estimation due to a small number of laser emissions should be small. The diameter of the DISTO laser dot is likely to be narrow enough to pass through leaf gaps, giving a higher measurement accuracy than other rangefinders, as mentioned in section 2.3. This characteristic would be important in detecting leaves in higher canopies, even with the small number of laser measurements in our study. More importantly, although our method using DISTO is relatively time-consuming, the manual laser measurement in this study was necessary to distinguish between leaves and other woody organs (trunks and branches). This was made possible by the visible laser dot of the DISTO and use of the vertical telescopic viewfinder attached to the DISTO. Thus, our measurement scheme using the MH method combined with LAI estimation by the allometric method has several advantages over other methods that use high-speed range-finding systems.

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References

Aber, J.D. 1979a. A method for estimating foliage-height profiles in broad-leaved forests. Journal of Ecology 67: 35–40.

— 1979b. Foliage-height profiles and succession in northern hardwood forests. Ecology 60(1): 18–23.

Denson, R.F. 1997. Minimizing errors in LAI estimates from laser-probe inclined-point quadrats. Field Crops Research 51: 231–240.

Ford, E.D. & Newbould, P.J. 1971. The leaf canopy of a coppiced deciduous woodland. Journal of Ecology 59: 843–862.

Fukushima, Y., Hiura, T. & Tanabe, S. 1998. Accuracy of the MacArthur-Horn method for estimating a foliage profile. Agricultural and Forest Meteorology 92: 203–210.

Hollinger, D.Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. Functional Ecology 3: 53–62.

Hosoi, F. & Omasa, K. 2007. Factors contributing to accuracy in the estimation of the woody canopy leaf area density profile using 3D portable lidar imaging. Journal of Experimental Botany 58(12): 3463–3473.

Ishii, H., Kobayashi, T., Uemura, S., Takahashi, K., Hanba, Y., Sumida, A. & Hara, T. 2008. Removal of understory dwarf bamboo (Sasa kurilensis) induces changes in water-relations characteristics of overstory Betula ermanii trees. Journal of Forest Research 13: 101–109.

Johnson, I.R. & Thornley, J.H.M. 1984. A model of instantaneous and daily canopy photosynthesis. Journal of Theoretical Biology 107: 531–545.

Kira, T. & Shidei, T. 1967. Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. Japanese Journal of Ecology 17(2): 70–87.

Kubo, T., Kobayashi, T., Kato, K., Nishimura, S., Uemura, S., Ono, K., Sumida, A. & Hara, T. 2008. Estimating the three-dimensional structure of canopy foliage based on the light measurements in a Betula ermanii stand. Agricultural and Forest Meteorology 148: 1293–1304.

Kujiraoka, K. 2004. Seasonal changes in allometry and carbohydrate storage of Betula ermanii in Hokkaido. Master's. thesis, Graduate School of Environmental Earth Science, Hokkaido University. (In Japanese).

Kull, O., Broadmeadow, M., Kruijt, B. & Meir, P. 1999. Light distribution and foliage structure in an oak canopy. Trees 14: 55–64.

Laar, A. van & Akça, A. 2007. Forest Mensuration. Springer, Dordrecht, The Netherlands.

Lefsky, M.A., Harding, D., Cohen, W.B., Parker, G. & Shugart, H.H. 1999. Surface lidar remote sensing of basal area and biomass in deciduous forests of Eastern Maryland, USA. Remote Sensing of Environment 67: 83–98.

— , Turner, D.P., Guzy, M. & Cohen, W.B. 2005. Combining lidar estimates of aboveground biomass and landsat estimates of stand age for spatially extensive validation of modeled forest productivity. Remote Sensing of Environment 95: 549–558.

Leica Geosystems 2001. DISTOpro4/pro4a user manual, version 1.0. Leica Geosystems, Heerbrugg, Switzerland.

MacArthur, R.H. & Horn, J.W. 1969. Foliage profiles by vertical measurements. Ecology 50(5): 802–804.

Madgwick H. A. I.& Satoo, T. 1975. On estimating the aboveground weights of tree stands. Ecology 56 (6): 1446–1450.

Mäkelä, A. 2002. Derivation of stem taper from the pipe theory in a carbon balance framework. Tree Physiology 22: 891–905.

Mas, A.H. & Dietsch, T.V. 2003. An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. Ecological Applications 13(5): 1491–1501.

Morgan, J. & Cannell, M.G.R. 1994. Shape of tree stems – a re-examination of the uniform stress hypothesis. Tree Physiology 14: 49–62.

Nadkarni, N.M. & Sumera, M.M. 2004. Old-growth forest canopy structure and its relationship to throughfall interception. Forest Science 50: 290–298.

Ogawa, H. & Kira, T. 1977. Methods of estimating forest biomass. In: Shidei, T. & Kira, T. (eds.). JIBP Synthesis Vol. 16: Primary productivity of Japanese forests. University of Tokyo Press, Tokyo. p. 15–25. ISBN 978-4-13-068063-9.

Oker-Blom, P. & Kellomäki, S. 1983. Effect of grouping of foliage on the within-stand and within-crown light regime: comparison of random and grouping canopy models. Agricultural Meteorology 28: 143–155.

— , Kaufmann, M.R. & Ryan, M.G. 1991. Performance of a canopy light interception model for conifer shoots, trees and stands. Tree Physiology 9: 227–243.

Ormerod, D.W. 1973. A simple bole model. Forestry Chronicle 49: 136–138.

Parker, G.G., Harding, D.J. & Berger, M.L. 2004. A portable LIDAR system for rapid determination of forest canopy structure. Journal of Applied Ecology 41: 755–767.

Pearcy, R.W., Muraoka, H. & Valladares, F. 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. New Phytologist 166: 791–800.

Prusinski, M.A., Chen, H., Drobnack, J.M., Kogut, S.J., Means, R.G., Howard, J.J., Oliver, J., Lukacik, G., Backenson, P.B. & White, D.J. 2006. Habitat structure associated with Borrelia burgdorferi prevalence in small mammals in New York State. Environmental Entomology 35(2): 308–319.

Radtke, P.J. & Bolstad, P.V. 2001. Laser point-quadrat sampling for estimating foliage-height profiles in broad-leaved forests. Canadian Journal of Forest Research 31: 410–418.

Ryan, M.G., Binkley, D., Fownes, J.H., Giardina, C.P. & Senock, R.S. 2004. An experimental test of the causes of forest growth decline with stand age. Ecological Monographs 74(3): 393–414.

Shidei, T. & Kira, T. 1977. JIBP Synthesis Vol. 16: Primary productivity of Japanese forests. University of Tokyo Press, Tokyo. ISBN 978-4-13-068063-9.

Shinozaki, K., Yoda, K., Hozumi, K. & Kira, T. 1964a. A quantitative analysis of plant form: The pipe model theory. I. Basis analyses. Japanese Journal of Ecology 14(3): 97–105.

– , Yoda, K., Hozumi, K. & Kira, T. 1964b. A quantitative analysis of plant form: The pipe model theory. II. Further evidence of the theory and its application in forest ecology. Japanese Journal of Ecology 14(4): 133–139.

Sprugel, D.G. 1983. Correcting for bias in log-transformed allometric equation. Ecology 64(1): 209–210.

Sumida, A. 1993. Growth of tree species in a broad-leaved secondary forest as related to the light environment of crowns. Journal of the Japanese Forestry Society 75(4): 278–286.

— 1995. Three-dimensional structure of a mixed broad-leaved forest in Japan. Vegetatio 119: 67–80.

Tadaki, Y. 1977. Leaf biomass. In: Shidei, T. & Kira, T. (eds.). JIBP Synthesis Vol. 16: Primary productivity of Japanese forests. University of Tokyo Press, Tokyo. p. 39–44. ISBN 978-4-13-068063-9.

Takahashi, K., Uemura, S. & Hara, T. 2002. Effects of understory dwarf bamboo on seasonal changes in soil temperature in a Betula ermanii forest, Northern Japan. Eurasian Journal of Forest Research 5: 49–53.

— , Uemura, S., Suzuki, J. & Hara, T. 2003. Effects of understory dwarf bamboo on soil water and growth of overstory trees in a dense secondary Betula ermanii forest, Northern Japan. Ecological Research 18: 767–774.

Tanaka, T., Park, H. & Hattori, S. 2004. Measurement of forest canopy structure by a laser plane range-finding method: Improvement of radiative resolution and examples of its application. Agricultural and Forest Meteorology 125: 129–142.

Toda, M., Yokozawa, M., Sumida, A., Watanabe, T. & Hara, T. 2007. Simulating the carbon balance of a temperate larch forest under various meteorological conditions. Carbon Balance and Management 2:6. [Online journal]. Available at: http://www.cbmjournal.com/content/2/1/6. doi: 10.1186/1750-0680-2-6.

Tripathi, S.K., Sumida, A., Shibata, H., Uemura, S., Ono, K. & Hara, T. 2005. Growth and substrate quality of fine root and soil nitrogen availability in a young Betula ermanii forest of northern Japan: Effects of the removal of understory dwarf bamboo (Sasa kurilensis). Forest Ecology and Management 212: 278–290.

— , Sumida, A., Ono, K., Shibata, H., Uemura, S., Takahashi, K. & Hara, T. 2006a. The effects of understorey dwarf bamboo (Sasa kurilensis) removal on soil fertility in a Betula ermanii forest of Northern Japan. Ecological Research 21: 315–320.

— , Sumida, A., Shibata, H., Ono, K., Uemura, S., Kodama, Y. & Hara, T. 2006b. Leaf litterfall and decomposition of different above- and below-ground parts of birch (Betula ermanii) trees and dwarf bamboo (Sasa kurilensis) shrubs in a young secondary forest in Northern Japan. Biology and Fertility of Soils 43: 237–246.

Utsugi, H., Araki, M., Kawasaki, T. & Ishizuka, M. 2006. Vertical distributions of leaf area and inclination angle, and their relationship in a 46-year-old Chamaecyparis obtusa stand. Forest Ecology and Management 225: 104–112.

Warren Wilson, J. 1963. Errors resulting from thickness of point quadrats. Australian Journal of Botany 11: 178–188.

Watanabe, T., Yokozawa, M., Emori, S., Takata, K., Sumida, A. & Hara, T. 2004. Developing a multilayered integrated numerical model of surface physics-growing plants interaction (MINoSGI). Global Change Biology 10: 963–982.

Welles, J.M. & Cohen, S. 1996. Canopy structure measurement by gap fraction analysis using commercial instrumentation. Journal of Experimental Botany 47(302): 1335–1342.

Zianis, D., Muukkonen, P., Raisa Mäkipää, R. & Mencuccini, M. 2005. Biomass and stem volume equations for tree species in Europe. Silva Fennica Monographs 4. 63 p.

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