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Vertical integration of leaf area index in a Japanese deciduous broad-leaved forest

Kenlo Nishida NASAHARA [a*], Hiroyuki MURAOKA [b], Shin NAGAI [b], and Hiroaki MIKAMI [a]

[a] Graduate School of Life and Environmental Science, University of Tsukuba, 1-1 Tennoudai, Tsukuba, Ibaraki 305-8572, Japan

[b] Institute for Basin Ecosystem Studies, Gifu University, 1-1 Yanagido, Gifu 501-1193, Japan

* Corresponding author: Tel./Fax: +81-29-853-4897. E-mail address: kenlo@sakura.cc.tsukuba.ac.jp

Abstract

Leaf area index (LAI) is an important quantity in the study of forest ecosystems, but field measurements of LAI often contain errors because of the vertical complexity of the forest canopy. In this study, we established a practical method for field measurement of LAI in the canopy of a deciduous broadleaved forest by accounting for its vertical complexity. First, we produced a semi-empirical model for the vertical integration of leaf dry mass per unit leaf area. We also quantified the litterfall for each tree species. These data enabled us to estimate the LAI of each species in autumn. By periodic *in situ* monitoring of some fixed sample shoots throughout the growing season, we were able to estimate the seasonality of leaf area (as a proportion of the annual maximum value at each point in time) of each species. By using this seasonality to extrapolate LAI values as a proportion of the LAI data in the leaf-fall season, we were able to estimate LAI throughout the year. We applied this method in a cool-temperate deciduous forest in central Japan (Takayama) in 2006 and validated our results using two conventional methods of LAI measurement: the plant canopy analyzer (LAI-2000) and the Tracing Radiation and Architecture of Canopies (TRAC) approach. LAI estimated by TRAC was in good agreement with our results, but LAI estimated using the LAI-2000 was only half the value estimated using our method. The use of basal area data as a proxy for species-specific leaf areas may save labor and time. Our method will be useful for studying the dynamics and interactions of multiple species because it can estimate LAI and its seasonal changes for each species.

Keywords: Leaf area index; Leaf mass per unit leaf area (LMA); Phenology; Litter traps

1. Introduction

The leaf area in a forest canopy is an important quantity in understanding many ecosystem processes and characteristics of the forest. For example, photosynthesis, transpiration, aerodynamic roughness, autotrophic respiration, and other important parameters can be represented by integrating the functions of individual leaves for each tree's total leaf area. This idea, originating from the proposition by Monsi and Saeki (1953; republished in 2005), has been verified in various ecosystems from various standpoints (e.g., Hirose, 2005) and has become the theoretical basis for studying the functional interactions between a forest and its environment (e.g., Aber et al., 1996; de Pury and Farquhar, 1997; Watanabe et al., 2004; Walcroft et al., 2005). Most such studies have described leaf area using the leaf area index (LAI) parameter, which is defined as half of the total leaf area (i.e., the area for only one leaf surface) divided by the ground surface area beneath those leaves (e.g., Chen and Black, 1992; Jonckheere et al., 2004). However, field measurements of LAI often contain errors because of the vertical complexity of a forest canopy's structure, such as the mixture of multiple species with different characteristics, the presence of stems and branches, variation among the leaves (e.g., in their size, angle, thickness), and temporal changes in these factors.

Indirect optical methods for the field measurement of LAI, such as the LAI-2000 Plant Canopy Analyzer (Li-Cor Inc., Lincoln, NE, USA; e.g., Norman and Campbell, 1989), the Tracing Radiation and Architecture of Canopies approach (TRAC, 3rd Wave Engineering, Nepean, Ontario, Canada; Chen and Cihlar, 1995;

61 Leblanc and Chen, 2001), hemispherical photography (e.g., Muraoka and Koizumi,
62 2005) and light transmittance (e.g., Saigusa et al., 2002), assume a simple canopy
63 architecture with little vertical complexity. Therefore, the accuracy of these methods
64 is controversial (e.g., Jonckheere et al., 2004). In contrast, destructive sampling
65 methods can directly provide the LAI value for each species (hereafter, the
66 “component LAI”). However, it is difficult to monitor temporal changes in LAI with
67 this method because we cannot always repeatedly destructively sample forest stands
68 and because the method is prohibitively time-consuming. Allometric approaches
69 (e.g., Macfarlane et al., 2007) can replace destructive sampling, but it remains
70 difficult to monitor seasonal changes using this approach.
71 For a deciduous forest, it is possible to overcome some of these problems
72 using litter traps (e.g., Jonckheere et al., 2004): If leaf expansion and leaf fall do
73 not take place simultaneously, we can estimate the biomass of leaves in the canopy
74 during the leaf-fall season by collecting leaf litter in litter traps on the forest floor.
75 We can then estimate the component LAI by sorting the leaf litter by species (e.g.,
76 Tateno et al., 2005). However, this method provides little information about LAI
77 during the leaf-expansion season. Moreover, to convert the biomass value into leaf
78 area values, we must calculate either the leaf dry mass per unit of leaf area (LMA)
79 or the specific leaf area (SLA), which is the reciprocal of LMA. In order to estimate
80 LMA or SLA, we must account for their vertical variability (e.g., Eriksson et al.,
81 2005).
82 In the present study, we aimed to develop a practical method for field

measurement of LAI in the canopy of a deciduous broadleaved forest that accounts for the canopy's vertical complexity and for seasonal changes. Our method combines three components. First, we propose a semi-empirical model for the vertical integration of LMA within a canopy. Second, using this model and litter-trap observations, we estimate the component LAI during the leaf-fall season. Third, by periodically obtaining *in situ* observations of sample shoots, we can estimate the pattern of relative change (hereafter, "seasonality") of the component LAIs. By scaling the seasonality of the component LAIs so that they are continuously connected to the component LAI in the leaf-fall season, we can extend our estimation of component LAI into the leaf-expansion season. By adding the component LAI of all species, we can then obtain LAI for the entire canopy from the initial leaf expansion to leaf fall. We implemented this method in a Japanese cool-temperate deciduous broadleaved forest. Using this result as a reference value, we validated it against two conventional indirect optical methods (LAI-2000 and TRAC).

2. Materials and methods

2-1. Study site

The study site is a cool-temperate deciduous broadleaved forest near Takayama, in central Japan (137.4231°N, 36.1462°E, 1420 m a.s.l.; Fig. 1). The annual mean air temperature and the mean annual rainfall from 1980 to 2002 were 7.2°C and 2275 mm, respectively. The site is covered by a snowpack that ranges from 100 to 180 cm

105 in depth from December until April (Mo et al., 2005). A tree census has been
106 carried out every year since 1999 (Ohtsuka et al., 2005). The fluxes of CO_2, water
107 vapor, and sensible heat have been observed at a flux tower since 1993 (Yamamoto
108 et al. 1999; Saigusa et al. 2002, 2005; Fig. 1). Leaf physiology (photosynthesis and
109 respiration) of some dominant species has been observed using a canopy-access
110 tower that is 18 m tall (Muraoka and Koizumi, 2005; Fig. 1). Some ecophysiological
111 models have been developed and tested for this site (Higuchi et al., 2005; Ito et al.,
112 2005, 2006).
113 (Insert Fig. 1 here)
114 The species composition of the canopy trees at the study site is as follows:
115 The dominant tree group consists of *Quercus crispula* and *Betula ermanii*, with some
116 *Fagus crenata*, *Betula platyphylla*, and *Magnolia obovata*. The co-dominant trees
117 include *Acer distylum*, *Acer rufinerve*, *Acanthopanax sciadophylloides*, *Tilia japonica*,
118 *Sorbus alnifolia*, and *Kalopanax pictus*. The suppressed trees include *Hydrangea*
119 *paniculata* and *Viburnum furcatum*. Under the suppressed trees, the forest floor is
120 covered by an understory of evergreen dwarf bamboo (*Sasa senanensis*) with a
121 height of 1.0 to 1.5 m. The height of the dominant forest canopy ranges from 13 to
122 20 m.
123 Most observations were carried out from April to November 2006. For the
124 study area, the leaf-expansion season is the period from April to mid-August, and
125 the leaf-fall season is the period from late August to November.
126

2-2. A model for the vertical integration of LMA within a canopy

Even within the same species or the same individual, leaf characteristics vary within the canopy, mainly due to variations in light conditions. For the sake of simplicity, we have considered only two extreme cases of this variation as a function of height, namely the leaf at the top position on the stem (hereafter, the "top leaf") and a leaf at the lowest position (hereafter, called "bottom leaf"). Using these two extremes, we can approximate the entire canopy as a mixture of these two leaf types.

In our model, we define the z-axis as extending vertically downward from the canopy surface ($z = 0$). At the forest floor, $z = Z$. We denote total LAI as L. We denote the cumulative leaf area over a unit area of ground from $z = 0$ to z as $l(z)$. Obviously, $l(0) = 0$ and $l(Z) = L$. Let m = LMA, which depends on z.

To begin our analysis, let us consider a canopy composed of a single species. For a thin layer between z and $z + dz$ within the canopy, the leaf area in this layer (dL) is $dL = L(z + dz) - L(z)$. The leaf dry mass (dM) in this layer is represented as: $dM = mdL$. Therefore, the total dry mass (M) of the entire canopy per unit of ground area is:

$$M = \int dM = \int_0^L m\, dl \quad . \tag{1}$$

Niinemets and Tenhunen (1997) proposed the following relationship based on field study data and a semi-empirical model of a deciduous broadleaved forest:

$$m = a \exp(-bL), \quad (2)$$

where a and b are constants that depend on the species and site. Dufrêne et al. (2005) adopted this function in their numerical model. We have assumed that this formula is generally valid for deciduous broadleaved forests.

We denote the LMA values of the top leaf and the bottom leaf as m_0 and m_1, respectively. From equation (2), it is obvious that $m_0 = m(0) = a$ and $m_1 = m(Z) = m_0 \exp(-bL)$. Therefore,

$$a = m_0 \quad \text{and} \quad b = \frac{1}{L} \ln \frac{m_0}{m_1}. \quad (3)$$

By substituting equations (2) and (3) into equation (1), we get:

$$M = L \frac{m_0 - m_1}{\ln m_0 - \ln m_1}. \quad (4)$$

From this equation, the average LMA (m_a) of the entire canopy can be defined as the total dry leaf mass divided by the total leaf area:

$$m_a = \frac{M}{L} = \frac{m_2 - m_1}{\ln m_2 - \ln m_1} . \quad (5)$$

Now, let us extend this formula to a complex canopy with multiple species. First, let us consider a layer occupied by a single species between $z = z_2$ and $z = z_3$ in the canopy. We describe $l(z_2)$ as l_2 and $l(z_3)$ as l_3. We can describe LMA at z_2 and z_3 as m_2 and m_3, respectively. We assume that equation (2) is valid for the layer occupied by the single species within the complex canopy. From this assumption, $m_2 = a \exp(-bl_2)$ and $m_3 = a \exp(-bl_3)$. Therefore,

$$b = \frac{1}{L_{23}} \ln \frac{m_2}{m_3} . \quad (6)$$

where, $L_{23}=l_3-l_2$. The leaf dry mass in this layer (M_{23}) can be calculated in the same way as equation (4):

$$M_{23} = L_{23} \frac{m_2 - m_3}{\ln m_2 - \ln m_3} \quad (7)$$

If we define the average LMA in this layer (m_{a23}) as M_{23} / L_{23},

$$m_{a23} = \frac{M_{23}}{L_{23}} = \frac{m_2 - m_3}{\ln m_2 - \ln m_3} , \quad (8)$$

which is similar to equation (5).

Now let us consider how the canopy (or a layer) of a single species can be represented as a mixture of top and bottom leaves. Because the LAI of the canopy is the sum of the LAI of the two types of leaves, $L = L_0 + L_1$. Then, the total leaf dry mass (M) can be represented as $M = m_0 L_0 + m_1 L_1$. This must be equal to equation (4). Therefore,

$$m_0 L_0 + m_1 L_1 = L \frac{m_0 - m_1}{\ln m_0 - \ln m_1} . \quad (9)$$

We can simplify this equation to eliminate L_1 by using the relationship $L = L_0 + L_1$, producing the following formula:

$$\frac{L_0}{L} = \frac{1}{\ln m_0 - \ln m_1} - \frac{m_1}{m_0 - m_1} . \quad (10)$$

This tells us about the fraction of top leaves in the canopy. We can estimate the fraction of the bottom leaves by subtracting this result from 1.

In a field study in southern Swedish forest stands, Eriksson et al. (2005) used equal proportions of the top and bottom leaves when estimating average tree SLA. In that case, the equation corresponding to equation (8) is $1 / m_{ae} = [(1 / m_0) + (1 / m_1)] / 2$, or equivalently:

205 $$m_{ae} = \frac{2 m_0 m_1}{m_0 + m_1} \quad (11)$$

206

207 where m_{ae} is the average LMA under the assumption of Eriksson et al. (2005).

208

209 2-3. Observation of LMA

210 In order to determine the LMA of each species, we sampled the top and bottom
211 leaves of each dominant species in August, September, and October in 2006 and
212 2007. We measured LMA of each leaf as follows: First, we measured the area of
213 each leaf by scanning the leaf with an ES-7000H image scanner (SEIKO EPSON Co.,
214 Japan, 300 dpi resolution). We calculated the leaf's area by counting the number of
215 leaf pixels and multiplying this total by the pixel size using the LIA-32 image-
216 analysis software (http://www.agr.nagoya-u.ac.jp/%7Eshinkan/LIA32). Most
217 leaves were flat. The non-flat leaves (wrinkled or rolled) were flattened by the lid of
218 the image scanner. After the area measurement, we dried the leaf samples in an
219 oven at 80°C for more than 48 h. We then measured the dry mass of each sample.
220 By dividing the dry mass by the leaf area, we obtained LMA for each sample. Then,
221 using equation (8), we obtained the average LMA for each species. Strictly
222 speaking, LMA can change along with growth and aging of the leaves. However, we
223 neglected this change because the change was estimated to be insignificant so far as
224 we limit it in the late summer and autumn.

225

226 2-4. Litter-trap observations

227 At the study site, we installed 14 litter traps within a 1-ha permanent sample plot
228 that is being used for ecological surveys (Fig. 1). Each trap had a square aperture of
229 1 m^2. Their locations were chosen so that they covered a wide range of site
230 topographic conditions (ridge, slope, and valley) and tree species. In particular, we
231 avoided placing multiple traps under the crown of a single tree. The litter (leaves,
232 branches, seeds, etc.) caught in the traps were recovered on August 25, September
233 17, September 30, October 9, October 22, November 4, and November 18. During
234 each litter collection, we sorted the litter in each trap into the leaves of each species.
235 Because it was difficult to distinguish between the leaves of *B. ermanii* and *B.*
236 *platyphylla*, we treated them as a single *Betula* category. The tree census data for
237 this site (Ohtsuka et al., 2005) suggest that *B. ermanii* occupied 63% of the total
238 basal area in the *Betula* category. We discarded the leaves of evergreen trees such as
239 *Pinus parviflora* because their amount was small. In fact, the evergreen trees
240 occupied only 2.8% of the site's basal area and only 1.0% of the individuals that
241 formed the entire canopy (Ohtsuka et al., 2005). After oven-drying the leaves at
242 approximately 70°C for longer than 48 h, we measured the mass of the dried leaves.
243 By dividing this mass by the average LMA, we estimated the area of the fallen leaves
244 of each species at the time of sampling. By adding the area of the fallen leaves from
245 August 25 to November 18, we obtained a total LAI, and were able to estimate the
246 component LAI at each point between these dates for the leaf-fall season.
247

248 2-5. Leaf seasonality observations

249 We carried out leaf seasonality observations by means of periodic *in situ* observation
250 of sample shoots. We selected 20 shoots of 18 individuals of 8 species for these
251 samples, all of which we could directly access from the canopy access tower or the
252 forest floor (Table 1). The selection of the 8 species was based on their relative rank
253 in the total tree biomass for the site (Ohtsuka et al., 2005). The selection of the 20
254 sample shoots was based on ease of access and the goal of measuring shoots at a
255 variety of positions.

256 (Insert Table 1 here)

257 On May 12, May 22, June 2, June 16, June 29, July 30, August 18,
258 September 17, September 30, October 9, October 22, and November 5, we obtained
259 the following observations for each sample shoot: the number of all leaves on the
260 shoot and the size (length and width) of about 20 randomly selected leaves on each
261 shoot. By approximating the shape of the leaves as an ellipse and assuming that the
262 measured length and width represented the longest and shortest axes of the ellipse,
263 respectively, we estimated the area of each leaf. Summation of these leaf areas gave
264 us an estimate of total leaf area on the shoot at that point in time. Thus, we
265 obtained a time series for the seasonal changes in total leaf area on each shoot. By
266 normalizing these data so that the seasonal peak value became 1.0, we obtained the
267 seasonality of the leaf area (i.e., the proportion of the maximum value at each point
268 in time) for each shoot. By averaging these results within each species, we obtained
269 the seasonality of the overall leaf area of each species. For *Betula* and *Quercus*, we

averaged the seasonality at the top position and at the bottom position separately, and then averaged the result using a fractional weight derived from equation (10).

These seasonality data were assumed to represent the seasonality of the component LAI. The average seasonality of *A. distylum* and *A. rufinerve* was assumed to represent the seasonality of the other codominant tree species. In the same way, the average seasonality of *H. paniculata* and *V. furcatum* was assumed to represent the seasonality of other suppressed tree species.

2-6. Development of seasonal LAI

We multiplied the seasonality of the component LAI so that it continuously connected to the component LAI for the leaf-fall season estimated by the litter-traps. This allowed us to extrapolate our results to obtain estimates of component LAI throughout the leaf-expansion season. By combining these results, we were able to estimate component LAI throughout the growing season. We also obtained the total LAI of the entire canopy (excluding *Sasa*) by adding the component LAI values for all the species.

LAI of *Sasa* on the forest floor in this site was estimated in April 1999 at 119 sampling points (Sakai et al., 2002), and the result was a mean of 1.71, with a standard deviation of 0.933. Assuming statistical independence among the 119 samples, the standard error of the mean was 0.09. Leaf biomass of *Sasa* at this site was mostly stable for all seasons in 1993 and 1994 (Nishimura et al., 2004). Based on these two results, we assumed a constant LAI of 1.71 for *Sasa*, with a standard

292 error of 0.09.

293

294 2-7. Observations of LAI using indirect optical methods

295 We used LAI-2000 to measure LAI on May 14, June 2, June 30, July 31, September
296 8, and October 23. We used two LAI-2000 instruments simultaneously: one to
297 measure incoming light from the sky above the canopy, and the other to measure
298 transmitted light at ground level. The LAI-2000 at the top of the canopy access
299 tower was operated in automatic mode, with measurements recorded at 15-s
300 intervals. The LAI-2000 at ground level was moved around the site by a researcher
301 to obtain measurements above the *Sasa* canopy (approximately 1.5 m above the
302 ground), taking five measurements within 10 s each time at each location (mostly
303 at or near the litter traps). LAI-2000 measurements were also obtained below the
304 *Sasa* canopy (approximately 0.1 m above the ground) on May 14 in order to
305 estimate the LAI of *Sasa*. We analyzed the data from the two LAI-2000s using the Li-
306 Cor FV2000 software (version 1.06), with all the initial parameters and conditions
307 left at the software's default values.

308 We performed TRAC measurements on June 3 and June 29 along the two
309 100-m transects shown in Figure 1. During each measurement, we also monitored
310 the photosynthetic photon flux density (PPFD) every 5 s with a quantum sensor
311 (IKS-27, Koito Industries, LTD., Yokohama, Japan) at the top of the canopy access
312 tower. We analyzed the TRAC data using the TRACWIN software (version 3.9.1).
313 We tested four groups of parameter settings for each TRAC measurement using two

values for “PPFD above” (the maximum and minimum PPFD values measured at the canopy tower) and two values for “mean element width” (the upper and lower limits of the range within one standard error of the mean leaf diameter estimated using the litter-trap and leaf-seasonality observations).

In general, these indirect methods inevitably observe not only leaves but also stems and branches within their field of view. Therefore, their results are not true LAI values, but rather PAI (plant area index) values, which equal the sum of LAI and SAI (stem area index; the total stem and branch area per unit of ground surface area). We assumed SAI to be invariant and equal to the PAI value observed with the LAI-2000 on May 14, when all the deciduous trees had no leaves. By subtracting this SAI value from the PAI values taken by the LAI-2000 and TRAC, we estimated LAI. Because we obtained these indirect observations above *Sasa* on the forest floor in most cases, these PAI and LAI values excluded the values for *Sasa*.

3. Results

3-1. LMA

We obtained LMA values for the study species that ranged from 25 to 92 g m^{-2} (Table 2). The standard error of each LMA value was less than 6% of the mean. In all species except for *V. furcatum*, the LMA of the top leaves was 1.5 to 2.1 times that of the bottom leaves; for *V. furcatum*, there was little difference between the two leaf types. The average LMA derived using equation (8) ranged from 32 to 76 g m^{-2}.

(Insert Table 2 here)

We tested equation (11) with our data and found that the resulting average LMA was 74.4 g m^{-2} for *B. ermanii*, 68.5 g m^{-2} for *Q. crispula*, and 30.7 g m^{-2} for *H. paniculata*. These values were smaller than the average LMA calculated using equation (8), but the difference was less than the standard error.

3-2. Litter-trap observations

As of late summer (August 25), the canopy LAI (excluding *Sasa*) equaled 5.0, of which 70% was accounted for by the dominant group, 16% by the codominant group, and 14% by the suppressed group. The standard error of the total LAI was 0.3. This error was attributable to both the limited number of the litter traps (14) and the error associated with LMA.

3-3. Leaf-seasonality observations

All the species showed clear seasonality of leaf number, single-leaf size, and leaf area per shoot (Fig. 2). As seen in the changing number of leaves (left column of Fig. 2), most species except *B. ermanii* had a single leaf flush (a rapid emergence of leaves) in May. In contrast, *B. ermanii* showed two leaf flushes: the first one in late May and the second in late June. Because of the small new leaves produced during the second flush, the mean single-leaf area of *B. ermanii* decreased in late June. The new leaves in the second flush never grew as large as the leaves in the first flush, thus the mean single-leaf area after June did not recover to the maximum level

358 attained in May. For some species (*Q. crispula* and *F. crenata* in particular), the
359 single-leaf area decreased slightly from the leaf flush until August, probably because
360 of herbivory by insects.
361 (Insert Fig. 2 here)
362 After summer, the single-leaf area of some species showed irregular changes.
363 For example, the single leaf area of *M. obovata* decreased temporarily in early
364 October and then recovered. This irregularity could occur in the following manner:
365 when large leaves on the shoot fell, the average single-leaf area decreased
366 temporarily, but thereafter, when small leaves fell, the average single-leaf area
367 recovered. Conversely, the single-leaf area of *F. crenata* temporarily increased in
368 October. Such irregularity is partly attributable to statistical errors resulting from
369 the small sample size.
370 The seasonality of leaf area per shoot during the leaf-fall season differed even
371 within a species (particularly for *B. ermanii* and *H. paniculata*), so that the standard
372 error of the leaf area was larger than that during the leaf-expansion season. Except
373 for the leaf-fall period, the standard error of seasonality of leaf area per shoot was
374 mostly less than 0.1. This magnitude of error suggests that the selection of 20
375 sample shoots offers a valid method for representing the seasonality of the
376 component LAI only during the leaf-expansion season.
377
378 3-4. LAI in all seasons
379 By combining the litter-trap data with the leaf seasonality data, we were able to

estimate the component LAI during all seasons (Fig. 3). *Betula* had the largest peak LAI, followed by *Q. crispula*.

(Insert Fig. 3 here)

The total LAI (Fig. 4) also showed clear seasonal changes with a maximum of 7.0 on July 30. Throughout most of the study period, the dominant group accounted for the majority of the total LAI. However, *Sasa* accounted for the majority of LAI in May and November because most of the deciduous trees had no leaves on their branches at this time. The codominant group and the suppressed group also accounted for higher fractions than the dominant group in mid-May because their leaf flush happened earlier than that of all trees in the dominant group except for *F. crenata*.

(Insert Fig. 4 here)

3-5. LAI estimation using indirect optical methods

SAI was estimated to be 0.8 from the LAI-2000 observations on May 14. By subtracting this SAI value from PAI, we estimated LAI with the LAI-2000 and the TRAC approach (Fig. 5). The LAI-2000 gave obviously lower LAI values (by about half) than those provided by our method throughout the study. Moreover, the pattern of seasonal change was different: in July, the LAI-2000 showed a continuing increase of LAI (by as much as 20% of the annual peak), whereas our method showed little increase. In contrast, the TRAC LAI values were close to those provided by our method. The LAI of *Sasa* was estimated to be 1.55 (with a standard

402 error of 0.10, $n = 21$) using the LAI-2000 observations on May 14, which was close
403 to our assumption of 1.71.
404 (Insert Fig. 5 here)
405
406 4. Discussion
407 4-1. Reliability and utility of the proposed method
408 The average LMA of each species derived using equation (8) showed little difference
409 from the average LMA calculated using equation (11). However, if L_0 and L_1 differ
410 greatly, the choice of equation becomes more critical. In order to address this issue,
411 we need further tests of the relationship between the cumulative leaf area and the
412 LMA proposed by Niinemets and Tenhunen (1997). This would require
413 stratification of the number of the fallen leaves (leaf litter) in each LMA category,
414 something we could not do in the present study because it was difficult to measure
415 the area of the fallen leaves, which were deformed and distorted as a result of
416 drying between collection dates.
417 The eight species that we selected for the leaf-seasonality observations
418 accounted for 84% of LAI (on August 25, excluding *Sasa*) estimated from the litter-
419 trap data. This means that the seasonality of about 16% of total LAI was uncertain.
420 Therefore, in order to attain more accurate assessments of the seasonality of LAI,
421 we should obtain observations for more species (especially for *T. japonica*) that
422 were ignored in the present study.
423 From a practical standpoint, our method offers the advantage that it can

work under any weather and light conditions. In contrast, the LAI-2000 and TRAC approaches require suitable weather and light conditions, which are not always available. However, our method is laborious in comparison to these alternatives. In particular, the process of sorting the leaf litter requires considerable time and a certain amount of expertise. If we could eliminate this part of the process, our method would become more convenient. To do so, it would be helpful to have a reliable proxy for the component LAI that is easier to measure in the field.

Figure 6 shows that the fraction of the component LAI (excluding evergreen trees and *Sasa*) of the major species in August corresponded well to the fraction of their total basal area estimated from a tree census study (Ohtsuka et al., 2005). This relationship is consistent with a study of the allometric relationship for 46 North American deciduous species, in which Niklas (1994) found that leaf area increased with the square of stem diameter (i.e., with increasing basal area). Based on this relationship, it may be possible to eliminate the process of sorting the leaf litter.

(Insert Figure 6 here)

4-2. Validation of LMA used in previous studies

From the total leaf dry mass of 315 g m^{-2} and the total LAI (excluding *Sasa*) of 5.0 on August 25, the LMA for the entire canopy (excluding *Sasa*) was estimated as 63 g m^{-2}. In comparison, a previous ecophysiological process model (Ito et al., 2005) reported LMA equal to 67 g m^{-2} (based on an SLA value of 150 $cm^2 g^{-1}$), which is slightly higher than our value. On the other hand, Ito et al. (2006) reported that

446 LMA equaled 93.1 g m^{-2} for *Q. crispula* and 69.2 g m^{-2} for *Betula* in another
447 modeling study, and these values differed greatly from our estimates of 69.7 and
448 76.3 g m^{-2}, respectively (Table 2). We believe that this discrepancy is mostly
449 attributable to the vertical scaling that we performed, which was not attempted in
450 previous studies at this site.
451
452 4-3. Comparison with indirect optical methods of LAI estimation
453 Obviously, it is impossible for every study to carry out such detailed measurements
454 as those in the present study. Therefore, it is desirable to validate and improve the
455 indirect optical methods because they are easier and quicker to carry out. In
456 comparison with our method, the TRAC method provided comparable LAI values
457 (although we did not validate this approach for the later parts of the growing
458 season), but the LAI-2000 gave lower LAI values and a dissimilar pattern of
459 seasonal change. One possible cause for this discrepancy is the clumping effect (e.g.,
460 Leblanc and Chen, 2001), which is accounted for by the TRAC method but not by
461 the LAI-2000 method. The clumping index must equal about 0.5 to explain the
462 discrepancy between these two instruments. However, the actual clumping index
463 estimated using the TRAC data ranged between 0.91 and 0.95. Therefore, the
464 clumping index alone cannot explain the discrepancy.
465 Our results also suggest underestimation of LAI values derived by indirect
466 methods in previous studies at this site. In 1997 and 1998, Saigusa et al. (2002)
467 used transmittance of PPFD to estimate the annual peak PAI (excluding *Sasa*),

468 which ranged between 3 and 4. In 2003, using hemispherical photography,
469 Muraoka and Koizumi (2005) estimated an annual peak PAI of 4.0 (excluding *Sasa*)
470 at 14 locations at this site (mostly corresponding to the litter traps in the present
471 study). If we assume that SAI = 0.8, then the annual peak LAI (excluding *Sasa*) in
472 these two studies should be between 2.2 and 3.2, which is smaller than our estimate
473 of 5.3 on July 30 for the annual peak LAI (excluding *Sasa*). However, the PAI values
474 reported by Muraoka and Koizumi (2005) showed seasonal changes that were
475 consistent with the pattern revealed using our proposed method.
476 To learn the reasons for the discrepancy among the methods, we will need to
477 validate each step in the derivation of LAI in each method, which is the next step
478 after the present study. Along with the leaf seasonality observations, we also
479 observed the distribution of leaf angles and leaf transmittance of each tree species.
480 These data, which we will present in a future paper, should provide more detailed
481 evidence for the causes of errors in the indirect methods.
482
483 4-4. Ecological implications
484 In general, the tree species in cool-temperate deciduous forests in Japan are
485 categorized into “single leaf flush” types such as *Fagus* spp., *Quercus* spp., and *Acer*
486 spp., and “indeterminate leaf production” types such as *Betula* spp. (Koike, 1988;
487 Kikuzawa, 2005). Trees of the “single leaf flush” type have a leaf flush that occurs
488 within a single short period in the early growing season, whereas trees of the
489 “indeterminate leaf production” type have either a gradual leaf flush or several

consecutive leaf flushes. The former type has smaller LMA values than the latter type. All these characteristics are considered to be related to their adaptation strategy to maximize light acquisition and utilization. In this study, these characteristics were obvious (Table 2, Fig. 2, Fig. 3).

These characteristics were reflected in the seasonal changes in component LAI. For example, trees in the codominant group accounted for the majority of total LAI (excluding *Sasa*; Fig. 4) early in the growing season (May). This may relate to the favorable light conditions created by the slower leaf expansion of the dominant trees. Such favorable light conditions for the codominant group, which has been called the “seasonal gap” (Yamamoto, 2000), should depend on the species composition and ecophysiological characteristics of the dominant group. For example, if *Q. crispula* become the majority of the dominant group (currently *Betula* spp.), the earlier leaf-flush and later leaf-fall of *Q. crispula* will create a shorter “seasonal gap,” resulting in a more severe environment for the trees below this canopy. Such an influence could be demonstrated using a numerical model that describes the regeneration process as well as the seasonality of leaf area for each species. This modeling would give insights into the consequences of interactions between forest canopy structure, the resulting light environment, and regeneration processes (Pearcy, 1990; Kuppers, 1994), all of which are affected by the vertical complexity of the canopy. Our method can contribute to such quantitative studies by providing fundamental data that can be used to explain the seasonal changes in the component LAI.

5. Conclusions

We were able to estimate the total LAI of a Japanese deciduous broadleaved forest by accounting for the vertical complexity of the canopy and its seasonal changes. This method can provide not only total canopy LAI but also the component LAI (i.e., LAI values for each species) and its seasonal changes. In this method, it may be possible to eliminate the most laborious step (sorting of leaf litter by species) if the basal area of each species is available. Our method provided considerably higher LAI values than those estimated using the LAI-2000 approach, but comparable values to those provided by the TRAC approach.

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535 University).

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638 Captions

639 Table 1. Sample shoots for the *in-situ* leaf-seasonality observation

640 Table 2. Leaf mass per unit leaf area (LMA; gm^{-2}) of the major tree species

641 Fig. 1. Top: Location of the Takayama (TKY) site in Japan. Bottom: Arrangement of
642 the litter traps and the Tracing Radiation and Architecture of Canopies (TRAC)
643 measurement transects at the Takayama Site. Each litter trap is identified with a
644 label made of a symbol "L" and a two-digit number from L03 to L17 (L01, L02, and
645 L06 do not exist).

646 Fig. 2. Seasonality of leaf characteristics for the tree species. For *B. ermanii* and *Q.*
647 *crispula*, the top and bottom shoots in the canopy are presented separately. Error
648 bars represent the standard error. Each time series for the data was normalized
649 using the annual maximum value set to 1.0.

650 Fig. 3. Leaf area index (LAI) of the tree species (component LAI) estimated by
651 combining the leaf-seasonality data (until August 25) with the litter-trap data (after
652 August 25).

653 Fig. 4. Top graph: Leaf area index (LAI) of the entire canopy and of the dominant,
654 codominant, and suppressed tree groups, and the understory layer (*Sasa* dwarf
655 bamboo), estimated by the proposed method. Bottom graph: The corresponding
656 fractions of total LAI for each group.

657 Fig. 5. Leaf area index (LAI) of the canopy (excluding *Sasa*) estimated by three
658 methods: the method proposed in this study (which combines litter-trap data with
659 leaf-seasonality observations), the LAI-2000 canopy analyzer, and the Tracing

660 Radiation and Architecture of Canopies (TRAC) approach. The LAI values for the
661 LAI-2000 and TRAC approaches were estimated from the observed plant area index
662 (PAI) under the assumption that the stem area index (SAI) equaled 0.8. The error
663 bar represents standard error except for TRAC. The error bar of TRAC represents
664 the range between the minimum and maximum of the LAI values calculated with
665 the four groups of the parameter setting.
666
667 Fig. 6. Fraction of total LAI accounted for by the major species at the study site
668 (*Betula*, *B. ermanii* and *B. platyphylla* combined; *Quercus crispula*; *Magnolia*
669 *obovata*; *Acer rufinerve*; *Tilia japonica*; *Hydrangea paniculata*; and *Viburnum*
670 *furcatum*) in late summer (August 25) versus the corresponding fraction of total
671 basal area (Ohtsuka et al., 2005). Error bars represent the standard error.
672

673 Table 1. Sample shoots for the *in-situ* leaf-seasonality observation

	ID of the individual	Height of the shoot	Leaf positions	Maximum number of leaves
Dominant tree group				
Betula ermanii	Be_A	14 m	top	66
	Be_B	18 m	top	51
		15 m	bottom	
165				
	Be_C	16 m	bottom	55
Quercus crispula	Qc_A	15 m	top	94
	Qc_B	14 m	top	149
		10 m	bottom	80
	Qc_C	11 m	bottom	93
	Qc_D	14 m	top	50
Magnolia obovata	Mo_A	14 m	middle	34
Fagus crenata	Fc_A	1.2 m	bottom	59
Codominant tree group				
Acer distylum	Ad_B	1.3 m	bottom	37
	Ad_C	1.3 m	bottom	42
Acer rufinerve	Ar_A	4.0 m	middle	72
Suppressed tree group				
Hydrangea paniculata	Hp_A	1.5 m	middle	163
	Hp_B	0.8 m	middle	68
	Hp_C	1.5 m	middle	96

Viburnum furcatum	Vf_A	2.5 m	middle	91
	Vf_B	1.0 m	middle	18
	Vf_C	1.0 m	middle	20

Table 2. Leaf mass per unit leaf area (LMA; g m^{-2}) of the major tree species

Species	Position	Mean	s.d.	Sample size	std. error
Dominant group					
Betula ermanii	top	92.2	4.3	5 leaves	2.1
	bottom	62.3	3.6	5 leaves	1.8
	average	**76.3**	---	---	**2.8**
Quercus crispula	top	81.9	15.7	13 leaves	4.5
	bottom	58.8	10.0	8 leaves	3.8
	average	**69.7**	---	---	**5.9**
Magnolia obovata	top	91.6	0.1	2 leaves	0.1
	bottom	44.0	0.2	2 leaves	0.2
	average	**64.9**	---	---	**0.2**
Fagus crenata	top	79.9	6.1	5 leaves	1.6
	bottom	52.0	3.5	2 leaves	4.3
	average	**64.9**	---	---	**2.6**
(Mean of averages)		69.0	---	---	**5.6**
Codominant group					
Acer distylum	top	44.0	2.3	5 leaves	1.2
	bottom	24.6	2.3	5 leaves	1.2
	average	**33.4**	---	---	**1.7**
Acer rufinerve	top	64.0	6.8	5 leaves	3.4
	bottom	31.3	2.5	5 leaves	1.3
	average	**45.7**	---	---	**3.6**
Acanthopanax	top	42.5	1.3	5 leaves	0.7

	sciadophylloides	bottom	27.7	0.4	5 leaves	0.2
		average	**34.6**	---	---	**0.6**
	(Mean of averages)		37.9 [1)]	---	---	**6.9**
	(Mean of averages, *Acer* only)		39.5 [2)]	---	---	**9.1**
Suppressed group						
	Hydrangea paniculata	top	39.9	3.8	5 leaves	1.9
		bottom	25.0	2.0	5 leaves	1.0
		average	**31.9**	---	---	**2.1**
	Viburnum furcatum	top	43.3	1.9	5 leaves	0.9
		bottom	43.5	4.3	5 leaves	2.1
		average	**43.4**	---	---	**2.3**
	(Mean of averages)		37.6 [3)]	---	---	**8.5**

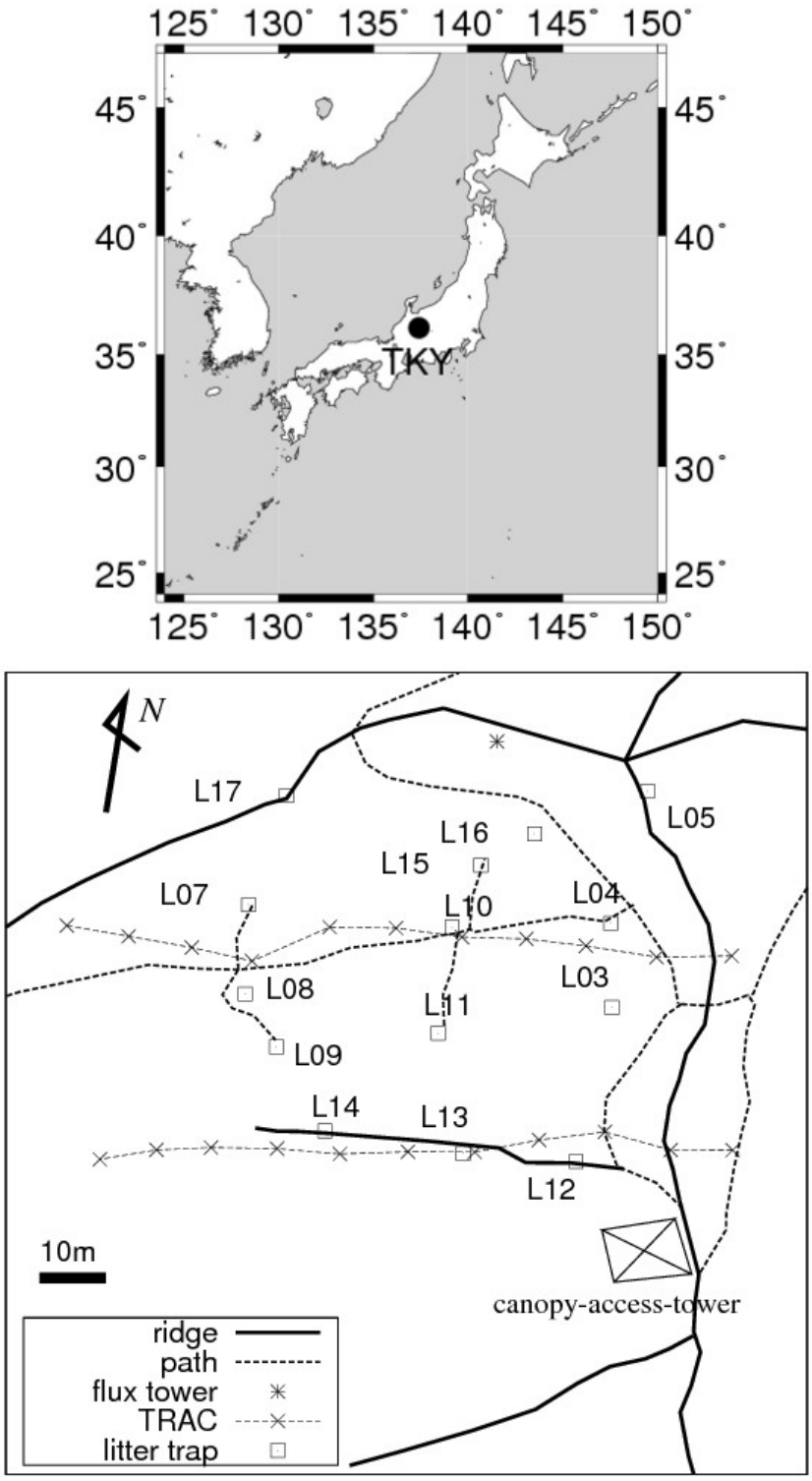
Note:

"top" means leaf samples from the highest part of the tree crown; "bottom" means the leaf samples from the lowest part of the tree crown; "s.d." means standard deviation; "std. error" means standard error (standard deviation of the mean). The boldfaced "**average**" values means the averaged LMA based on equation (8), whereas the "mean of averages" means the arithmetic mean of the **averaged** LMA.

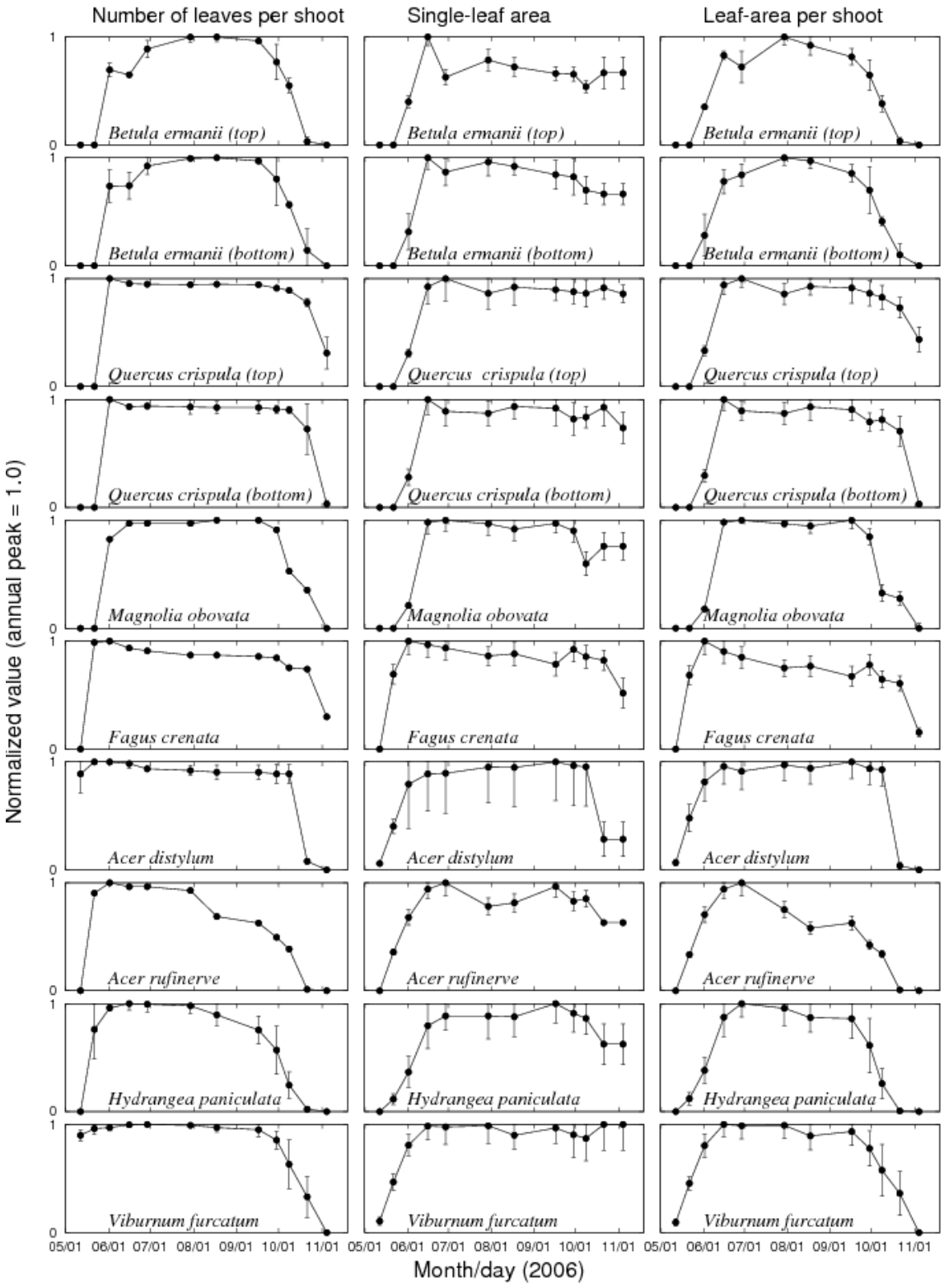
1) This value was used as the surrogate LMA for all other codominant species, including *T. japonica*, *S. alnifolia*, and *K. pictus*.

2) This value was used as the surrogate LMA for all other *Acer* species.

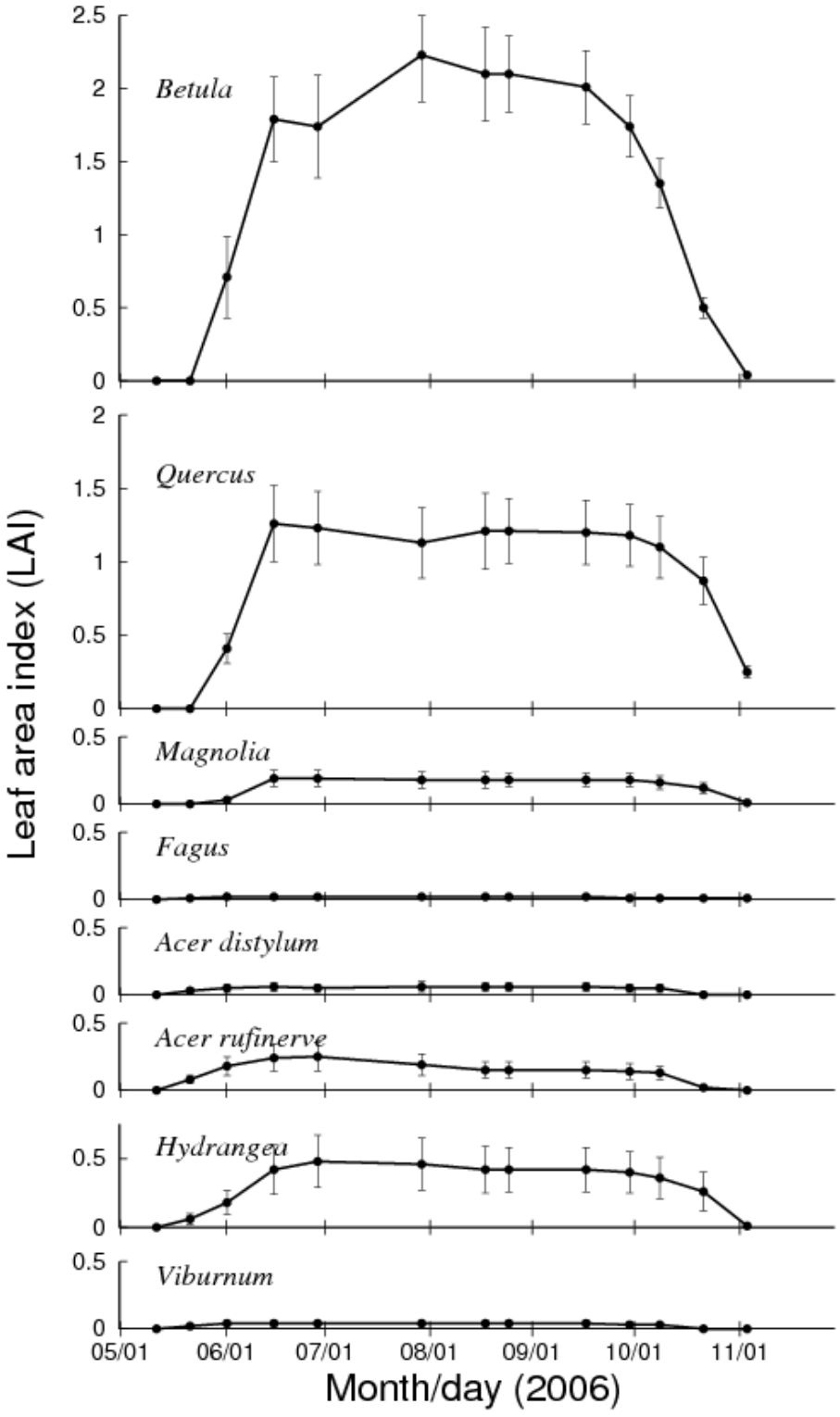
3) This value was used as the surrogate LMA for all other suppressed species.


125° 130° 135° 140° 145° 150°
45°
40°
35°
30°
25°
TKY
N
L17
L16
L15
L07
L10
L04
L05
L08
L11
L03
L09
L14
L13
L12
10m
canopy-access-tower
ridge
path
flux tower
TRAC
litter trap

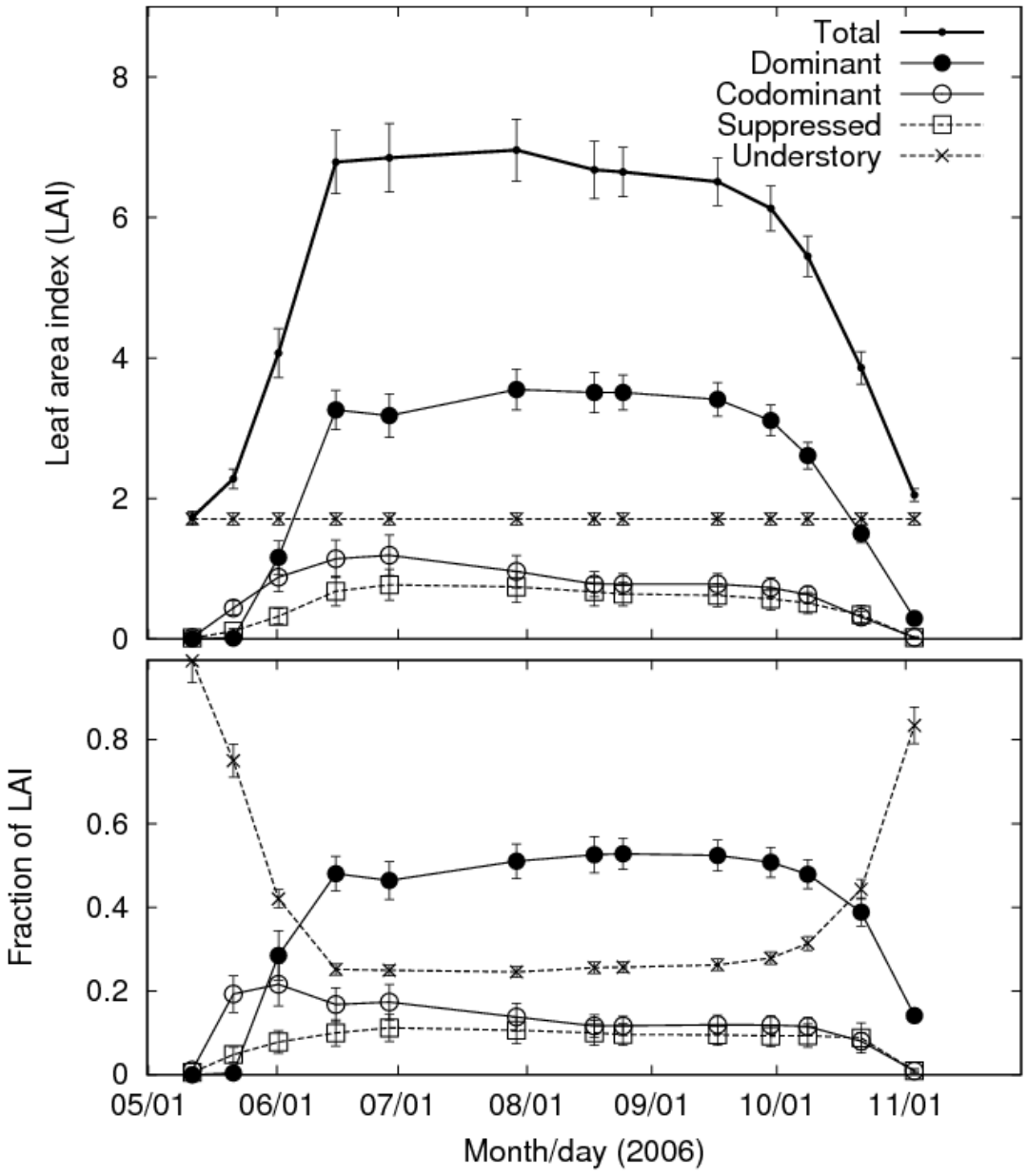
747 Fig. 1


Number of leaves per shoot
Single-leaf area
Leaf-area per shoot
Betula ermanii (top)
Betula ermanii (bottom)
Quercus crispula (top)
Quercus crispula (bottom)
Magnolia obovata
Fagus crenata
Acer distylum
Acer rufinerve
Hydrangea paniculata
Viburnum furcatum
Normalized value (annual peak = 1.0)
0
1
05/01 06/01 07/01 08/01 09/01 10/01 11/01
Month/day (2006)

748 Fig. 2


Leaf area index (LAI)
Betula
Quercus
Magnolia
Fagus
Acer distylum
Acer rufinerve
Hydrangea
Viburnum
2.5
2
1.5
1
0.5
0
05/01
06/01
07/01
08/01
09/01
10/01
11/01
Month/day (2006)

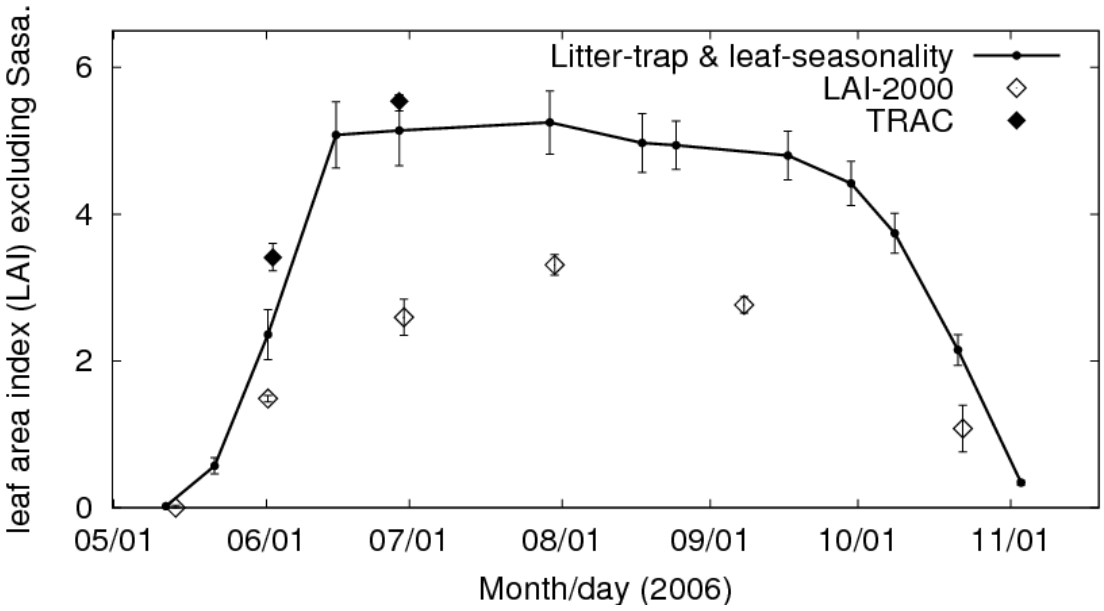
749 Fig. 3


Total
Dominant
Codominant
Suppressed
Understory
Leaf area index (LAI)
0
2
4
6
8
Fraction of LAI
0
0.2
0.4
0.6
0.8
05/01
06/01
07/01
08/01
09/01
10/01
11/01
Month/day (2006)

751 Fig. 4

752

753



754 Fig. 5

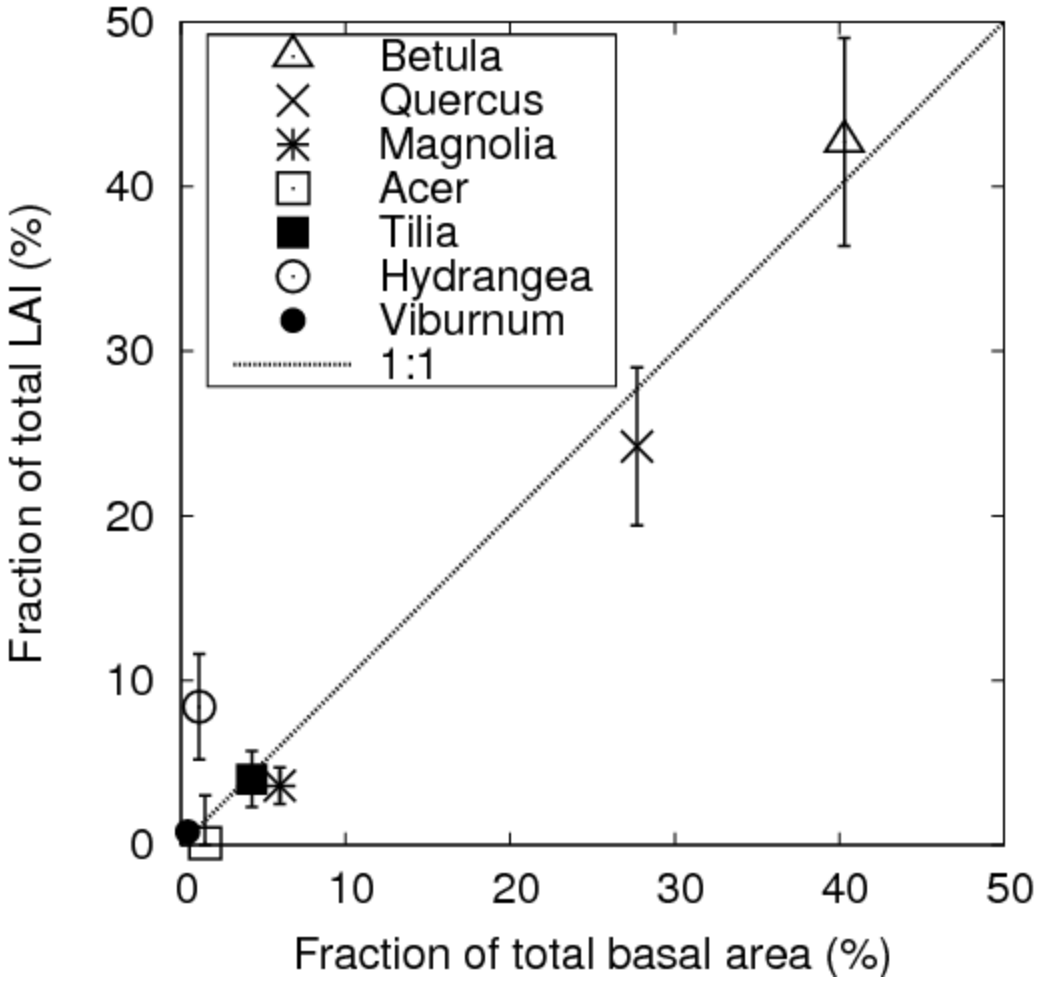

Betula
Quercus
Magnolia
Acer
Tilia
Hydrangea
Viburnum
1:1
Fraction of total LAI (%)
Fraction of total basal area (%)
0
10
20
30
40
50

Fig. 6