

Spatial variability of leaf area index in homogeneous forests relates to local variation in tree characteristics

Keywords: Error, sample size, sampling strategy, tree height, crown length, distance

Abstract

Forest canopy density can be highly variable within one stand. The accuracy of indirect methods to quantify stand leaf area index (LAI) is often unknown, and intensive sampling strategies are required. Our objectives were to study the drivers of the spatial LAI variability, and to improve the sampling strategy based on a sampling protocol as a function of the local canopy pattern. We examined the spatial variability of hemispherical photography (HP) based LAI estimates of European beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.) and Scots pine (*Pinus sylvestris* L.) in Flanders, Belgium. Within the 30 selected forest stands, a regular grid of 16 LAI measurement points and a circular forest inventory plot were established. The LAI estimates of the grid points were used to calculate the LAI of the squared cells (defined as ‘patches’), within the regular grid. Local forest inventory data were used to study the drivers of the deviation of patch LAI (LAI_{dev}) relative to the average plot LAI. Average tree distance from a patch centre was negatively related with the LAI_{dev} . Tree structural characteristics (diameter at breast height (DBH), tree height, crown length and crown cover) were all positively related to the LAI_{dev} . Based on our findings, we suggest that for the analysed forest types, sampling layouts for HP-based LAI estimates should follow a pattern of selecting two (beech and pine) or three (oak) sample points and positioning the camera at a distance of approximately 20% of the dominant height from one (beech) or two (oak and pine) large trees.

Introduction

The leaf area index (LAI; $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$) is a generic ecosystem characteristic determined by and, in turn, influencing, several key processes of the forest ecosystem. LAI is a key determinant of the total photosynthetic carbon uptake, and therefore, of forest productivity (Waring 1983; Maguire et al. 1998). LAI also determines other crucial aspects of forest canopy functioning, such as rainfall interception and evapotranspiration. Furthermore, LAI directly influences radiation intensity reaching the ground (Smith 1981). It is therefore important to accurately quantify LAI (Eckhardt et al. 2003).

Direct methods of assessing LAI are the most accurate (Bréda 2003; Jonckheere et al. 2004). However, they are extremely labour intensive and time consuming which makes them less applicable for large-scale and long-term monitoring. Direct techniques can be considered as calibration methods for indirect LAI assessments (Jonckheere et al. 2004). Indirect methods are non-destructive, and generally allow faster measurements and automated analysis. It makes them more suitable for assessments at larger spatial scales and long-term monitoring. Among these, optical methods such as hemispherical photography (HP) are the most commonly implemented methods in forest research (Chason et al. 1991); they are based on the measurement of light transmission through canopies (Gower et al. 1999). With the development of affordable high resolution digital cameras, research has mainly focused on the development of automated processing of these hemispherical images (Jonckheere et al. 2004; Fuentes et al. 2008). Yet, the sampling strategy (design and intensity) for indirect LAI measurements remains a source of inaccuracy (Strachan and McCaughey 1996).

Within every forest – even inside homogeneous even-aged stands – LAI is spatially highly variable. Furthermore, site parameters and management practices might over time induce canopies to become heterogeneous regarding foliage distribution (Seidling 2007). Spatial sampling is therefore a key issue when performing ground measurements that need to be representative for the entire canopy (Weiss et al. 2004). Several systematic sampling strategies have been proposed depending on (i) the

LAI measurement method considered, (ii) the canopy architecture, and (iii) the size of the studied area. The reader is referred to Weiss et al. (2004) for a detailed review on this subject. Transects, regular or criss-cross grids associated with a particular number of observations have been proposed to capture the spatial variability of a forest stand. A minimum sampling intensity of 12 (Weiss et al. 2004) or 15 observations (Nackaerts et al. 2000) has been suggested. Another systematic approach consists of adapting the sampling strategy to the local variation of the canopy. Herewith, the sample point is chosen based on its distance from the nearest trees, allowing the stand to be characterized with only a few systematic measurements (López-Serrano et al. 2000). No other study has further considered a systematic approach for measuring LAI indirectly. Adopting a sampling strategy in function of the variation in the local canopy pattern could strongly reduce the observed spatial LAI variability within stands, and, consequently reduce the number of measurements required for an accurate LAI assessment.

The current study focused on the relationships between the spatial variability of LAI and tree structural characteristics in small-scale plots (around 1000 m²) during the period of peak LAI for two broad-leaved species (European beech and pedunculate oak) and a coniferous species (Scots pine). The study aims (i) to determine the spatial variability of LAI inside a plot, (ii) to analyze whether the observed spatial variability is related to structural characteristics (i.e. tree size and distance to the sampling point), (iii) to propose and test a new sampling protocol based on the results and insights obtained on the local canopy pattern, and (iv) to compare the newly developed sampling protocols to a traditional LAI sampling scheme (regular grid) based on measurement points randomly chosen within the forest stand. The main rationale of the new protocols was to reduce the sample size while maintaining the same accuracy. This was achieved by reducing the deviation of LAI measurement to the average plot LAI at each sampling point.

Materials and methods

Experimental sites

We studied 10 pedunculate oak (*Quercus robur* L.), 10 European beech (*Fagus sylvatica* L.), and 10 Scots pine (*Pinus sylvestris* L.) stands distributed over 16 forests in Flanders (Belgium), which has a moderate maritime (North-Atlantic) climate. For all species the investigated stands were selected to cover the entire productivity range within Flanders. Table 1 summarizes the main stand characteristics. All stands were homogeneous and composed of even-aged mature trees, i.e. older than 50 years.

A study plot of about 1000 m² was established in each of the 30 forest stands. We assumed homogeneity of site quality parameters within these plots. Every study plot consisted of a circular forest inventory plot (18 m in radius) centred around a dominant and vital sample tree. A 16-point regular grid (10 m spacing) in a square of 30 m by side (Fig. 1) was established around the sample tree for the LAI measurements.

LAI measurements

Hemispherical photographs were taken on each of the 16 points of the regular grid within each plot (according to Nackaerts et al. 2000). Photographs were taken in mid-July 2008 during the period of peak development of LAI (Gond et al. 1999; Bequet et al. 2012). LAI was indirectly quantified by an optical method, i.e. the digital HP (Rich 1990; Jonckheere et al. 2004). Images of the canopy were acquired from the ground using a fish-eye lens with a 180° field of view (8 mm, f/4, Sigma Corporation, Tokyo, Japan) mounted on a Canon 5D digital professional camera (Canon Inc., Tokyo, Japan). Hemispherical photographs were taken at the highest camera resolution (13.3 mega pixels) and with ISO set at 200. The focus ring was set to infinity as depth of field was practically infinite. The camera was placed on a tripod with the top of the lens 1.3 m above the ground and the camera oriented in such a way that the magnetic north was always located at the top of the photograph. The lens position was

manually fitted in the vertical and horizontal axes with the help of a double water-level. Calibration of the camera's white balance was done before the measurement of every plot by using a standard grey card (Eastman Kodak Company, New-York, USA). Photographs were taken during conditions of diffuse sky light (blue sky or evenly overcast) to achieve an even sky illumination (Rich 1990). Hemispherical photographs were analyzed using the Hemisfer program (version 1.4) (Schleppi et al. 2007).

We selected the clustering-based threshold of Ridler and Calvard (1978) to distinguish visible sky and foliage pixels (Jonckheere et al. 2005). The algorithm of Norman and Campbell (1989) was chosen to compute the LAI values as all rings received equal weights in the calculations. Consequently, LAI values per measurement point were not homogenized over the different zenithal rings, but each ring was considered independent to calculate its LAI value. The segregation among zenithal rings increases the spatial variability of LAI per plot (higher standard deviation). Optical methods are incapable of detecting the surface area contributed solely by green leafy material. Therefore, Chen and Black (1992) introduced the term "effective LAI" to refer to optically obtained LAI estimates. The effective LAI underestimates the true LAI when foliage in the canopy is clumped (Gower et al. 1999). To amend this problem, we applied the correction factor of the crown and branch clumping as defined by Chen and Cihlar (1995).

Transformation of circular LAI estimates into squared LAI patches

The study of the spatial variability of LAI was facilitated (i.e. the number of within plot replications increased) by transforming the 16 circular hemispherical photographs into a dataset of 25 squared LAI estimates. To do so, the zenith angle of each photograph was first reduced to a maximum zenith angle of 40° to 68°. This was done to avoid inclusion of mixed pixels (zenith angles above 60° or closer to the horizon) that reduce the magnitude of foliage-sky segregation (Rich 1990; Jonckheere et al. 2004) as well as to avoid overlapping of the field of view – and thus LAI information – of two

neighbouring measurement points. Then, each hemispherical photograph was divided in quadrants oriented NE, SE, SW and NW (Fig. 1A). Overlapping quadrants from adjacent measurement points were subsequently averaged to fit a squared patch. Each LAI patch consisted of one cell (10 x 10 m) of the new sampling grid (Fig. 1B). A novel LAI value (named “patch LAI”) was associated to the patch centre (or fictive sample point) located in the centre of the square. In further analysis this new patch LAI substituted the circular LAI estimate. As a result, the 16 circular hemispherical photographs in each plot were transposed into 25 squared LAI patches (Fig. 1B). We could only use the inner five patches (out of 25) for establishing relationships with the tree structural data because the other 20 patches were only partially covered by the inventory plot (Fig. 1B).

The relative patch LAI (LAI_{dev}) was defined and calculated as the deviation of the patch LAI to the average plot LAI (average of the 16 hemispherical measurements). A positive, respectively negative LAI_{dev} indicated an overestimation, respectively underestimation of the plot LAI.

Tree structural characteristics

Various tree structural characteristics described the actual state of the tree layer in the studied plots. Structural characteristics were measured during the winter 2008-2009 in a circular inventory plot (Fig. 1B), and included diameter at breast height (DBH), tree height (H), crown length (CL) and crown cover (CC). H, CL and CC were *in situ* measured on direct competitors of the sample tree within the forest inventory plot. Values of H, CL and CC for other trees in the forest inventory plot were derived from plot-specific allometric relationships developed for the measured trees (i.e. the direct competitors and the sample tree). Within the inventory plot, only trees with a DBH exceeding 30 cm were considered. Preliminary results showed that the overall analysis was not significantly affected by considering smaller trees (6 cm < DBH < 30cm).

Driving variables of LAI_{dev}

155

156 We tested different driving variables that could be related to LAI_{dev} , based on the data
157 available for the inventory plot. Among the driving variables, the total basal area per patch, the
158 average tree structural characteristics (i.e. DBH, H, CL and CC) and the average “tree-to-patch
159 centre” distance (D) were restricted to the one to four nearest trees to the patch centre. Relationships
160 between this set of driving variables and patch LAI were determined for the five central LAI patches
161 of each study plot by calculating linear models based on 50 observations per species (five LAI
162 patches x 10 plots per species). For each application, mixed-effect models including a random-effect
163 for possible within-plot autocorrelations were calculated in SPSS (SPSS 16.0, Chicago, USA). Only
164 significant ($p < 0.05$) linear regressions resulting in LAI_{dev} between 0.9 and 1.1 (i.e. $\pm 10\%$ deviation
165 of the average plot LAI) were selected. The selected ranges of values of the driving variables were
166 expressed as a relative value to facilitate its transposition to other forest types. H was expressed
167 relative to dominant height of the plot, i.e. average height of the four highest trees. DBH and CC
168 were expressed relative to maximum DBH and CC of the plot, respectively. CL was expressed as a
169 relative proportion to H. The relative distance was expressed as a proportion of the dominant height.

170

171 *Protocol testing on full zenith angle circular hemispherical photographs*

172

173 Based on the selection of significant linear models (Table 2) values of driving variables
174 giving LAI with $\pm 10\%$ around the average, were calculated for circular hemispherical photographs at
175 full zenith angle (up to 60° ; following Jonckheere et al. 2004). We tested two different sampling
176 strategies on sampling accuracy, sampling error and sample size. The first sampling strategy
177 included a dataset that corresponded to the ‘original’ LAI estimates calculated from the 16 circular
178 hemispherical photographs (16-point regular grid) and was named ‘*grid sampling*’. The second
179 sampling strategy included a dataset that corresponded to a subset of the grid sampling, i.e. only the
180 measurements taken at locations that met the allowed values of driving variables as reported in Table

2. This second datasets was named '*local sampling*'. Besides, the local sampling dataset consisted at least of a minimum of two LAI estimates (two observations). In total, we had a one '*grid sampling*' and three (oak) or four (beech and pine) '*local sampling*' strategies per plot and per species (Table 3). Because the LAI estimates of the '*local sampling*' were selected based on a narrow range of driving variables, this sampling strategy was considered as a systematic approach for LAI measurements as a function of the local canopy pattern.

For both strategies, i.e. the '*grid sampling*' (16 observations) and the '*local sampling*' (minimum two observations), we calculated the relative root mean squared error (*rRMSE*) on the resampled LAI values (Kint et al. 2004). When the *rRMSE* was below the level of 10% precision for a set of n observations, we recalculated *rRMSE* for $n-1$ observations after random resampling. Finally, we obtained plot-specific *rRMSE* and sample size for both sampling strategies (Table 3). Considering a target precision of estimated LAI, we compared the different sampling strategies (grid versus local) and the differences among '*local sampling*' strategies for full zenith angle HP-based LAI estimates.

Results and Discussion

Spatial LAI variability

Substantial spatial variability of LAI was observed in every plot based on hemispherical photographs. For the plot illustrated in Fig. 1B (i.e. the plot with the highest spatial LAI variability), LAI_{dev} ranged from -34% (underestimation of the average plot LAI) to +186% (overestimation of the average plot LAI). Table 1 contains the average plot LAI, the standard deviation (SD) and the coefficient of variation (CV_{LAI}) for each study plot. The average LAI ranged around 2.3–3.5 for beech, around 2.2–3.0 for oak and around 1.6–2.3 for pine. The CV_{LAI} ranged from 7–24% for

207 beech, from 10–21% for oak and from 5–17% for pine. In the literature, spatial variations in stand
208 LAI measured by HP from the ground are reported to be rather limited with a CV_{LAI} of about 10% in
209 a mixed oak forest (Wang et al. 1992) and of about 15% in an aspen-birch forest (Strachan and
210 McCaughey 1996). Consequently, our results coincide well with previous studies of spatial LAI
211 variability.

212 213 *Relationships between LAI_{dev} and driving variables*

214
215 The relationships between the driving variables and the LAI_{dev} were strongly significant ($p <$
216 0.005); the equation coefficients were mostly moderate ($0.43 < r < 0.78$) and the significance was
217 strong (Table 2). The absence of a significant relationship between LAI_{dev} and basal area per patch
218 resulted in the exclusion of this variable for further protocol testing. Overall, LAI_{dev} was positively
219 related to the tree structural characteristics. This implies that HP taken in locations with on average
220 high DBH, H, CL or CC, overestimate the average plot LAI. For all species D was an important
221 driver (and negatively related to LAI_{dev}). Therefore, when trees were close to the measurement point,
222 LAI tended to be higher than the average plot LAI. Tree height was an important driver because it
223 ranked among the two best drivers for oak and pine (highest equation coefficient; Table 2). The
224 effect of woody elements (branches and stem) on indirect LAI measurements has seldom been
225 quantified. Deblonde et al. (1994) concluded that indirect LAI measurements (made with a Li-Cor
226 LAI-2000 instrument) underestimated the direct LAI values in a red pine forest if direct
227 measurements of woody-to-foliage hemi-surface area ratios were under 10%. However, forest stands
228 reaching a ratio above 20% provided an overestimation of indirect LAI values compared to the direct
229 values. Our study was not designed to determine the portion of woody elements on indirect LAI
230 measurements. However, to a certain extent, our results are in agreement with those of Deblonde et
231 al. (1994). Measurements made at close proximity of large trees imply that a larger proportion of the
232 stem is considered in the LAI assessment (Kucharik et al. 1998). Very high correlations between tree

structural characteristics and indirect values of stand LAI (López-Serrano et al. 2000) suggested that very large trees (high DBH, H, CL and CC) support a large amount of leaves, and thus have a high LAI (overestimation of the average stand LAI).

Results of Table 2 suggested that the nearest one or two trees to the point of measurements had a larger impact on LAI than the nearest three or four trees. Among our results, the drivers of LAI_{dev} varied among species. In particular, beech and oak had different driving variables. Those that were shared (D, DBH) had a different importance among the driving variables, i.e. their ranking based on the equation coefficients differed. For instance, D was common between beech and oak (Table 2), but D was dominant compared to the other drivers in beech while D had the lowest fit for oak. On the other hand, the main drivers of LAI_{dev} were common for beech and Scots pine despite the high differences in canopy structure and management practice between these two species. In addition, the ranges of tree structural characteristics for oak and pine suggested that the largest trees of a plot (i.e. close to maximum DBH or to dominant height) provided accurate plot LAI estimates. Ranges of tree structural characteristics varied from 55 to 96% for both species (Table 2). For beech, co-dominant large trees suited best for LAI measurements. The relative ranges for tree structural characteristics varied from 12 to 49%. For all three species, the distance “tree-to-patch centre” was similar and ranged between 17 and 28% of the dominant height (Table 2).

Protocol testing on full zenith angle circular hemispherical photographs

The high CV_{LAI} (Table 1) was representative for a high spatial variability of LAI. Consequently, it is necessary to take a large sample size when LAI is measured with indirect methods. Nackaerts et al. (2000) and Weiss et al. (2004) reported a minimum of 12 to 15 measurement points to estimate the average LAI of a stand (or a plot). A large sample size is a prerequisite when establishing sampling schemes (transects, regular grids) randomly in the forest

without considering the canopy heterogeneity. But sample size could be drastically reduced by using a sampling strategy based on the local canopy pattern (López-Serrano et al. 2000).

Our study revealed that spatial variability in LAI was well related to structural characteristics of large trees (DBH > 30 cm; Table 2). Mixed-effect linear models gave the driving variables' range that allowed accurate LAI measurements (i.e. $\pm 10\%$ deviation around plot LAI; Table 2). Consequently, '*local sampling*' strategies were as numerous as driving variables in Table 2 (i.e. three strategies for oak and four strategies for beech and pine). The LAI values and the amount of sampling points of all sampling strategies (grid and local) were separately tested for sampling error and minimum sample size (Table 3). By choosing for a '*local sampling*' strategy, one can reach: (i) a higher sampling accuracy (sample point selected within the optimal range of a driving variable of LAI_{dev}), (ii) a lower sampling error, and (iii) a lower sample size for measuring the average plot LAI than when choosing for a random '*grid sampling*' strategy.

- *Sampling accuracy*: Relative ranges of tree structural characteristics and distance are reported for beech, oak and pine (Table 2). When applied to the selection of the sample point those ranges provide accurate LAI values (i.e. close to the plot LAI) using HP.
- *Sampling error*: Every '*local sampling*' strategy showed a lower sampling error (i.e. a lower *rRMSE*) than the corresponding '*grid sampling*' strategy (for similar sample sizes; Table 3). The lower error associated to the plot LAI by adopting a '*local sampling*' strategy relies in the fact that the observations were made for similar canopy characteristics.
- *Sample size*: Besides accurately measuring plot LAI, we aimed to determine the minimum sample size (i.e. minimum amount of observations) of both sampling strategies necessary to stay under the targeted sampling error of 10% (i.e. *rRMSE* < 10%). Table 3 represents the minimum sample size and its associated sampling error for all tested strategies. In the '*grid sampling*' beech plots required between 7 and 11 observations (except B7; Table 3) to reach the targeted error. Oak plots reached a sample size of 6 to 9 observations (except O2; Table 3). Scots pine plots performed as well as oak plots and needed a minimum of 5 to 10

observations (except P4 and P6; Table 3) to reach an $rRMSE$ of 10% using the ‘*grid sampling*’ strategy. As expected, the plots with a low sample size (for instance B7, O2, P4 and P6) also had a low CV_{LAI} (Table 1) and, thereby, had a more homogeneous canopy. The ‘*local sampling*’ strategies reached the targeted error with a number of observations that was much lower than the one of the corresponding ‘*grid sampling*’. Exceptions to this were several plots of Scots pine as well as two oak plots, all marked with an “*” in Table 3. For those exceptions the number of observations was equivalent in both sampling strategies. The reason might be that the driving variable ranges for those species were larger (Table 2) than the *in-situ* (measured) variable ranges within those plots (data not shown). Apart from these exceptions, most ‘*local sampling*’ strategies proposed a sample size of maximum 5 observations, and a large majority of those sampling strategies could be performed on only 1 to 3 observations (Table 3). No difference was found concerning the sample size of the different ‘*local sampling*’ strategies.

Overall, the best sampling protocols with ‘*local sampling*’ strategy consisted of selecting two (beech and pine) or three (oak) sample points, and positioning the camera at a distance of approximately 20% of the dominant height (Table 2) from one (beech) or two (oak and pine) trees. This protocol based on the “tree-to-sample-point” distance led to an estimation of the average stand LAI with an error below 10% in at least 80% of the cases (Table 3). A sampling protocol focused on DBH consisted in selecting two (beech), three (pine) or four (oak) sample points at 40% of the maximum DBH of the two nearest large trees for beech or at 75-80% of the maximum DBH of the nearest large tree for oak and pine (Table 2). This protocol led to an accurate estimation of plot LAI in at least 80% of the studied plots for beech and in 50% of the plots for oak and pine (Table 3). Other tree structural variables (H, CL, CC) were successful for establishing ‘*local sampling*’ strategies, but they did not apply for all tree species. Besides, they might be more difficult to

implement in forest stands as they are more difficult to measure than DBH and distance “tree-to-sample point”.

Conclusion

Forest canopies are generally heterogeneous as a consequence of natural (windfall, diseases, site characteristics) and man-made (planting density, selective thinning) factors. Indirectly measuring LAI at stand level requires a high sample size because of the important spatial variability of LAI. This study highlighted the impact of tree structural characteristics (tree height, crown depth, diameter at breast height) and distance “tree-to-sample point” on the optimal sampling scheme and intensity in temperate homogeneous forests. Instead of a general and random approach for indirect LAI measurements of the stand level, this research on three forest species in Belgium showed the possibility of applying a local sampling strategy which provided more accurate and precise measurements, and strongly reduced the sample size. Measuring stand LAI with an error below 10% was, in most cases, possible by using two or three sample points. The distance “tree-to-sample point” was the best variable to take into account for local sampling.

The new sampling approach is likely to be a good investment when implementing a campaign involving many plots within a limited number of well-defined compositional and structural types (e.g. stand LAI monitoring). On the other hand, this approach might prove less effective for smaller studies or those encompassing a great deal of heterogeneity in composition or structure. In any case, the innovative methodological approach and the relative values of driving variable ranges reported might serve as a useful starting basis for future studies around sampling strategies.

References

- Bequet, R., V. Kint, M. Campioli, D. Vansteenkiste, B. Muys, and R. Ceulemans. 2012. Influence of stand, site and meteorological variables on the maximum leaf area index of beech, oak and Scots pine. *Eur. J. For. Res.* 131:283-295.
- Bréda, N. 2003. Ground-based measurements of leaf area index: a review of methods, instruments and controversies. *J. Exp. Bot.* 54:2403–2417.
- Bivand, R. 2009. spdep: Spatial dependence: weighting schemes, statistics and models. R package version 0.4-34.
- Chason, J.W., D.D. Baldocchi, and M.A. Huston. 1991. A comparison of direct and indirect methods for estimating forest canopy leaf-area. *Agr. For. Meteorol.* 57:107-128.
- Chen, J.M., and T.A. Black. 1992. Defining leaf-area index for non-flat leaves. *Plant Cell Environ.* 15:421-429.
- Chen, J.M., and J. Cihlar. 1995. Quantifying the effect of canopy architecture on optical measurements of leaf-area index using two gap size analysis-methods. *IEEE Trans. Geosci. Rem. Sens.* 33:777-787.
- Deblonde, G., M. Penner, and A. Royer. 1994. Measuring leaf area index with the Li-Cor LAI-2000 in pine stands. *Ecol.* 75:1507-1511.
- Eckhardt, K., L. Breuer, and H.G. Frede. 2003. Parameter uncertainty and the significance of simulated land use change effects. *J. Hydrol.* 273:164-176.

359

360 Fuentes, S., A.R. Palmer, D. Taylor, M. Zeppel, R. Whitley, and D. Eamus. 2008. An
361 automated procedure for estimating the leaf area index (LAI) of woodland ecosystems using digital
362 imagery, MATLAB programming and its application to an examination of the relationship between
363 remotely sensed and field measurements of LAI. *Funct. Plant Biol.* 35:1070-1079.

364

365 Gond, V., D.G.G. de Pury, F. Veroustraete, and R. Ceulemans. 1999. Seasonal variations in
366 leaf area index, leaf chlorophyll, and water content; scaling-up to estimate fAPAR and carbon
367 balance in a multilayer, multispecies temperate forest. *Tree Physiol.* 19:673-679.

368

369 Gower, S.T., C.J. Kucharik, and J.M. Norman. 1999. Direct and indirect estimation of leaf
370 area index, f(APAR), and net primary production of terrestrial ecosystems. *Rem. Sens. Environ.*
371 70:29-51.

372

373 Jonckheere, I., S. Fleck, K. Nackaerts, B. Muys, P. Coppin, M. Weiss, and F. Baret. 2004.
374 Review of methods for in situ leaf area index determination. Part I. Theories, sensors and
375 hemispherical photography. *Agr. For. Meteorol.* 121:19-35.

376

377 Jonckheere, I., K. Nackaerts, B. Muys, and P. Coppin. 2005. Assessment of automatic gap
378 fraction estimation of forests from digital hemispherical photography. *Agr. For. Meteorol.* 132:96-
379 114.

380

381 Kint, V., R. De Wulf, and N. Lust. 2004. Evaluation of sampling methods for the estimation
382 of structural indices in forest stands. *Ecol. Model.* 180:461-476.

383

Kucharik, C.J., J.M. Norman, and S.T. Gower. 1998. Measurements of branch area and adjusting leaf area index indirect measurements. *Agr. For. Meteorol.* 91:69-88.

Lopez-Serrano, F.R., T. Landete-Castillejos, J. Martinez-Millan, and A. del Cerro-Barja. 2000. LAI estimation of natural pine forest using a non-standard sampling technique. *Agr. For. Meteorol.* 101:95-111.

Maguire, D.A., J.C. Brissette, and L.H. Gu. 1998. Crown structure and growth efficiency of red spruce in uneven-aged, mixed-species stands in Maine. *Can. J. For. Res.* 28:1233-1240.

Nackaerts, K., P. Coppin, B. Muys, and M. Hermy. 2000. Sampling methodology for LAI measurements with LAI-2000 in small forest stands. *Agr. For. Meteorol.* 101:247-250.

Norman, J.M., and G.S. Campbell. 1989. Canopy structure. P. 301-325 in: *Plant Physiological Ecology: Field Methods and Instrumentation*, Pearcy, R.W., J.R. Ehleringer, H.A. Mooney, and P.W. Rundel (eds.), Chapman and Hall, New York.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available online at <http://www.R-project.org>; last accessed Oct. 12, 2010.

Rich, P.M. 1990. Characterizing plant canopies with hemispherical photographs. *Remote Sens. Rev.* 5:13-29.

Ridler TW, Calvard S (1978) Picture thresholding using an iterative selection method. *IEEE Trans. Systems Man Cybernetics* 8:630-632

410

411 Schleppi, P., M. Conedera, I. Sedivy, and A. Thimonier. 2007. Correcting non-linearity and
412 slope effects in the estimation of the leaf area index of forests from hemispherical photographs. *Agr.*
413 *For. Meteorol.* 144:236-242.

414

415 Seidling, W. 2007. Signals of summer drought in crown condition data from the German
416 Level I network. *Eur. J. For. Res.* 126:529-544.

417

418 Smith, H. 1981. Light quality as an ecological factor. In: Grace, J., E.D. Ford, and P.G.
419 Jarvis (eds). *Plants under their Atmospheric Environment*. Blackwell, Oxford, pp 93-110.

420

421 Strachan, I.B., and J.H. McCaughey. 1996. Spatial and vertical leaf area index of a
422 deciduous forest resolved using the LAI-2000 plant canopy analyzer. *For. Sci.* 42:176-181.

423

424 Wang, Y.S., D.R. Miller, J.M. Welles, and G.M. Heisler. 1992. Spatial variability of canopy
425 foliage in an oak forest estimated with fisheye sensors. *For. Sci.* 38:854-865.

426

427 Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf-area.
428 *Adv. Ecol. Res.* 13:327-354.

429

430 Weiss, M., F. Baret, G.J. Smith, I. Jonckheere, and P. Coppin. 2004. Review of methods for
431 in situ leaf area index (LAI) determination. Part II. Estimation of LAI, errors and sampling. *Agr.*
432 *For. Meteorol.* 121:37-53.

433 Figure legends

434

435 **Figure 1** (A) Plot configuration (grid of 16 points, black dots) of hemispherical photographs (HP).
436 Transformation of HP into squared LAI patches (shown for the LAI patch centred around the open
437 circle in panel A and indicated with 1 in panel B) consisted of: (i) a reduction of zenith angles
438 (shown for the measurement point “x”), (ii) a division in quadrants, and (iii) averaging of quadrants
439 facing each other (small arrows). (B) Spatial LAI variability (gray scale) within a beech plot with
440 average LAI of $3.36 \text{ m}^2 \text{ m}^{-2}$. The five dashed squares numbered 1 to 5 are the LAI patches included
441 in the forest inventory plot (circle) established around the central sample tree (full square).

Tables

Table 1 Average plot leaf area index (LAI), its standard deviation (SD) and coefficient of variation (CV_{LAI} ; $n = 25$) in combination with the stand characteristics (site index (SI), age, average diameter at breast height (DBH), tree density and total basal area) of the 30 selected mature study plots of beech (B), oak (O) and Scots pine (P).

Study plot	SI m	Age y	DBH cm	Tree density trees ha ⁻¹	Basal area m ² ha ⁻¹	LAI m ² m ⁻²	SD m ² m ⁻²	CV_{LAI} %
B1	30.1	82	36.7	403	28.1	3.29	0.44	13.5
B2	35.1	84	41.8	206	29.2	2.89	0.41	14.3
B3	32.6	85	48.4	187	30.8	2.79	0.53	19.1
B4	39.1	74	45.2	236	29.4	2.97	0.43	14.5
B5	40.6	71	48.8	314	29.9	3.36	0.80	23.9
B6	38.2	68	43.6	275	22.5	3.53	0.51	14.5
B7	35.5	84	74.0	88	26.9	2.27	0.16	7.0
B8	28.0	138	90.3	216	32.5	2.92	0.41	14.1
B9	27.6	147	64.9	118	27.2	2.74	0.37	13.4
B10	40.2	71	54.7	138	22.9	3.18	0.64	20.0
O1	32.1	73	38.1	216	27.3	2.31	0.31	13.2
O2	25.4	74	31.7	354	20.8	2.66	0.25	9.6
O3	23.2	54	30.2	285	17.7	2.34	0.34	14.4
O4	35.0	71	47.3	246	26.7	2.60	0.54	20.8
O5	28.2	70	62.1	69	16.0	2.29	0.47	20.5
O6	27.5	70	45.7	98	18.4	2.19	0.28	12.8
O7	28.3	117	54.9	305	30.8	2.82	0.41	14.6
O8	27.6	121	54.3	442	28.8	2.95	0.45	15.2
O9	34.7	61	37.7	177	17.9	2.44	0.34	13.8
O10	34.7	61	40.6	216	20.2	2.50	0.41	16.3
P1	30.4	61	34.2	196	16.0	1.69	0.17	10.3
P2	30.3	61	34.3	305	26.1	1.62	0.25	15.4
P3	23.1	81	36.2	216	22.6	1.88	0.15	8.2
P4	27.3	73	33.4	393	30.0	1.98	0.11	5.4
P5	15.8	80	21.5	717	27.9	2.30	0.26	11.4
P6	22.2	63	24.3	698	30.4	2.08	0.15	7.2
P7	19.4	65	30.2	403	28.3	2.23	0.28	12.6
P8	26.1	67	29.3	393	24.2	1.74	0.20	11.6
P9	21.0	72	30.4	452	28.7	2.07	0.32	15.7
P10	22.9	71	29.5	648	38.1	1.72	0.30	17.2

Table 2 Correlation coefficients (r) between the deviation of leaf area index (LAI) estimates from the average plot LAI, the average “tree-to-patch centre” distance and structural characteristics of the one or two nearest surrounding trees (with DBH > 30 cm) in the five inner LAI units of the study plot (see Fig . 1B). The variable ranges (minimum and maximum values) are relative values derived from the linear regression equations.

Species	Variable	Unit	Model's statistics			Variable range for a $\pm 10\%$ deviation	
			r	p	n	Min (%)	Max (%)
Beech	D 1	M	-0.78	< 0.001	47	17	22
	DBH 2	Cm	0.55	< 0.001	46	30	49
	CL 1	M	0.54	< 0.001	48	26	40
	CC 2	proj. m ² leaves	0.52	< 0.001	46	12	35
Oak	DBH 1	Cm	0.57	< 0.001	48	59	92
	H 1	M	0.56	< 0.001	48	55	90
	D 2	M	-0.56	< 0.001	46	20	28
Scots pine	DBH 1	Cm	0.53	< 0.001	49	57	94
	H 1	M	0.49	< 0.001	47	64	96
	D 2	M	-0.45	0.003	49	17	23
	CC 1	proj. m ² leaves	0.43	0.005	47	59	83

p = significance level, n = number of observations.

Numbers 1 and 2 (in column “variable”) refer to the nearest one or two large trees to the patch centre.

H = tree height; CL = crown length; DBH = diameter at breast height; CC = crown cover; D = average distance “tree-to-patch centre”.

Tree height is relative to plot dominant height; crown length is relative to tree height; DBH is relative to maximum plot DBH; crown cover is relative to maximum plot crown cover; distance is relative to dominant height.

Table 3 Minimum sample sizes (n) and relative root mean squared errors (rRMSE, in %) for two sampling techniques in ten beech (B), Scots pine (P) and oak (O) plots considering trees with diameter at breast height (DBH) > 30 cm. In the local sampling several driving variables (Var. 1 to Var. 4) were tested towards sample size and precision.

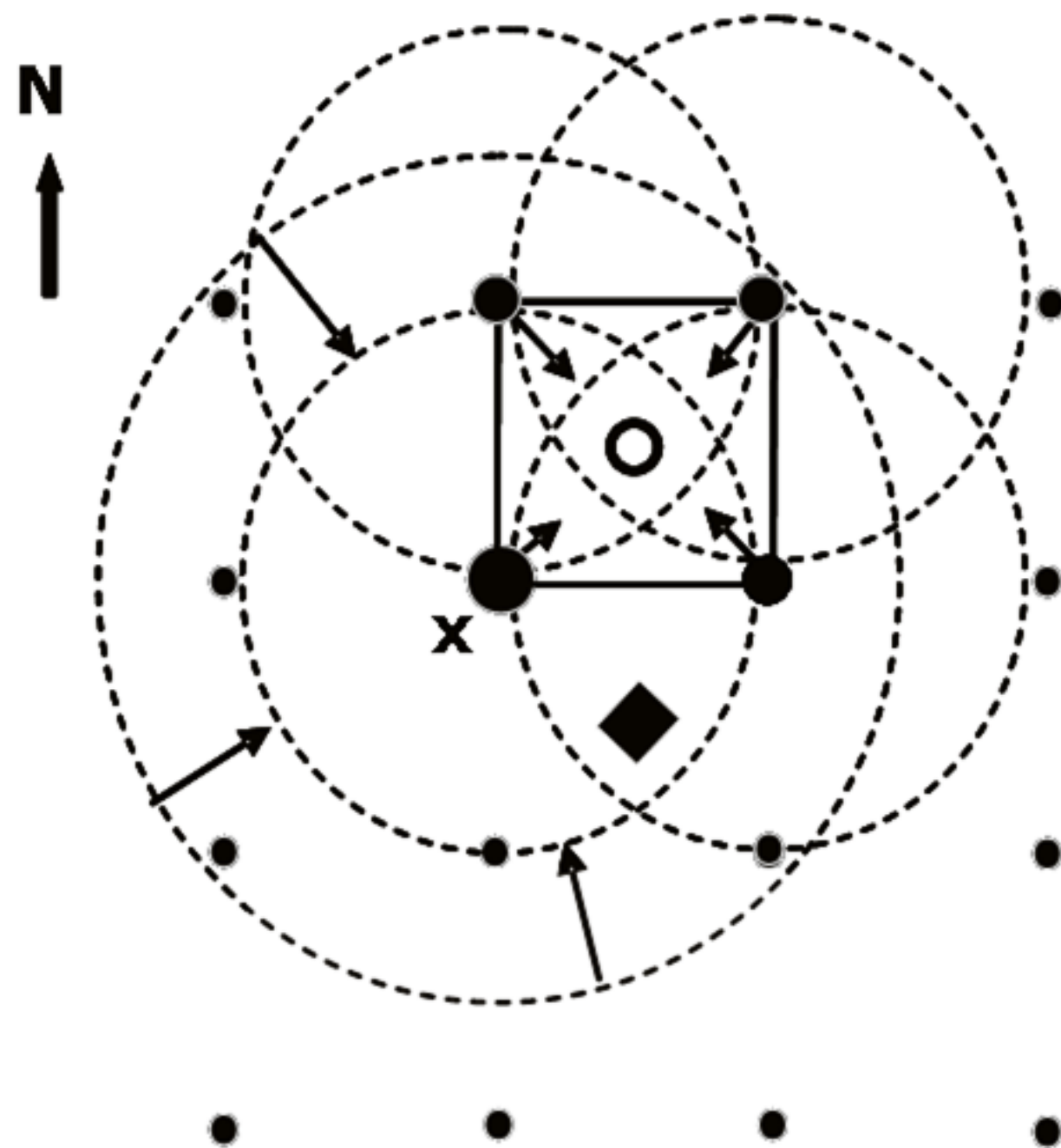
	Grid sampling		Local sampling		Var. 2		Var. 3		Var. 4	
	n	rRMSE	N	rRMSE	n	rRMSE	n	rRMSE	n	rRMSE
Beech			D1		DBH2		CC2		CL2	
B1	9	< 9.6	2	< 6.3	3	< 7.9	1	< 7.0	2	< 9.2
B2	8	< 9.9	1	< 9.0	1	< 7.7	--	--	--	--
B3	10	< 9.8	2	< 8.9	--	--	--	--	--	--
B4	9	< 9.6	1	< 5.2	--	--	2	< 6.6	--	--
B5	11	< 9.2	5	< 9.9	2	< 7.5	2	13	5	15
B6	9	< 9.5	3	< 9.4	2	< 9.5	6	< 9.2	4	< 9.4
B7	1	< 8.8	1	< 9.3	1	< 7.7	--	--	--	--
B8	8	< 9.8	2	< 8.0	--	--	2	< 5.8	1	< 7.7
B9	7	< 9.7	2	< 7.8	1	< 9.3	--	--	2	< 5.6
B10	10	< 9.9	1	< 7.4	--	--	--	--	--	--
Pine			D2		DBH1		H1		CC1	
P1	6	< 8.9	1	< 2.6	3	< 8.7	2	< 9.4	3	10
P2	9	< 9.2	2	< 8.7	9 *	< 9.2	3	< 9.1	3	< 9.2
P3	5	< 9.1	1	< 6.6	1	< 9.7	5 *	< 9.1	1	< 8.5
P4	1	< 8.5	1	< 2.8	1	< 8.3	1	< 5.6	1	< 3.0
P5	6	< 9.7	--	--	1	< 9.5	2	< 9.8	3	< 9.2
P6	1	< 9.6	--	--	1	< 6.5	1 *	< 9.6	1	< 6.5
P7	7	< 9.3	1	< 6.4	7 *	< 9.3	7 *	< 9.3	1	< 8.3
P8	7	< 9.1	1	< 3.8	7 *	< 9.1	7 *	< 9.1	2	< 7.5
P9	9	< 9.9	3	< 9.2	9 *	< 9.9	9 *	< 9.9	5	< 9.1
P10	10	< 9.2	1	< 3.5	10 *	< 9.2	10 *	< 9.2	2	< 9.6
Oak			D2		DBH1		H1		none	
O1	6	< 9.3	2	< 7.7	4	< 9.6	3	< 7.8	--	--
O2	2	< 9.7	2	< 9.2	3	< 9.6	2	< 9.6	--	--
O3	7	< 9.9	3	12	5	< 9.2	6	< 8.7	--	--
O4	9	< 9.8	7	< 9.8	7	< 8.8	5	< 9.7	--	--
O5	9	< 9.2	3	< 8.2	--	--	3	< 9.8	--	--
O6	8	< 9.9	2	< 9.6	2	< 8.4	--	--	--	--
O7	8	< 9.2	1	< 8.3	1	< 7.4	1	< 6.4	--	--
O8	9	< 9.5	2	< 8.5	4	< 8.3	2	< 7.2	--	--
O9	7	< 9.9	2	< 7.6	7 *	< 9.9	2	< 9.7	--	--
O10	8	< 9.2	4	< 8.9	8 *	< 9.2	3	< 9.3	--	--

Numbers 1 and 2 (in the variable names) refer to the nearest one or two large trees to the measurement point.

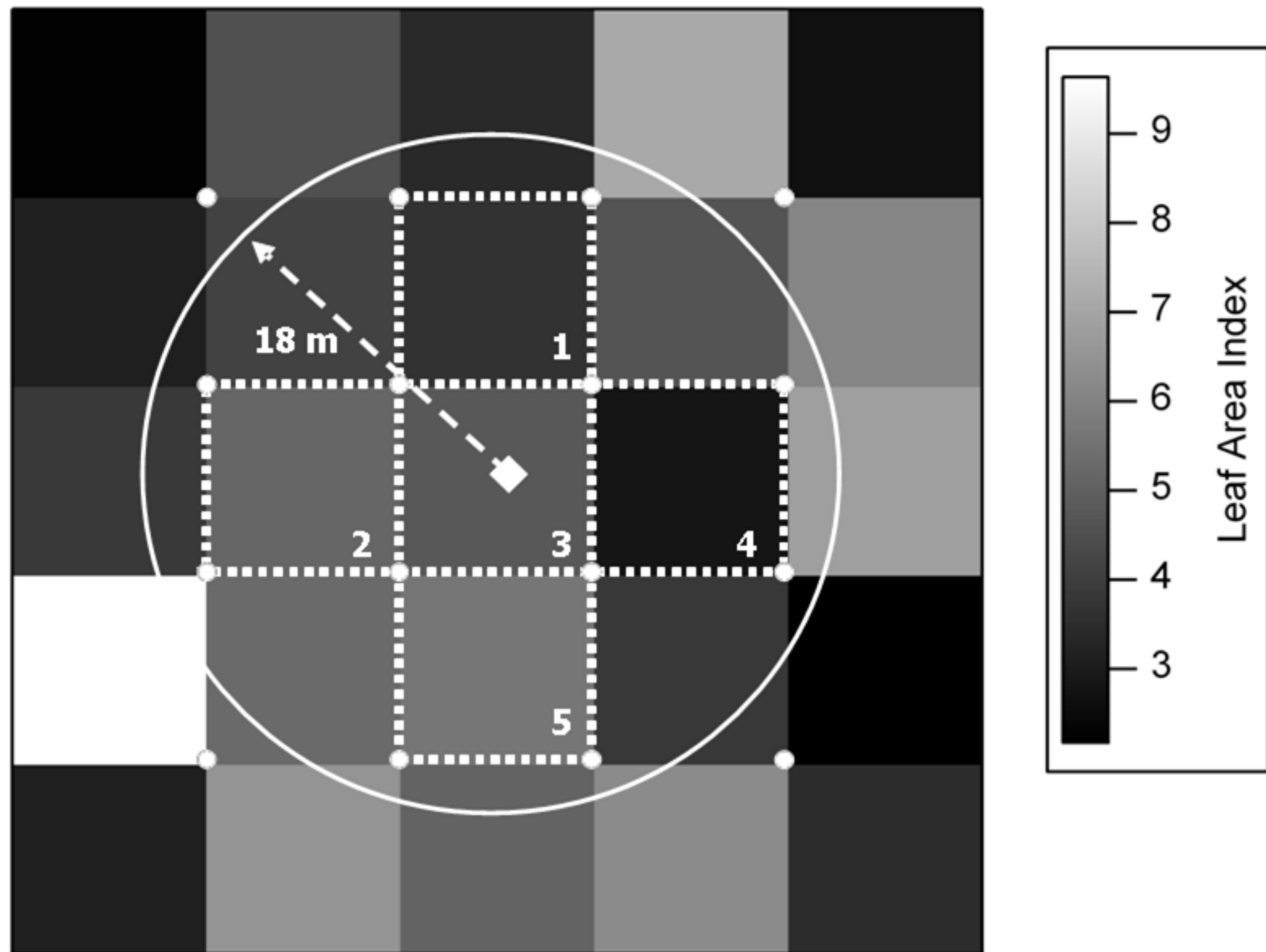
* local sampling observations are equivalent to the grid sampling observations.

D = distance to the nearest tree; DBH = diameter at breast height; CC = crown cover; CL = crown length; H = tree height; '--' = not applicable.

A



B



Spatial variability of leaf area index in homogeneous forests relates to local variation in tree characteristics

General comment:

We are very glad for the positive feed-back from the Associate Editor concerning our previous modifications to the manuscript. We applied all three new proposals of modifications suggested by the Associate Editor. We hope our manuscript conforms now to the editorial standard of Forest Science.

Reply to the Associate Editor :

1. The final part of the Conclusions has been rewritten, clearly stating the potential of the new sampling approach for large sampling campaigns in homogeneous stands and the limitations of the approach for small-scale studies in heterogeneous stands (see lines 326-331);
2. The Figure caption 1 has been shortened by circa 30% (see lines 435-441);
3. The "Equation coefficients" in Table caption 2 has been replaced by "Correlation coefficients" (see line 451).
4. Additional (minor) changes have been made concerning the citation and reference of the article of Bequet et al. 2011. A full reference (year, journal number, pages) is now available and it has been added to the text on lines 95 and 334-336.