Dr. Akihiko Ito
Associate Editor
Biogeosciences
Email: itoh@nies.go.jp

Dear Editor,

Please find attached our previous manuscript entitled "Spatial and seasonal variations of leaf area index (LAI) in subtropical secondary forests related to floristic composition and stand characters" (No. bg-2016-5) for final publishing as a research paper in the ***Biogeosciences***.

At first, we thank you and the three referees for the constructive and helpful comments on the previous manuscript. We have revised the manuscript accordingly and all changes are highlighted in blue font. You will find our point by point reply to the comments and a marked-up manuscript version in the following pages.

Thank you very much for your consideration. We look forward to hearing from you.
With best regards,

Yours sincerely

Wenhua Xiang

Faculty of Life Science and Technology
Central South University of Forestry and Technology
No. 498 Southern Shaoshan Road
Changsha 410004, Changsha, Hunan
Email: xiangwh2005@163.com

Responses to comments

We thank two anonymous referees, Dr. X. Zhang and Associate Editor Dr. Akihiko Ito for their valuable comments on the previous manuscript. We have carefully taken the comments raised by all referees into consideration in revising our paper. Our detailed responses to the comments are presented as follows.

Editor' comments:

Thank you for sending your revised manuscript. I confirmed that you improved clarity of description and made sufficient revision. So, the manuscript is acceptable for publication.

Re: Thanks for the positive comments!

Referee #1' s comments:

The authors investigated seasonal variation, spatial heterogeneity of LAI and its controlling factors by using spatial statistics and generalized additive models (GAM) based on observed values of three forests in subtropical China. They found that LAI values differed greatly by forest types and seasons and showed strong spatial autocorrelation. Species diversity and stand variables like stand density affected LAI values. The work is new for subtropical forests. This is a well-written manuscript well suited for biogeoscience. The topic is of general interest to readers in the field of forest ecosystem process. I only have a few questions/comments on model parts.

Re: Thanks for the overall positive and valuable comments on our manuscript. Based on comments, we have revised the manuscript. Please see the detailed responses below.

1. The authors mentioned they used GAM followed by linear step regression (LSR). You may directly use GAM for stepwise regression by MGCV packages in R and not necessary perform LSR since GAM could describe both linear and nonlinear relationship.

Re: It is a good point. Based on this comment, we used GAM model directly instead of fitting the model by two steps (that is LSR and GAM). Because there are two packages (“gam” and “mgcv”) developed in R project for GAM and the two packages have the same function, we still used gam package for GAM analysis. Our results (see Table 4, Fig. 3 and Fig. 4) showed that the factors affecting LAI variations differed slightly from the results in the previous manuscript, but the effects were significant. We have revised the manuscript accordingly. We hope that our results are satisfactory for publication.

2. In the methods, you need to report which smooth method you used for GAM.

Re: Based on this comment, we have described the method (smooth spline method with two splines) for GAM (see line 227-228 on page 12).

3. For the results of model fitting, you listed some variables which were not statistically significant ($p>0.1$). For example, BA ($p=0.258$), crown width ($p=0.327$) and crown coverage ($p=0.333$) in Table S1 for LSR and crown width ($p=0.209$) and crown coverage ($p=0.456$) for GAM in Table 2. This will change the conclusion on the variables related with LAI. Although the model is not for prediction, you may lower the significant level. Please carefully check the results.

Re: Based on the comments above, we re-run the gam package directly and the variables with statistical significance are presented in the Table 4. Thus, the variables that are not significant are not shown. And we have revised the results and conclusions accordingly in this revision (see Table 4 and the Results and Conclusion sections).

4. Page 11 Line 11. “Tree species diversity” is better than “species diversity”.

Re: Changed as suggested (see line 222 on page 12).

5. Page 21 Lines 395-396. It is interesting the authors recommended 30m as a reference for sampling plot size to estimate LAI in subtropical forests. However, you may use a range not point value to account this according to table 3.

Re: Good point! We have replaced the point value with the range value (i.e. from 13m to 27m) based on this comment (see line 431-432 on page 23).

6. As the author mentioned, there are many factors affecting LAI. As an important stand structure characteristic, stand structural diversity (tree size diversity in this case) may explain LAI variation partially. I suggest testing the factor in the study.

Re: Good suggestion! We calculated the tree size diversity based on the reference (Lei XD, Wang WF, Peng CH. 2008. Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. Can. J. For. Res., 39, 1835-1847). Then we have added this variable to run GAM model (see lines 152-155 on pages 8-9). However, we found no significant effect of tree size diversity on LAI, so did not present the result.

7. Fig. 1. *P. massoniana-L. glaber* and *C. axillaris* cannot be recognized clearly. Please change the legend.

Re: Good point! We have changed as suggested (see Fig. 1).

8. Fig.3. I am wondering you may have wrong values for BA (range from 0 to 6000?) and crown coverage (range from 0 to 1000?). What is the unit for them? Same as Fig. 4. Please carefully check them.

Re: In the previous manuscript the unit for BA was cm^2 and for crown coverage was m^2. We only used the data of individual trees with height larger than average height in each stand, so some values of BA and crown coverage were within the range. After re-running the GAM model, only total crown coverage of the stand is a significant variable. We have checked the data carefully and presented the right results (see Fig. 3).

9. Table S1. The summary of values of stem density, BA and IV by species are not equal to the whole stand.

Re: Yes, you are right. In the previous manuscript, the data in Table S1 were for the all species and the top five tree species. The data of other species were not provided in Table S1. Sorry for our carelessness. We have added one row to show the summed data for the rest species (see Table S1).

10. Table S2. Parts of the columns of mean sq and sum aq are the same? Actually you need not to report these values besides parameters, F values and p values.

Re: We have deleted the Table S2 because we used GAM model directly instead of fitting the model by two steps (that is LSR and GAM) based on your comment.

Referee #2’ s comments:

GENERAL COMMENT The topic of the manuscript lies within the field of the journal Biogeosciences. It reports on spatial and temporal variability of the leaf area index in forests. The overall importance of reliable LAI measurements is undoubted and systematic studies of spatial variability within forest stands are seldom. In this sense, the present study is justified. Unfortunately, the description of the methods is insufficient and the obtained results remain therefore questionable.

Re: Thanks for the positive comments and suggestions on our manuscript. Based on the comments, we have revised the methods and results sections. The detailed responses are presented as follows.

DETAILED COMMENTS Material and methods Since this determines the canopy structure, it should be stated if the studied forest plots where planted or if they are from natural regeneration, further if they were thinned or selectively cut at some point in time. According to the supplementary table S1, it appears that the stands are unevenaged, but a clear information about their history would be useful.

Re: Good point! The forests are originated from natural regeneration after human disturbance was prohibited in the middle 1960s and no thinning or selectively cutting were applied there till to investigation. The history of the forests was described in the Materials and Methods (see line 125-132 on page 7).

The material used for the hemispherical photography is only poorly described. The camera type is given, but not its manufacturer. There is no information about the lens, not even its viewing angle (or focal length). The choice of picture exposure is not described although it is essential to achieve a good contrast without overexposure. The resolution of the pictures is not given, nor their format.

Re: Thanks for valuable suggestion. We have provided clear information about the material of the hemispherical photography, such as the manufacturer (Shiya Scientific and Technical Cooperation, China), the lens (Pentax TS2V114E, Japan), the viewing angle (180°), the picture exposure (automatic exposure set by the manufacturer), the picture resolution and format (768×494 pix, BMP) (see line 159-164 on page 9).

The picture analysis is also insufficiently described. There is no indication of the software used, of the pixel classification (thresholding), of the considered viewing angle and if it was divided into rings. The viewing angle would be very important to know here because, in conjunction with the tree height, it determines the integration area of the LAI measurement (which is, in turn, important for understanding the spatial variability).

Re: We have revised the manuscript by adding the description of the picture analysis such as the software (the plant canopy analysis software developed by the manufacturer), the pixel classification (thresholding) (752(H)×582(V)), the considered viewing angle (150°) and it was divided into 5 rings (see line 165-168 on page 9).

The method to estimate a clumping factor does not state the number of sectors used. The estimation of the contribution of leaves versus wood to the plant area index would be a positive aspect of this study, but here also the methods are poorly described. It is not stated if all of the woody elements on all pictures were painted or only sub-samples. Further, "replace the woody materials with surrounding of non-woody materials" is either a wrong wording or a wrong method. Woody areas should neither be replaced by "non-woody materials" nor by sky pixels, they should be excluded from the analysis because it is essentially not known how much leaf area or sky area they hide.

Re: Sorry for our unclear description. We originally described the method according to the reference (Liu ZL, Jin GZ, Chen JM, Qi YJ. 2015. Evaluating optical measurements of leaf area index against litter collection in a mixed broadleaved-Korean pine forest in China. Trees, 29: 59-73), where the word “replace” used means “exclude the pixels of woody materials”. We have changed the sentence into “In Photoshop software, we used the Clone Stamp Tool to select the image of the woody materials (e.g., stems) and excluded the pixels, leaving only leaves on the photos” (see line 172-173 and 176-178 on page 10).

Statistical tests are partly done after different types of data transformation. I’m not sure if cutting outliers back to "normally maximal values" is an appropriate method, but at least the measure of this transformation in table 1 should be described in an understandable manner. Using non-parametric statistics would probably make the tests more convincing than the different transformations applied here.

Re: Yes, you are right. Our description is not clear, so we have changed the sentences into “According to Chiang et al. (2003), we regarded the LAI values as the normal values when the LAI values were within mean value±3×standard deviation. Otherwise, the LAI values were outliers and replaced with the maximum or the minimum of normal values. Because the geostatistics analysis requires that the data meet normal distribution, the transformation was applied if the data did not meet normal distribution”. To support our method, we have cited the references (Chiang LH, Pell RJ, Seasholtz MB. 2003. Exploring process data with the use of robust outlier detection algorithms. Journal of Process Control, 13(5): 437-449; Dai FQ, Zhou QG, Lv ZQ, Wang XM, Liu GC. 2014. Spatial prediction of soil organic matter content integrating artificial neural network and ordinary kriging in Tibetan Plateau. Ecological Indicators, 45: 184-194) in the text and added them in the reference list. We hope this revision is clearer than it was before (see line 192-196 on page 11).

Crown coverage is used as a factor in statistical models, but it is not described what this parameter means and how it was measured. A crown coverage is often derived from hemispherical photographs. Is it also the case here, or is it an independent measurement? This can completely change the interpretation of the obtained statistical relationship.

Re: Sorry for our ambiguous description. The crown coverage was not derived from hemispherical photographs and it was calculated from crown diameter measured for individual trees within a stand (see line 145 on page 8).

The kriging is also insufficiently described in the methods section (it is only in a figure legend that it is given as "ordinary"). The maps produced by this kriging show island structures that probably correspond to the grid of picture taking. If this is true, then it indicates a methodological problem. Either the photographs were systematically taken in some spatial relation to the trees (e.g. on a regular grid in a regularly planted stand). Or the very goal of kriging, i.e. interpolating between discrete measurements, was missed.

Re: According to this comments, we have added description of the Kriging in the methods section. Although the ordinary Kriging has the drawback, it is a commonly used interpolating method in the geostatistics reported by other studies (Elbasiouny H, Abowaly M, Abu_Alkheir A, Gad A. 2014. Spatial variation of soil carbon and nitrogen pools by using ordinary Kriging method in an area of north Nile Delta, Egypt. Catena, 113: 70-78. Dai FQ, Zhou QG, Lv ZQ, Wang XM, Liu GC. 2014. Spatial prediction of soil organic matter content integrating artificial neural network and ordinary kriging in Tibetan Plateau. Ecol. Indic., 45: 184-194) (see line 211-218 on page 12).

Results and discussion The presented results would probably be interesting, but due to the poor description of the methods they are all more of less doubtful.

Re: We have revised the Methods section (see Materials and Methods section) and hope this revision is satisfactory.

Tables and figures Table 1 and 2 should use the same structure to be comparable. Table 3 should include the sample size, otherwise the column RSS is meaningless. Table 4 gives statistical tests without giving any information on how the different factors affect the dependent variable. Since this is not so easy to put in a table in the case of non-linear relationships, table 4 should make a reference to fig. 3. Figure 1: the two grey tones cannot be distinguished.

Re: We have used the same structure for Table 1 and Table 2, and added the sample size in Table 3 as suggested. We have changed Table 4 and Fig. 3, which showed the effect factors and relationship between LAI and factors, respectively. The two grey bars in

Figure 1 have been changed into empty and grey, respectively.

Language The English of the manuscript is well understandable but some sentences are not well structured. At least in one case the wording is inappropriate: "throughout four measurement seasons" would mean at least several measurements in each season (while there is actually one per season).

Re: We asked a native English editor from the Charlesworth Group to improve the language (see http://www.charlesworth-group.com).

X. Zhang’s comments:

The manuscript entitled “Spatial and seasonal variations of leaf area index (LAI) in subtropical secondary forests related to floristic composition and stand characters” by Zhu et al. is an interesting study on the spatial heterogeneity of LAI and its controlling factors in subtropical forests in China. The paper covers an important issue. The investigation is in-depth and thorough. The results are interesting and fill the gap of LAI measurement in subtropical forests. The paper is well-written and duly illustrated. Publication is therefore recommended with minor revisions suggested as follows:

Re: First of all, we thank X. Zhang very much for the positive comments and valuable suggestions. Based on the following comments, we have revised the manuscript and our detailed replies are presented below.

1. Line 33-34: insert a word “and” after the geostatistics method.

Re: We have added “and” as suggested (see line 28 on page 2).

2. Line 46: remove the keywords "Deciduous species". In your paper, more than one tree species were investigated and the constituents of forests or tree species richness was one of the controlling factors of LAI values. In other words, "deciduous species" is not a proper substitute for the proportion of deciduous species.

Re: We replaced the keyword with “Geostatistical analysis” as suggested (see line 40 on page 3).

3. Line 51, 55-56 and throughout main text, the reference should be arranged by the published year.

Re: Based on the comments, we have changed all references in the entire manuscript according to a chronological order (see line 45 on page 3 and the others).

4. Line 59: insert a word “as” between “used” and “parameter”.

Re: Instead of adding “as”, we have changed the sentence into “Leaf area index (LAI), defined as total one-sided leaf area per unit ground surface area (Biudes et al., 2014), is a widely used parameter to: : :.” (see line 50-55 on page 3).

5. Line 109: change “stand character” to “stand characters”.

Re: Changed as suggested (see line 96 on page 6).

6. Line 133-134: the mean temperature of the study site should be a fixed value, please correct it.

Re: We have changed the mean annual air temperature into “16.5 C°”(see line 118 on page 7).

7. Line 148: check and correct the plot size of *P. massoniana* - *L. glaber* mixed forests.

Re: We have checked and the plot size is correct because the plot of *P. massoniana* - *L. glaber* mixed forests is irregular with 90 m × 190 m (see line 135 on page 8).

8. Line 170: please add the manufacturer and country to the LAI measuring instrument (SY-S01A).

Re: Added as suggested (see line 159 on page 9).

9. Line 199-200: coefficient of variation (CV) does not need full name here.

Re: We have used abbreviation CV here (see line 189 on page 10).

10. Line 234-238: the author need to report which smooth method used for GAM in this study.

Re: Good point. We have indicated that the smooth method for GAM is smooth spline (see line 227-228 on page 12).

11. Line 250: it is better to illustrate the version of R software used in this study.

Re: We have added the version of R (R 3.2.1) in the manuscript (see line 238 on page 13).

12. Line 255: consider changing "month" in Table 1 into "measurement seasons". Do the same modifications in other tables and Fig. 1.

Re: Change as suggested (see all Tables and Fig. 1 in this manuscript).

13. Line 265: How did you calculate the mean LAI values? I'm a little confused that why you think it's necessary to report the minimum, maximum and mean values of LAI at the same time. what's the differences or the particular meaning between them?

Re: We calculated average LAI values of 100 plots in each forest at a given measurement season. The minimum and maximum values within a forest at different measurement seasons to examine the variations in LAI (see line 190 on page 10).

14. Line 350: ": : :. but they are not suitable for LAI correction in subtropical forests", why? Is this a conclusion drew by yourself or from other's research?

Re: The previous studies by Liu et al. (2015a) and Liu et al. (2015b) showed that the α values ranged from 0.04±0.01 to 0.69±0.12 and Ω_E values ranged from 0.88±0.04 to 0.96±0.01. These values were measured in temperate forest in northeastern China and differed from our study (α ranged from 0.04±0.03 to 0.15±0.09 and Ω_E ranged from 0.84±0.09 to 0.92±0.08). Therefore, we drew the conclusion and revised the sentence (see line 330-333 on page 18).

15. Line 360: change "is" to "was".

Re: Changed as suggested (see line 340 on page 18).

16. Line 695-700: the “RSS” in the first line in Table 3 need to be clarified.

Re: We have offered the full name of RSS (residual sum of squares) (see Table 3).

17. Line 745-750: In Fig.1, the y-axis should change into "mean LAI value", x-axis should change into “Month”.

Re: We remained the axis labels (see the reply to comment 12).

18. Fig 3 and 4: These two figures are new and unique, and the results might be interesting. It’s a pity that you didn’t thoroughly discuss these figures except simply described in Results Line 326-330. I suggest to add some discussion about these two figures in you manuscript.

Re: Good suggestions. We have added some sentences to discuss the results of Fig. 3 and Fig. 4 (see line 385-417 on page 21-22).

Spatial and seasonal variations of leaf area index (LAI) in subtropical secondary forests related to floristic composition and stand characters

Wenjuan Zhu[1,2], Wenhua Xiang[1,2,3*], Qiong Pan[4,1], Yelin Zeng[1], Shuai Ouyang[1,2,3], Pifeng Lei[1,2,3], Xiangwen Deng[1,2,3], Xi Fang [1,2,3], Changhui Peng[5,1]

1 Faculty of Life Science and Technology, Central South University of Forestry and Technology, Changsha 410004, Hunan Province, China

2 Huitong National Field Station for Scientific Observation and Research of Chinese Fir Plantation Ecosystem in Hunan Province, Huitong 438107, China

3 National Engineering Laboratory of Applied Technology for Forestry & Ecology in Southern China, Changsha 410004, China

4 Changsha Environmental Protection College, Changsha 410004, China

5 Institute of Environment Sciences, Department of Biological Sciences, University of Quebec at Montreal, Montreal, QCH3C 3P8, Canada

* *Correspondence to*: Wenhua Xiang, Email: xiangwh2005@163.com, Tel.: +86 0731 85623483

Abstract. Leaf area index (LAI) is an important parameter related to carbon, water and energy exchange between canopy and atmosphere, and is widely applied in process models that simulate production and hydrological cycles in forest ecosystems. However, fine-scale spatial heterogeneity of LAI and its controlling factors have yet to be fully understood in Chinese subtropical forests. We used hemispherical photography to measure LAI values in three subtropical forests (*Pinus massoniana-Lithocarpus glaber* coniferous and evergreen broadleaved mixed forests, *Choerospondias axillaris* deciduous broadleaved forests, and *L. glaber-Cyclobalanopsis glauca* evergreen broadleaved forests) from April 2014 to January 2015. Spatial heterogeneity of LAI and its controlling factors were analysed using geostatistical methods and the generalised additive models (GAMs), respectively. Our results showed that LAI values differed greatly in the three forests and their seasonal variations were consistent with plant phenology. LAI values exhibited strong spatial autocorrelation for the three forests measured in January and for the *L. glaber-C. glauca* forest in April, July and October. Obvious patch distribution pattern of LAI values occurred in three forests during the non-growing period and this pattern gradually dwindled in the growing season. Stem number, crown coverage, proportion of evergreen conifer species on basal area basis, proportion of deciduous species on basal area basis and forest types affected the spatial variations in LAI values in January, while stem number and proportion of deciduous species on basal area basis affected the spatial variations in LAI values in July. Floristic composition, spatial heterogeneity and seasonal variations should be considered for sampling strategy in indirect LAI measurement and application of LAI to simulate functional processes in subtropical forests.

Keywords: Leaf area index; Spatial heterogeneity; Geostatistical analysis; Generalised additive models (GAMs)

1 Introduction

Many fundamental ecological processes in forest ecosystems, such as carbon (C) flux as well as water and energy exchanges, take place between the canopy layer and atmosphere (GCOS, 2006; Brut et al., 2009; Alonzo et al., 2015; Liu et al., 2015b). At a finer scale, leaves within the canopy are the primary organ to perform a series of physiological activities (i.e. photosynthesis, respiration and evapotranspiration) (Aragão et al., 2005) and physical reactions (i.e. rainfall and radiation interception) (Aston, 1979; Smith, 1981; Crockford & Richardson, 2000). Therefore, the amount of leaves in a forest is the determinant of above-ground ecological processes and ecosystem functions. Leaf area index (LAI), defined as total one-sided leaf area per unit ground surface area (Biudes et al., 2014), is a widely used parameter (Kross et al., 2015) to quantitatively describe the vegetation canopy structure (Woodgate et al., 2015), to simulate ecological process models (Brooks et al., 2006; Sprintsin et al., 2007; Facchi et al., 2010; Gonsamo & Chen, 2014) and to reveal tree growth and productivity in forests at stand scale and landscape level (Lee et al., 2004; Liu et al., 2015b). In addition, LAI is listed as one of the essential variables for observation of global climate (Mason et al., 2003; Manninen et al., 2009) and for remote sensing data validation (Asner et al., 2003; Clark et al., 2008). Thus, accurate estimates of LAI value are important to understand ecological processes in forest ecosystems.

At present, various direct and indirect methods have been developed to measure LAI in forests. Direct estimation methods including leaf harvest (Clark et al., 2008), allometric equations and litter collection (Ryu et al., 2010; Liu et al., 2015a) are recognised as the most accurate. However, leaf harvest and allometric equations methods need time-consuming, labour-intensive and destructive sampling processes, while litter collection is more feasible for temperate deciduous forests. Obviously, the direct methods are less applicable to large-scale and long-term LAI monitoring (Bequet et al., 2012; Biudes et al., 2014). Indirect methods include using a plant canopy analyser (Licor LAI-2000), hemispherical or fisheye photography (Macfarlane et al., 2007) and remote sensing (Biudes et al., 2014). The indirect methods retrieve LAI value from light transmittance through canopies or from canopy image analysis. For large-scale LAI estimates, remote sensing is the most effective method but requires validation with ground-based LAI data. LAI estimates on the ground at small scales are still a challenge due to the problems of sampling strategies associated with accepted level of accuracy, time and cost considerations (Richardson et al., 2009). Hemispherical photography is a relatively simple and easily operated method among many indirect methods to retrieve LAI value at small scales (Demarez et al., 2008). Correction of the effects of woody materials, clumping and zenith angels or exposure is critical to improve the accuracy of LAI estimation (Liu et al., 2015b). Analysis software development and portable and timely characteristics allow hemispherical photography to measure spatial heterogeneity and seasonal variations of LAI in forests.

Forest canopy structure is highly complex so LAI values show great temporal and spatial variations at scales ranging from stand to global scale. For example, LAI values in the 7.9 ha plot of an old humid temperate forest tended to increase spatially as elevation increased and showed a temporal variation with plant phenology (Naithani et al., 2013). The spatial patterns of LAI values at stand scale were significantly influenced by spatial distribution of tree species, which was dependent on topography and soil types (Naithani et al., 2013). The coefficient of variation (CV) in LAI decreased as the scale increased and LAI values did not have any relationship with biome type and climate patterns, but were influenced by land use and land cover, terrain features, and soil properties at stand scale (Aragão et al., 2005). The CV of LAI of three species (i.e. beech, oak and pine) had different degrees of spatial variation in a 1 ha plot at stand level (Bequet et al., 2012). LAI values in sagebrush displayed strong spatial patterns with time after disturbance and increased with stand age and total plant cover (Ewers & Pendall, 2007). The LAI values derived from MODIS data (Myneni et al., 2002; Huang et al., 2008) revealed strong spatial variations at global scale, which were correlated with latitude (Tian et al., 2004). At the global scale, temperature is the limiting factor for LAI under cool conditions while water plays a predominant role under other conditions, and this pattern differed among plant functional types (Iio et al., 2014). The factors that govern the spatial variations in LAI values at stand level include forest types, stand structure (Bequet et al., 2012), climate (Shao & Zeng, 2011), topography, soil moisture condition (Breshears & Barnes, 1999), and human disturbance and management activities (Huang & Ji, 2010). Although effects of topography, soil properties (Aragão et al., 2005; Naithani et al., 2013) and stand characters (Bequet et al., 2012; Yao et al., 2015) on LAI values have been investigated in detail, the effect of forest type, stand structural diversity and stand structure on spatial heterogeneity and seasonal variations of LAI has yet to be fully understood.

Chinese subtropical forests contain a diversity of tree species with complex canopy structure that mostly grow on heterogeneous topography and soil conditions. As a result, LAI in subtropical forests may exhibit great spatial and seasonal variations, which is worthy of further investigation. However, LAI data of subtropical forests are relatively deficient in the global database (see Asner et al., 2003). In this study, we selected three different forests: *Pinus massoniana*-*Lithocarpus glaber* coniferous and evergreen broadleaved mixed forests, *Choerospondias axillaris* deciduous broadleaved forests, and *L. glaber*-*Cyclobalanopsis glauca* evergreen broadleaved forests, in which to measure LAI values were measured by using hemispherical photography. Spatial heterogeneity of LAI was investigated through geostatistical analysis, and generalised additive models (GAMs) were used to examine how stand structural diversity and stand characters affect LAI variations in the three forests. Specifically, the objectives of this study were: (1) to examine differences and seasonal variations in LAI among three forests in subtropical China; (2) to analyse spatial heterogeneity of LAI values within a specific forest; and (3) to identify how forest types, stand structural diversity and stand characters control the spatial heterogeneity and seasonal variations of LAI values in three forests.

2 Materials and methods

2.1 Study site description

The study was carried out at Dashanchong Forest Farm (latitude 28°23′58″-28°24′ 58″

N, longitude 113°17′46″-113°19′08″ E), Changsha County, Hunan Province, China. The farm experiences a humid mid-subtropical monsoon climate. Mean annual air temperature was 16.5 °C, with a mean monthly minimum temperature of -11°C in January and maximum temperature of 40°C in July. Mean annual precipitation ranged from 1412 mm to 1559 mm, mostly occurring between April and August. The topography is characterized by a typical low hilly landscape with an altitude between 55 m and 260 m above sea level. Soil type is designated as well-drained clay loam red soil developed on slate and shale rock, classified as Alliti-Udic Ferrosols, corresponding to Acrisol in the World Reference Base for Soil Resource (IUSS Working Group WRB, 2006). Evergreen broadleaved forest is the climax vegetation of the region. As a result of human disturbance and management activities, the farm has no primary forest, and possesses a range of secondary forests in different stages of succession (based on species composition) dominated by different tree species, including (1) early stage *P. massoniana-L. glaber* coniferous and evergreen broadleaved mixed forests dominated by the shade-intolerant coniferous species typical of early succession, (2) middle stage *C. axillaris* deciduous broadleaved forests dominated by shade-intolerant deciduous broadleaf species, and (3) late stage *L. glaber-C. glauca* evergreen broadleaved forests dominated by the shade-tolerant evergreen broadleaved species commonly observed in the late stage of succession in this farm (Xiang et al., 2015; Ouyang et al., 2016).

2.2 Determination of stand characteristics

We established a permanent plot for each of three forests (i.e. 90 m × 190 m irregular plot for *P. massoniana*-*L. glaber* mixed forests, 100 m × 100 m plot for *C. axillaris* deciduous forests, and 100 m × 100 m plot for *L. glaber*-*C. glauca* evergreen broadleaved forests). Each plot was divided into 10 m × 10 m subplots, where tree species, diameter at breast height (DBH, cm), tree height (H, m), height under the lowest live branch (m) and crown width (m) were measured for the individual stem with DBH larger than 1 cm. Stand characteristics for the trees with DBH >4 cm of the three forests are presented in Table S1.

To identify the factors that control spatial heterogeneity of LAI values in the forests, we selected individual trees with H larger than average height of each stand (see Table S1) and calculated their stem number, average DBH, H, total basal area at breast height (BA), crown width, crown coverage (calculated from crown diameter measured for individual trees within a stand), tree species diversity, tree size diversity, the proportion of BA of three functional group (coniferous, deciduous and evergreen broadleaved species) to total stand BA within a subplot. Tree species diversity (biodiversity index, BDI) was determined using the Shannon-Wiener index as follows:

$$BDI = -\sum P_i \ln P_i \qquad (1)$$

where P_i is important value of *i*th species and is calculated by dividing the sum of relative abundance degree (*A*r) and relative dominance degree (*D*r) of *i*th species within a subplot by two.

Based on the Shannon-Wiener index, 2 cm was used for the DBH class, so tree size diversity (*H*) was determined using the formula of Lei et al. (2009):

$$H = -\sum P_i \ln P_i \qquad (2)$$

where P_i is the proportion of basal area for the *i*th diameter class.

2.3 Sampling design for LAI measurement

At the centre of each subplot of the three forests, hemispherical photographs were taken using a LAI measuring instrument (SY-S01A, Shiya Scientific and Technical Cooperation, Hebei, China) throughout four measurement seasons, i.e. in April (spring), July (summer) and October (autumn) in 2014 and January (winter) in 2015. The operation was carried out below canopy with the fisheye lens (Pentax TS2V114E, Japan) 1.0 m above the ground (Manninen et al., 2009) with a viewing angle of 180°. The picture exposure is automatic exposure set by the manufacturer, and we took the photographs (768 × 494 pix, BMP) in the morning, at dusk or when cloudy, in order to minimize influence of direct sunshine (Rich, 1990; Bequet et al., 2012). The images were processed and effective LAI values (L_e) were recorded using plant canopy analysis software developed by the manufacturer, for which appropriate pixel classification (thresholding) was chosen (752(H) × 494(V)), viewing angle considered (150°), and the hemispherical photography was divided into five rings to obtain results. To obtain accurate LAI (L), the correction was made to L_e based on previous theory (Chen, 1996):

$$L = \frac{(1-\alpha)L_e\gamma_E}{\Omega_E} \tag{3}$$

where α is the ratio of woody to total area and reflects the contribution of woody materials to L_e, and Ω_E is the clumping index that quantifies the effect of foliage clumping beyond shoots level. In the method getting accurate Ω_E values, the hemispherical photography was divided into ten sectors. γ_E is the needle to shoot area ratio and quantifies the effect of foliage clumping within shoots.

Photoshop Software (Adobe Photoshop CS5, Adobe Systems Incorporated, North America) was used to calculate α. After total pixel number of L_e image was determined, in the Photoshop software, we used the Clone Stamp Tool to select the image of the woody materials (e.g. stems) and excluded the pixels, leaving only leaves on the photos, recorded as LAI of leaves ($\mathrm{LAI}_{\mathrm{leaf}}$). The value of α was calculated accordingly:

$$\alpha = (L_e - \mathrm{LAI}_{\mathrm{leaf}})/L_e \tag{4}$$

The logarithm averaging method proposed by Lang and Xiang (1986) was applied to calculate Ω_E:

$$\Omega(\theta) = \frac{\ln[P(\bar{\theta})]}{\overline{\ln[P(\theta)]}} = \frac{n\ln[P(\bar{\theta})]}{\sum_{k=1}^{n}\ln(P_k(\theta)]} \tag{5}$$

where $P(\theta)$ is the average gap fraction (expressed without the bar in the text), $\ln[P(\theta)]$ is the logarithm average of the gap fraction, and $P_k(\theta)$ is the gap fraction of segment k. For deciduous and evergreen broadleaved species, γ_E=1.0, but for coniferous species, γ_E is always >1.0, but we ignored the effect of needle to shoot area on LAI in this study.

2.4 Data analysis

The minimum, maximum, mean value, standard deviation and CV were calculated for the LAI data measured in 100 plots within each forest. Two-way analysis of variance (ANOVA) was used to detect effect of forest type and measurement season on LAI value. The LAI data in the three forests were tested for normal distribution using the K-S test (P<0.05). We followed Chiang et al. (2003) in regarding LAI values as normal when they fell within the mean value ±3 standard deviations. Otherwise, the LAI values were regarded as outliers and replaced with the maximum or the minimum of normal values.

Because the geostatistical analysis requires that the data meet normal distribution, the transformation was applied if the data did not meet normal distribution (Dai et al., 2014). Most values required natural logarithm transformation to meet assumptions of normality. The exception is for *L. glaber*-*C. glauca* in April and in November which were artan-transformed.

To investigate spatial heterogeneity of LAI values over four seasons measured in the three forests, semivariance function was calculated as follows:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(x_i) - Z(x_i + h)]^2 \qquad (6)$$

where $\gamma(h)$ is semivariance value of lag distance h, $N(h)$ is the number of pair data for lag distance h, $Z(x_i)$ and $Z(x_i + h)$ represent LAI values at coordinate x_i and (x_i+h) (Rossi et al., 1992). Based on the semivariogram plotting $\gamma(h)$ values against h variable, the appropriate models were fitted and we obtained the values of nugget (C_0), sill (C_0+C), range (A_0) (Ewers & Pendall, 2007) and the ratio $[C/(C_0+C)]$ that reflected the degree of spatial autocorrelation of LAI values in a forest. Because spatial autocorrelation and semivariogram theory make unbiased optimal estimation for regional variables in a limited area (Bivand et al., 2013), the Kriging interpolation method, an unbiased estimation of the regional variables of the sampling points using the structure of the data and semivariogram function, was used to predict unknown LAI values in the forests from the data measured and to produce spatial distribution maps of LAI values for the three forests and four seasons. Compared with other methods, the Kriging method can overcome the difficulty in analysing error of interpolation, does not produce the boundary effect of regression analysis, and estimates the spatial variability distribution of measured parameters.

Ordinary Kriging - one of the Kriging methods - is a least-squares method of spatial prediction based on the assumption of an unknown mean. It is the most common type of Kriging in practice (Dai et al., 2014) and is widely used in soil spatial heterogeneity studies (Elbasiouny et al., 2014). In our study, we also used the ordinary Kriging interpolation method to investigate spatial heterogeneity of LAI values.

Because the largest amount of defoliated leaves occurs in January and leaves fully expand in July in subtropical forests, we chose LAI values measured in January and July in three forests as response variables. The explanatory variables include forest types, stand structural diversity (species richness, tree species diversity and tree size diversity) and stand characters (stem number, average DBH, H, BA, crown width, crown coverage, the proportion of two functional groups (deciduous and evergreen conifer species) to total stand BA). The generalised additive models (GAMs) are able to analyse complex and nonlinear relationships (Guisan et al., 2002; Austin, 2002; Wood, 2006). Therefore, we used GAMs to examine how the factors affect LAI values. The function of GAMs is the addition of many smooth functions and each smooth function has an explanatory variable. In our study, we chose smooth spline with two splines as the smooth method for GAMs. The variance inflation factor (VIF) - the ratio of the regression coefficient variance for a variable when fit with all variables to that for the variable if fit on its own - was used to test the multi-collinearity of explanatory variables (James et al., 2013). When the VIF of an explanatory variable is between 0 and 10, the variable was retained to the model; otherwise, we discarded the variable (Shen et al., 2015). The Akaike information criterion (AIC) or generalised cross validation (GCV) was used to determine whether the model was good or bad (Clark, 2013). The factors selected after the multi-collinearity test were used for multi-factor analysis. After all the possible models in multi-factor analysis, we determined the optimal model based on the significant influence of all explanatory variables in the model with the smallest AIC or GCV (Dong et al., 2012). Geostatistical analysis was performed with GS+ software (Gamma Design Software). Statistical analysis and GAMs analysis were operated in R 3.2.1 (R Development Core Team, 2015). The car packages were used to test multi-collinearity and the gam packages were used to select the optimal model.

3 Results

3.1 Variation in LAI values

The LAI values varied with forest type and measurement season (Table 1). Generally, LAI differed significantly between measurement season ($P<0.001$), but LAI difference was not significant among forest types ($P>0.05$). Interactive effects of measurement seasons and forest types on LAI were significant ($P<0.01$). Among three forests, LAI in the *P. massoniana-L. glaber* forest had relatively low variation, while LAI in the *L. glaber-C. glauca* forest had the highest variation. In the *P. massoniana-L. glaber* forest, LAI showed the largest variation (the highest CVs) in October and the lowest variation (the smallest CVs) in January. In the *C. axillaris* forest, the largest variation in LAI was found in April and the lowest was found in January. In the *L. glaber-C. glauca* forest, LAI showed the largest variation in April and had the lowest variation in July.

Mean LAI values in the three forests showed different seasonal variation patterns (Fig.

1). The *C. axillaris* forest exhibited a unimodal pattern of seasonal variation, with the maximum mean LAI value (3.11±1.18) occurring in July and the minimum mean LAI value (1.28±0.44) in January. In the *P. massoniana-L. glaber* forest and *L. glaber-C. glauca* forest, the maximum mean LAI values occurred in October and the minimum mean LAI values appeared in January. During the growing season (April and July), the *C. axillaris* forest had the highest mean LAI value and the *L. glaber-C. glauca* forest had the lowest mean LAI value. During the non-growing season (October and January), the *L. glaber-C. glauca* forest had the highest mean LAI value in January, while the *P. massoniana-L. glaber* forest had the highest mean LAI value in October, and the *C. axillaris* forest had the lowest mean LAI values.

Mean α values in the three forests showed different seasonal variation patterns (Table 2). The *C. axillaris* forest exhibited a unimodal pattern of seasonal variations in mean α value, with the maximum mean α value occurring in January and the minimum mean α value in July. No obvious seasonal variations were found for the mean α value in the *P. massoniana-L. glaber* forest and in the *L. glaber-C. glauca* forest. Mean Ω_E values in the three forests were between 0.84 and 0.92, but they did not show clear seasonal variations, and the standard deviations were small.

3.2 Spatial heterogeneity in LAI values

The semivariogram results for LAI across the three forests during different measurement seasons are summarised in Table 3. The spatially dependent variance [C] accounted for 88.9%-98.4% of the total variance [$C+C_0$] for LAI values measured in

January in the three forests and also in April, July and October in the *L. glaber-C. glauca* forest. This indicated the strong spatial autocorrelations of LAI values over short distances. These LAI data were best fitted with a Gaussian model or exponential model ($r^2>0.50$).

Spatial autocorrelation ranges of LAI values differed among forests and measurement seasons (Table 3). In January, the largest spatial autocorrelation range was found in the *P. massoniana-L. glaber* forest, and the lowest was found in the *C. axillaris* forest. In April, the largest spatial autocorrelation range of LAI was found in the *C. axillaris* forest, and the lowest was found in the *P. massoniana-L. glaber* forest. In July, the largest spatial autocorrelation range of LAI was in the *P. massoniana-L. glaber* forest, while the smallest was in the *C. axillaris* forest. In October, the largest spatial autocorrelation range of LAI was in the *L. glaber-C. glauca* forest, while the smallest was in the *P. massoniana-L. glaber* forest. Seasonal changes of range showed one peak pattern for *C. axillaris* forest and *L. glaber-C. glauca* forest, where the large range appeared in the growing season (April and July) and the small range appeared in the non-growing season (October and January).

Spatial distribution pattern of LAI values also varied with forest type and measurement season (Fig. 2). For example, LAI values in January across the three forests exhibited obvious patch and heterogeneous spatial distribution. In April and July, less spatial heterogeneity was found for LAI values especially in the *P. massoniana-L. glaber* forest. In October, heterogeneous and patch spatial distributions of LAI values appeared in the *L. glaber-C. glauca* forest, and banded spatial distributions of LAI values obviously appeared in the *C. axillaris* forest.

3.3 Factors affecting LAI variation

The multi-collinearity test indicated that the explanatory variables in January and July did not have multi-collinearity. Thus, forest type, species richness, tree species diversity, tree size diversity, stem number, average DBH, H, BA, crown width, crown coverage, and the proportion of two functional groups (deciduous and evergreen conifer species) to total stand BA were included as explanatory variables in multi-factor analysis for LAI values measured in January in the three forests. After comparing all possible models, the best fitted GAMs for LAI values in January were expressed as LAI ~ s(stem number, 2) + s(crown coverage, 2) + s(PESB, 2) + s (PDSB, 2) + factor (forest types) (Table 4). For LAI values measured in July, all these factors selected by the multi-collinearity test were included as explanatory variables in multi-factor analysis. The best fitted GAMs for LAI values in July were expressed as LAI ~ s(stem number, 2) + s(PDSB, 2) (Table 4).

The explanatory variables included in GAMs reflected their effects on or relationship with LAI variations. Given that other variables were fixed, LAI measured in January tended to decrease as stem number increased. LAI showed a positive nonlinear relationship with crown coverage up to ~200 m^2, and then decreased with increasing crown coverage. The LAI values tended to increase as the proportion of evergreen conifer species to total stand BA increased, and tended to decrease as the proportion of deciduous species to total stand BA increased (Fig. 3). Given that other variables were fixed, LAI measured in July tended to increase as stem number increased up to ~7 and then decreased at higher values. The effect of the proportion of deciduous species to total stand BA on

LAI appeared more complicated, in that LAI increased as the proportion of deciduous species to total stand BA increased up to ~0.7, and then decreased at higher values (Fig. 4).

4 Discussion

4.1 Seasonal variation in LAI value among forest type

LAI data in subtropical forests in southern China are lacking compared to other global regions (Asner et al., 2003). This study provided seasonal LAI data in three subtropical forests that consist of contrasting functional types of species. Their mean LAI values varied from 1.28±0.44 to 3.28±1.26 (Table 1). This result is close to the LAI range (from 1.0 in winter to 4.0 in summer) retrieved by remote sensing techniques from the subtropical area of China from 2000 to 2010 (Liu et al., 2012). Compared with the LAI values estimated from allometric equations (Xiang et al., 2016) and specific leaf area (SLA) values in 40 m × 40 m plots in this study (5.29-9.19), the LAI values measured by hemispherical photography are low but significantly correlated (r^2=0.40 and P=0.035). Previous studies (see Lopes et al., 2015) have proved the underestimation of LAI using hemispherical photography. However, the method is feasible to obtain forest LAI data and to investigate spatial and seasonal variation in such values (Coops et al., 2004; Dovey & Toit, 2006).

The ratio of woody to total area (α) and the clumping index (Ω_E) have been recognised as the error sources in LAI measurement by optical methods (Chen et al., 1997; Bréda, 2003; Liu et al., 2015a). So far these two parameters have been measured in northeastern

China (Liu et al., 2015a; Liu et al., 2015b), which showed that the α values ranged from 0.04±0.01 to 0.69±0.12 and Ω_E values ranged from 0.88±0.04 to 0.96±0.01. These values were measured in temperate forest in northeastern China and differed from our study (mean α values varied from 0.04±0.03 to 0.15±0.09 and mean Ω_E values varied from 0.84±0.09 to 0.92±0.08) (Table 2), so they are not suitable for LAI correction in subtropical forests. Also literature on α and Ω_E values in subtropical forests is scarce. The variations in α are probably due to the seasonal variations and spatial heterogeneity of canopy structure in the three forests. In general, the α values are consistent with the amount of leaf litter. Our results showed that the large mean α values occurred in autumn for the *P. massoniana-L. glaber* forest and the *C. axillaris* forest, but in spring and autumn for the *L. glaber-C. glauca* forest (Table 2). This seasonal change in mean α value in three forests was generally consistent with the amount of leaf litter collected by a litter trap installed in each forest type (Guo et al., 2015). The average Ω_E value (0.87) in this study was smaller than the values of mixed broadleaved-Korean pine forest in northeastern China (Liu et al. 2015b) and this could be attributed to the different region and forests. The values of α and Ω_E obtained in this study fill the gap of calibration for optical measurement of LAI in subtropical forests.

Mean LAI values differed among the three forests and the differences were significant between the *C. axillaris* forest and the other two forests at a given measurement season. The *C. axillaris* forest had a relatively high mean LAI value during the growing season but changed to the lowest mean LAI value during the non-growing season. The change in mean LAI values in the *C. axillaris* forest was consistent with the study of a deciduous species-dominated forest reported by Naithani et al. (2013). It has been reported that the forests consisting of different plant functional types showed different LAI values (Asner et al., 2003; Iio et al., 2014). The differences and seasonal variations of LAI values in the three forests could be attributed to floristic composition and phenological defoliation patterns of tree species especially the deciduous species. The *C. axillaris* forest consisted of 74.15% deciduous species, 25.80% evergreen broadleaved species and 0.05% evergreen coniferous species, while the proportions of deciduous species were 10.05% and 25.70% in the *P. massoniana-L. glaber* and *L. glaber-C. glauca* forests, respectively. Seasonal growth and defoliation of different functional types of species lead to the change in leaf lifespan and foliage area (Niinemets, 2010) during different seasons related to temperature and water availability, which are responsible for the unimodal pattern of seasonal variation in mean LAI values. This agrees with the results of Liu et al. (2012), where the highest LAI was found in summer (July), followed by autumn (October) and spring (April), and the lowest was found in winter (January).

4.2 Within-forest spatial heterogeneity and factors controlling LAI

Semivariograms of LAI values in the three forests were fitted with spherical, Gaussian, exponential or linear models (Table 3). Based on the fitted models, the degree of spatial autocorrelation could be evaluated. Spatial autocorrelation is weak when the determination coefficient (r^2) of the best-fitted semivariogram model is less than 0.5 (Duffera et al., 2007). The ratio $[C/(C_0+C)]$ is also used to describe the degree of spatial autocorrelation. A ratio of between 0 and 0.25 indicates a weak spatial autocorrelation, of between 0.26

and 0.75 indicates moderate autocorrelation and of more than 0.75 indicates strong autocorrelation (Lopez-Granados et al., 2004). Spatial autocorrelation of LAI in this study varied with forest and measurement season (Table 3). Strong spatial autocorrelation in LAI values at a short range measured in January in all three forests indicated the sampling distance is reasonable for LAI variables within the spatial range (Liu et al., 2008). On the contrary, weak autocorrelation indicated that more samples and smaller sampling intervals should be taken to determine spatial dependency of LAI, such as for LAI measured in April in the *P. massoniana-L. glaber* forest.

Spatial heterogeneity in LAI values was different for forest type and measurement season. Our study described spatial variations in LAI value by CV and geostatistical analysis, and the results were largely consistent with each other. In general, the CVs of LAI values in the three forest types (in particular *C. axillaris* forest) were higher for the period of leaf onset (April) and senescence (October) than for the period of leaf maturity (July) (Table 1). This reflects changes in leaves due to plant phenology and is consistent with the study of Naithani (2013) where LAI became increasingly homogenous from leaf onset to maturity, but became more heterogeneous from maturity to senescence. As a result, degree of heterogeneity in LAI value for all three forests tended to dwindle from leaf non-growing season to growing season (Fig. 2).

The complex hydrothermal environment results in complex vertical and horizontal variation in canopy layer and formed unique spatial heterogeneity in LAI values. The effects of stand characters on LAI have been examined and positive and negative effects have been reported (Tobin et al., 2006; Bequet et al., 2012; Yao et al., 2015). In our study, results from GAMs showed that forest types, stand structural diversity and stand characters affected spatial heterogeneity of LAI values significantly in the three forests. This finding that floristic composition and stand characters affected LAI values measured in July is consistent with the study of Yao et al. (2015); LAI values increased with stem number but when stem number was larger than 7, LAI values decreased with stem number mainly due to the floristic composition in these study areas. Because July is the period of leaf maturity for deciduous species and leaves fully expand in this season, LAI values tended to increase as ratio of deciduous species increased, but when the ratio was higher than ~0.7, its negative relationship with LAI probably could be explained by the strong competition among tree species, with diverse species composition and the canopy overlap among tree species (Fig. 4). Our results indicated that LAI values did not exhibit a significant relationship with stand BA, consistent with the findings of Mcdowell (2007); total LAI did not exhibit a clear pattern in relation to stand BA.

Until now, the non-growing season relationship of LAI variation with forest type and stand characters has been seldom reported. In this study, forest type, stem number, crown coverage, proportion of evergreen conifer species to total stand BA and proportion of deciduous species to total stand BA and forest type were the factors significantly affecting LAI variation in January. As January is mainly the leaf senescence period of deciduous species, LAI values in January decreased with stem number and decreased with deciduous species ratio. The relationship between LAI value and the evergreen species ratio was generally the reverse of that between LAI and the deciduous species ratio. The fact that LAI values in January decreased with increasing crown coverage when crown coverage was larger than ~200 m^2 could be explained by large crown coverage resulting in more defoliation (in particular for deciduous species) in the forest in January (Fig. 3). The proportion of deciduous species to total stand BA both significantly affected LAI variations in January and July, and the relationship between LAI and the deciduous species proportion was reversed when the ratio was smaller than 0.7 in these two seasons, which is consistent with the growth law of deciduous species. Thus, deciduous species play an important role in LAI variations across seasons. Also the seasons have a significant effect on LAI variation by affecting leaf growth. The partial effects of stem number and crown coverage on the LAI values observed in January showed these smooth functions were large at both ends of the 95% confidence interval. This was due to the small sample number in this range, and most were concentrated in the middle parts, the same as the partial effects of stem number on the LAI values observed in January (Figs 3, 4).

Although the factors selected by regression could explain a small proportion (4%) of spatial heterogeneity of LAI measured in July, the factors selected in January could explain 35% of the LAI spatial heterogeneity (Table 4). The LAI heterogeneity also could be affected by several other factors, such as the topography (Naithani et al., 2012), soil feature (Chloer et al., 2010), soil temperature (Vitasse et al., 2009; Hardwick et al., 2015), microclimate, human activity and other physicochemical properties. However, full leaf expansion of all tree species, which covers up the effect of other physicochemical properties on LAI, leads to a small difference in LAI in July. The effects of environmental factors (e.g. temperate and rainfall) on LAI in the forests at the fine scale should be taken into account in future studies.

Spatial heterogeneity of LAI in the three forests can yield some useful information for sampling strategy to accurately estimate of LAI using indirect measurement. An optimal sampling strategy should consider appropriate sampling plot size and the lowest sampling number that, as far as possible, obtains a high sampling accuracy and a low sampling error (Bequet et al., 2012). Our study found that strong spatial autocorrelations range were ~13-27 m (the minimal range was 13.80 m, and the maximal range was 27.00 m) (Table 3), indicating that the range from 13 m to 27 m might serve as the reference for sampling plot size to estimate LAI in subtropical forests. In addition, LAI heterogeneity was closely related to floristic composition and stand characters, thus stand structural variables (BA or DBH) are important for sampling strategy to measure LAI in forests (Bequet et al., 2012).

5 Conclusions

This study measured LAI in three subtropical forests using a hemispherical photography method over four seasons, and offered reliable data to analyse spatial and seasonal variations in LAI. Our results indicated that LAI differed greatly with forest type and measurement season. Seasonal variation in LAI across the three forests reflects defoliation due to plant phenology. LAI values for all three forests exhibited different spatial autocorrelation in the four seasons. A clear patch distribution pattern in LAI value was found during the non-growing seasons and this pattern gradually dwindled in the growing seasons. While stem number, crown coverage, proportion of evergreen conifer species to total stand BA, the proportion of deciduous species to total stand BA, and forest type significantly affected spatial variations in LAI values in January, stem number and proportion of deciduous species to total stand BA significantly affected spatial variations in LAI values in July. These findings supplement LAI data for global synthesis, and will provide valuable information for sampling strategies to enable more accurate estimates of LAI for simulated models of production and hydrological cycles in subtropical forests.

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Table 1 Descriptive statistical characteristics of LAI values measured from April 2014 to January 2015 in *P. massoniana-L. glaber*, *C. axillaris* and *L. glaber-C. glauca* forests (n=100).

Measurement season	Forest type	Minimum value	Maximum value	Variance coefficient (%)	*P*-value of K-S test	Data transformation
January	*P. massoniana-L. glaber*	1.29	4.03	27.5	0.021	0.275
	C. axillaris	0.53	2.38	34.0	0.260	
	L. glaber-C. glauca	0.43	6.98	40.2	0.018	0.243
April	*P. massoniana-L. glaber*	1.57	7.83	36.4	0.076	
	C. axillaris	1.34	8.33	47.0	0.047	0.535
	L. glaber-C. glauca	1.34	10.22	59.6	0.000	0.158
July	*P. massoniana-L. glaber*	1.56	8.16	38.0	0.003	0.075
	C. axillaris	1.73	8.17	37.8	0.166	
	L. glaber-C. glauca	1.68	7.58	33.1	0.010	0.170
October	*P. massoniana-L. glaber*	1.55	6.79	38.3	0.321	
	C. axillaris	0.37	6.51	44.1	0.102	
	L. glaber-C. glauca	1.49	7.88	49.3	0.000	0.212

Table 2 Average woody to total leaf ration (α) and clumping index (Ω_E) values in *P. massoniana-L. glaber*, *C. axillaris* and *L. glaber-C. glauca* forests. Values in parenthesis are the standard deviation of α and Ω_E values (n=100).

Measurement season	Forest type	Mean value		Standard deviation	
		α	Ω_E	α	Ω_E
January	*P. massoniana-L. glaber*	0.06	0.88	0.04	0.09
	C. axillaris	0.15	0.92	0.09	0.08
	L. glaber-C. glauca	0.07	0.87	0.09	0.09
April	*P. massoniana-L. glaber*	0.08	0.87	0.05	0.09
	C. axillaris	0.07	0.85	0.06	0.10
	L. glaber-C. glauca	0.15	0.86	0.07	0.09
July	*P. massoniana - L. glaber*	0.07	0.87	0.04	0.09
	C. axillaris	0.04	0.90	0.03	0.07
	L. glaber-C. glauca	0.05	0.87	0.03	0.08
October	*P. massoniana-L. glaber*	0.09	0.85	0.10	0.08
	C. axillaris	0.14	0.87	0.14	0.10
	L. glaber-C. glauca	0.09	0.84	0.08	0.09

Table 3 Semivariogram theoretical models and fitted parameters for LAI values in *P. massoniana-L. glaber* (90 m × 190 m irregular shape), *C. axillaris* (100 m × 100 m) and *L. glaber-C. glauca* (100 m × 100 m) forests.

Measurement season	Forest type	Model	Nugget (C_0)	Sill (C_0+C)	$C/(C_0+C)$	Range (A_0/m)	r^2	Residual sum of squares (RSS)
January	*P. massoniana-L. glaber*	Exponential	0.0068	0.0614	0.889	27.00	0.607	9.762×10^{-5}
	C. axillaris	Exponential	0.0030	0.1820	0.984	13.80	0.504	1.219×10^{-4}
	L. glaber-C. glauca	Gaussian	0.0029	0.1178	0.975	15.42	0.888	3.468×10^{-5}
April	*P. massoniana-L. glaber*	Exponential	0.1220	0.7670	0.841	17.70	0.229	0.017
	C. axillaris	Linear	0.1760	0.1760	0.000	52.96	0.189	1.762×10^{-4}
	L. glaber-C. glauca	Exponential	0.0008	0.0152	0.951	26.40	0.978	2.290×10^{-7}
July	*P. massoniana-L. glaber*	Linear	0.0843	0.0843	0.000	92.69	0.074	1.383×10^{-4}
	C. axillaris	Exponential	0.1460	0.9340	0.844	17.70	0.258	0.017
	L. glaber-C. glauca	Exponential	0.0065	0.0684	0.905	22.80	0.951	5.781×10^{-6}
October	*P. massoniana-L. glaber*	Exponential	0.1620	1.6310	0.901	11.70	0.173	0.017
	C. axillaris	Spherical	0.0050	0.5830	0.991	11.90	0.000	1.870×10^{-3}
	L. glaber-C. glauca	Exponential	0.0005	0.0125	0.960	21.90	0.894	4.444×10^{-7}

Table 4 Estimated coefficients of the generalised additive models (GAMs) for the factors with effects on LAI values measured in *P. massoniana-L. glaber*, *C. axillaris* and *L. glaber-C. glauca* forests.

Measurement season	Parameter	*F*-value	*P*-value	r^2	AIC
January	s (Stem number, 2)	16.716	<0.0001***	0.3481	655.91
	s (Crown coverage, 2)	4.545	0.034*		
	s (PESB, 2)	26.105	<0.0001***		
	s (PDSB, 2)	27.281	<0.0001***		
	factor(Forest types)	39.847	<0.0001***		
July	s (Stem number, 2)	5.027	0.026*	0.040	880.93
	s (PDSB, 2)	7.115	0.008**		

The significance of the regressions (*P*) are *, **, *** for $P<0.05$, 0.01, and 0.001, respectively

Figure captions

Fig. 01 Seasonal variation in mean LAI value (with standard deviation) in *P. massoniana*-*L. glaber*, *C. axillaris* and *L. glaber*-*C. glauca* forests. The different letters by values indicate significant differences (P<0.05) among measurement seasons in a given forest.

Fig. 02 Spatial heterogeneity map of LAI values interpolated through ordinary Kriging method for *P. massoniana*-*L. glaber*, *C. axillaris* and *L. glaber*-*C. glauca* forests.

Fig. 03 Partial effects of stem number, crown coverage (m^2), the proportion of evergreen conifer species to total stand BA (PESB), the proportion of deciduous species to total stand BA (PDSB) and forest types (calculated for overstorey trees with height larger than average stand height) on the LAI values observed in January in *P. massoniana*-*L. glaber*, *C. axillaris* and *L. glaber*-*C. glauca* forests.

Fig. 04 Partial effects of stem number and the proportion of deciduous species to total stand BA (PDSB) (calculated for overstorey trees with height larger than average stand height) on the LAI values observed in July in *P. massoniana*-*L. glaber*, *C. axillaris* and *L. glaber*-*C. glauca* forests.

Figure 01

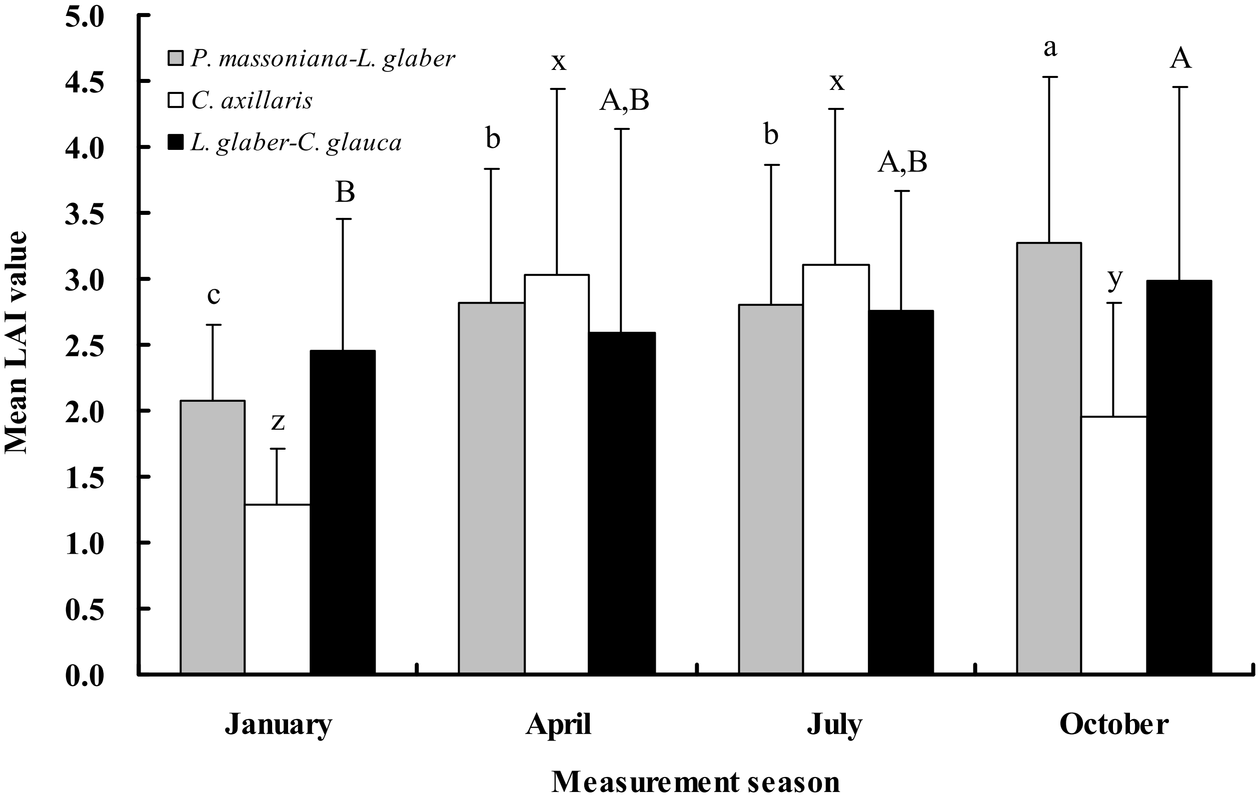
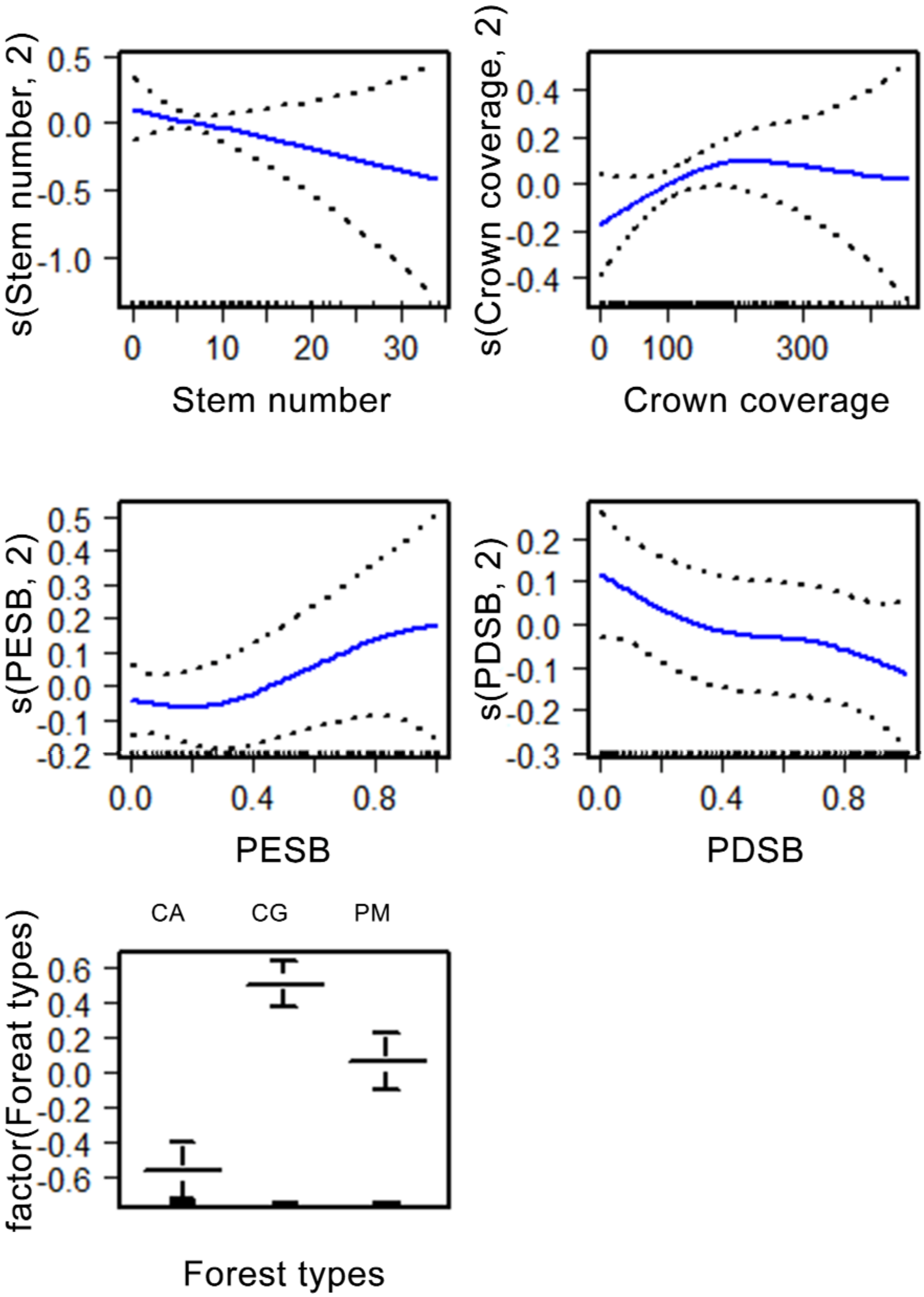

5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Mean LAI value
P. massoniana-L. glaber
C. axillaris
L. glaber-C. glauca
c
z
B
b
x
A,B
b
x
A,B
a
y
A
January
April
July
October
Measurement season

Figure 02

Figure 03


s(Stem number, 2)
0.5
0.0
-0.5
-1.0
0
10
20
30
Stem number
s(Crown coverage, 2)
0.4
0.2
0.0
-0.2
-0.4
0
100
300
Crown coverage
s(PESB, 2)
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
0.0
0.4
0.8
PESB
s(PDSB, 2)
0.2
0.1
0.0
-0.1
-0.2
-0.3
0.0
0.4
0.8
PDSB
CA
CG
PM
factor(Foreat types)
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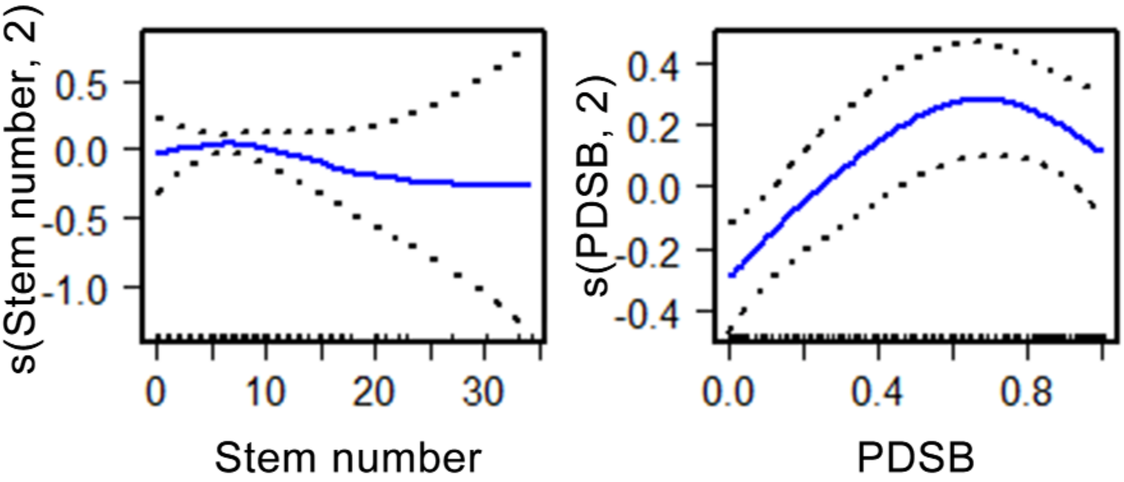
0.4
0.2
0.0
-0.2
-0.4
-0.6
Forest types

Figure 04


s(Stem number, 2)
0.5
0.0
-0.5
-1.0
0
10
20
30
Stem number
s(PDSB, 2)
0.4
0.2
0.0
-0.2
-0.4
0.0
0.4
0.8
PDSB