Thai J. For. 34 (3) : 69-82 (2015)

Original article

Spatial Biomass Variation, Biomass Dynamics and Species Diversity in Relation to Topographic Factors of Lower Tropical Montane Forest

Witchaphart Sungpalee[1*]
Kriangsak Sri-ngernyuang[3]
Mamoru Kanzaki[4]
Akira Itoh[2]
Satoshi Nanami[2]

[1]Faculty of Agricultural Production, Maejo University, Chiang Mai 50290, Thailand,
[2]Graduate School of Science, Osaka City University, Osaka 558-8585, Japan,
[3]Faculty of Architecture and Environmental design, Maejo University, Chiang Mai 50290, Thailand,
[4]Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan
[*]Corresponding Author, E-mail: sci.ocu@gmail.com

Received: May 25, 2015 Accepted: Jul 7, 2015

ABSTRACT

Forest biomass and biomass dynamics were used in this study of forest structure and environmental assessment as one of the most important criteria in order to understand forest ecosystem status and forest equilibrium. This research approach evaluated the effects of topographic indices consisting of elevation, slope aspect, slope inclination and index of convexity (IC) on the live-tree, aboveground biomass (AGB), biomass dynamics and species diversity of 5-year, inter-census intervals in a lower montane forest of a 15 ha forest dynamics plot at Doi Inthanon. Spatial variation of biomass dynamics was drawn up using 20 x 20 m subplots (n=375) and then estimating the biomass and biomass dynamics consisting of the AGB increment, AGB of ingrowth, AGB loss and AGB change of each subplot. Differences in biomass, biomass dynamics and species diversity among topography classes were analyzed using ANOVA. The results of this research revealed that elevation had a significant effect on the mean AGB, mean AGB of recruitment rate and mean AGB of increment rate. Slope aspect had a significant effect on the mean AGB recruitment rate and mean AGB loss rate. Slope inclination only had a significant effect on the AGB recruitment rate while IC had a significant effect on the mean AGB recruitment rate and mean AGB of increment rate. Changes in the species diversity index $(\Delta H')$ were significantly different based on topographic variables except for the slope aspect. The results suggested that the evaluation of forest biomass, biomass dynamics and changes in species diversity of the tropical lower montane forest should be based on data from various topographic sites. The relationship between the mean AGB, biomass dynamics, species diversity and topography may be mediated by differences in the stand turnover rates, which must be related to topography.

Keywords: forest biomass, forest dynamic, tropical lower montane forest, topography index, species diversity

INTRODUCTION

Since tropical forests hold a large stock of carbon, they play a major role in the global carbon cycle (Houghton *et al.,* 2001). Estimation of the biomass and carbon stock of tropical forests gained importance for the Climate Convention of the United Nations and the Kyoto Protocol. Tropical forest biomass estimation is a useful way to assess the changes in forest carbon stocks and emissions to the atmosphere that are caused by land use change and forest degradation (Fearnside, 1996; Houghton, 2005; Malhi and Grace, 2000). Biomass varies across environmental gradients of soils and topography (Clark and Clark, 2000; De Castilho *et al.*, 2006; Laurnce *et al.*, 1999; Luizao *et al.*, 2004; Valencia *et al.*, 2009). It is also known that biomass is related to differences in regimes of natural disturbance (Houghton, 2005). Therefore, spatial variation in biomass and its dynamics should be related to environmental gradients such as topography.

Topography has been known as an easily measured deputation for environmental resource availability and spatial distribution in plant species alignment (Bohlman *et al.*, 2008). Topography is closely interrelated to microhabitat gradients of soil moisture and soil fertility at the local scale (Balvanera *et al.*, 2011), with the valley being moister and more nutrient rich than sites near ridge tops (Gibbons and Newbery, 2003). Also steeper areas have higher water and nutrient output and thus generally have less water in the soil and less nutrients available than flat formed areas (Balvanera *et al.*, 2011). Given the significant relationships between topography and soil and/or water resource availability, it is not surprising that many researchers have found evidence of habitat associations of plant species along topographical gradients (Punchi-Manage *et al.*, 2013). However, Bellingham and Tanner (2000) found that there was not always an influence of topography on tree growth, mortality, and recruitment in a tropical montane forest in Jamaica. Furthermore, the results of a previous study in a 20 ha forest dynamics plot in Xishuangbanna, southern Yunnan, found that the species composition and diversity changed significantly along the topographical gradient (Liu *et al*., 2014).

Studies reporting the spatial variation of biomass, biomass dynamics and species diversity in Thailand are scarce and it is a challenge to understand the variation and state of forest in terms of any topographical effect. The specific objectives of this paper were: (1) to investigate the forest structure in term of biomass, biomass dynamics and species diversity at the spatial level and (2) to examine the effect of topography on the total aboveground biomass (AGB), biomass dynamics and species diversity in a 15 ha permanent plot.

MATERIALS AND METHODS

Study site

The study was conducted in a 15 ha forest dynamics plot, which was representative of the tropical, lower motane forests in the Doi Inthanon National Park, Chiang Mai province, Thailand. The aboveground biomass of each tree was estimated for the first tree census in 1997 and the second tree census in 2003. Trees with apparently strange sizes (such as, a mistake in measurement or typing error) were omitted from the biomass estimation because their inclusion may have produced large errors especially in the analysis of dynamics. In total, 254 individuals were omitted from the calculations (0.26% of all individuals). As a result, 88,904 trees of 165 species, in 110 genera and 55 families were used for the first census, and 96,627 trees of 156 species, 104 genera and 52 families for the second census. During the first and second censuses, 10,258 trees died and 17,981 trees were recruited.

Biomass estimation

We first estimated tree height (H) in meters from the stem diameter at breast height (D) in centimeters using Equation 1, which was obtained from 70 sample trees in the 15 ha plot consisting of various species.

$$\frac{1}{H}=\frac{1}{1.283D}+\frac{1}{56.626} \qquad (1)$$

In the method, Equation 2 was obtained by harvesting data from various moist tropical forests (Chave *et al.,* 2005). This equation estimated only total biomass (W_T) or AGB using diameter (D), total tree height (H) and species-specific wood density (ρ):

$$AGB = 0.0509\,\rho\,D^2 H\,, \qquad (2)$$

Species-specific wood densities were obtained from wood core samples of trees in the 15 ha plot (Sungpalee *et al*., 2009). If the species-specific mean was not available, we used a genus mean (Chave *et al.*, 2006; Slik, 2006; Sungpalee *et al*., 2009), and if the genus mean was not available, then the mean of all species (0.549 g cm^{-3}) was used.

Spatial variation of total above ground biomass

In order to analyze fine-scale variation in the total above ground biomass and biomass dynamics, we divided the 15 ha plot into 20 × 20 m subplots (n=375) and estimated biomass at the first (1998) and second (2003) censuses for each subplot. Following Chave *et al.*, (2003), we calculated the biomass increment, biomass of ingrowth (recruited trees), biomass loss (dead trees), biomass change and species diversity for each subplot.

The biomass increment of a surviving tree between the first and second censuses [$\Delta Biomass_{(Surviving)}$] (Mg) was defined as the increment in terms of biomass for a surviving tree by growth and calculated using Equation 3:

$$\Delta Biomass_{(Surviving)} = Biomass(t2) - Biomass(t1), \quad (3)$$

where, *Biomass*(*t1*) and *Biomass*(*t2*) is the biomass at the first and second census of the surviving tree, respectively. Then, the biomass increment rate (Mg ha^{-1} y^{-1}) in a subplot was calculated using Equation 4:

Biomass increment rate

$$= \left[\sum_i \frac{\Delta Biomass_{(Surviving)i}}{\Delta t_i} + \sum_j \frac{\Delta Biomass_{(Ingrowth)j}}{\Delta t_j}\right] \Big/ A\ , \quad (4)$$

where $\Delta Biomass_{(Surviving)\mathrm{i}}$ is the biomass increment of the *i*th surviving trees in the subplot, $\Delta Biomass_{(Ingrhowth)j}$ is the biomass of the jth ingrowth or recruited tree at the second census, $\mathrm{D}t_i$ and $\mathrm{D}t_j$ are the census interval of the ith and jth trees in years, respectively, and A is the total area of the subplot (0.04 ha).

The biomass loss rate (Mg ha^{-1} y^{-1}) for a subplot was calculated using Equation 5:

$$Biomass\ loss\ rate = \frac{1}{AT}\sum_{i=1}^{k} Biomass_{(dead)i}\,, \quad (5)$$

where $Biomass_{(dead)i}$ is the biomass at the first census for the ith tree that died between the first and second censuses in the subplot, k is the total number of dead trees, T is the average census period of the dead trees and A is the area of a subplot. The biomass change of a subplot (Mg ha^{-1} y^{-1}) was calculated as increment minus loss.

Species diversity in each subplot, was estimated using the Shannon diversity index (H') with a natural logarithmic base formula (Kent and Coker, 1992). Then, differences in the diversity index inter-census were calculated as the index of the first minus the second census and used as absolute values.

Spatial variation of biomass dynamics, species diversity and its relation to topography

Differences in biomass, biomass dynamics and species diversity among different topographic variables were examined. For each topographic variable (relative elevation, slope aspect, slope inclination and index of convexity), the 20 × 20 m subplots were grouped into three classes based on the values of the variable. Then, differences in the mean values of the total biomass or biomass dynamics (increment, ingrowth, loss and change) were analyzed using ANOVA. All statistical analyses were undertaken using the R 3.1.1 software (The R Development Core Team, http://www.r-project.org).

RESULTS AND DISCUSSION

Biomass and biomass dynamics

The overall total aboveground biomass (AGB) in the 15 ha plot increased from the first census (372.70 Mg ha^{-1}) to the second census (379.65 Mg ha^{-1}). The largest biomass at the first and the second tree census was in the diameter class 51–61 cm class (55.24 and 54.18 Mg ha^{-1}, respectively, Table 1). Within the census interval, the live trees biomass increment was estimated as 6.129 Mg ha^{-1} year^{-1} and the biomass loss by dead trees during the census interval was estimated as 4.235 Mg ha^{-1} year^{-1}. The largest positive biomass change rate was found in the diameter class 21–31 cm (0.597 Mg ha^{-1} year^{-1}) and the largest negative biomass change rate was found in the diameter class 131–141 cm (–0.649 Mg ha^{-1} year^{-1}) and the overall biomass change rate in the plot was estimated as 2.018 Mg ha^{-1} year^{-1}.

Estimation in this plot had a larger AGB than the temporary sample plot of deciduous dipterocarp forest at Khao Wong community forest, Chaiyaphum province which was estimated as 186.43 Mg ha^{-1} (dbh ≥ 4.5 cm) in a recent study by Ounkerd *et al.* (2015). In order to compare the current results with other large-scale plots, the biomass increment rate during the study period (1997–2003) was determined as 6.258 Mg ha^{-1}y^{-1}, the biomass recruitment rate was 0.04 Mg ha^{-1}y^{-1}, the biomass loss rate was 4.240 Mg ha^{-1}y^{-1} and the net biomass change was +2.018 Mg ha^{-1}y^{-1} in the Doi Inthanon forest. Table 2 compares these values to those in a recent study by

Chave *et al*. (2008) in several large-scale, tropical forest plots whose dataset included over 5 million stem-diameter measurements taken between 1985 and 2005 according to a standard census protocol (Table 2).

Based on a within-country comparison, Doi Inthanon had a truly larger AGB than tropical, dry forest in Huai Kha Khang. The AGB of the Doi Inthanon forest was estimated to be twice as high as a tropical, montane cloud forest in La Planada in Columbia, larger than in some lowland rain forests, such as Yasuni in Ecuador, Palanan in the Philippines and BCI in Panama, Pasoh in Peninsular Malaysia and Sinharaja in Sri Lanka, and smaller than other lowland rain forests, such as, Edoro and Lenda in the Republic of Congo and Lambir in Sarawak, Malaysia.

Table 1 Above ground biomass (AGB) for various diameter classes of the first and the second tree census. Biomass increment, biomass loss and biomass change rates between the first and second censuses are also shown. See text for definition of biomass loss and biomass change rates.

Diameter class (cm)	AGB at the first census (Mg ha^{-1})	AGB at the second census (Mg ha^{-1})	Increment (Mg ha^{-1}year^{-1})	Loss (Mg ha^{-1}year^{-1})	Change (Mg ha^{-1}year^{-1})
1 - 11	10.76	11.25	0.394	0.139	0.365
11 - 21	25.73	25.95	0.730	0.257	0.473
21 - 31	40.61	41.84	0.931	0.334	0.597
31 - 41	47.78	48.51	1.000	0.491	0.509
41 - 51	51.99	50.25	0.790	0.605	0.185
51 - 61	55.24	54.18	0.713	0.609	0.104
61 - 71	39.87	43.16	0.590	0.614	–0.025
71 - 81	20.33	23.51	0.285	0.264	0.020
81 - 91	14.89	13.96	0.090	0.061	0.029
91 - 101	14.22	12.96	0.160	-	0.160
101 - 111	7.92	12.01	0.106	0.135	–0.028
111 - 121	8.44	6.17	0.042	-	0.042
121 - 131	12.19	12.94	0.114	-	0.114
131 - 141	6.67	4.99	0.077	0.726	–0.649
141 - 151	4.54	6.39	0.056	-	0.056
151 - 161	6.97	7.03	0.051	-	0.051
161 - 171	-	-	-	-	-
171 - 181	4.54	4.54	0.001		0.001
	372.70	379.65	6.129	4.235	2.018

Table 2 Stocks and changes in total aboveground biomass (AGB) and biomass dynamics for eleven undisturbed tropical forest plots.

Site	AGB Mg ha^{-1}	Growth rate in Mg ha^{-1}y^{-1}	Recruitment in Mg ha^{-1}y^{-1}	Loss in Mg ha^{-1}y^{-1}	Net Biomass Change in Mg ha^{-1}y^{-1}
BCI	306.5	5.01	0.033	5.29	–0.25
Edoro	397.7	6.65	0.015	6.42	0.24
Lenda	541.6	5.78	0.016	4.36	1.44
HKK	211.2	3.56	0.058	3.85	–0.24
La Planada	177.6	4.75	0.091	3.57	1.27
Lambir	497.2	7.13	0.041	6.14	1.03
Palanan	290.1	4.8	0.102	4.69	0.21
Pasoh	339.8	6.96	0.024	5.37	1.61
Sinharaja	357.9	7.4	0.028	8.41	–0.98
Yasuni	282.4	6.76	0.050	6.22	0.38
Doi Inthanon*	372.7	6.24	0.018	4.24	2.018

Note: * Current study

Biomass dynamics in relation to topography

The mean AGB was significantly different among classes based on the ANOVA (Table 3), showing a significantly larger value for the middle elevation (mean ± SE, 416.16 ± 19.83 Mg ha^{-1}) than at the low and high elevation (349.52 ± 16.73 and 352.40 ± 14.67 Mg ha^{-1}, respectively). The mean biomass was not significantly different among slope aspect, slope inclination and index of convexity.

At the spatial level of the biomass dynamics of the inter-census interval, the aboveground biomass recruitment rate was highly significantly different among the classes of all topographic variables (relative elevation, slope inclination, aspect and convexity). The mean AGB recruitment rate at the high elevation (0.043 ± 0.005 Mg ha^{-1}y^{-1}) was larger than for the middle (0.022 ± 0.002 Mg ha^{-1}y^{-1}) and low elevation (0.015 ± 0.001 Mg ha^{-1}y^{-1}) sites, with significantly larger values on the eastern slope aspect, moderate slope inclination and rectilinear area.

The mean AGB of the surviving trees was greatest at high elevation (7.076 ± 0.241 Mg ha^{-1}y^{-1}) than at middle (5.319 ± 0.261 Mg ha^{-1}y^{-1}) and low elevation (5.991 ± 0.320 Mg ha^{-1}y^{-1}), and the mean biomass was significantly different among the convexity classes, being significantly larger for the convex (7.075 ± 0.258 Mg ha^{-1}y^{-1}) and rectilinear (6.388 ± 0.269 Mg ha^{-1}y^{-1}) than for the concave class (4.935 ± 0.289 Mg ha^{-1}y^{-1}). The mean biomass loss rate due to dead trees was significantly different among the slope aspect classes, with a significantly larger values for the east class (7.211 ± 1.777 Mg ha^{-1}y^{-1}). The net biomass change was significantly different among the slope aspect classes, with a significantly larger positive value on the west slope aspect (3.889

Table 3 Results of one-way ANOVA for mean total aboveground biomass (AGB), mean AGB recruitment rates, mean AGB increment rates, mean AGB loss rates and mean AGB change rates among three classes of four topography variables. Different letters indicate significantly different values among three classes of each topography variable using Tukey's multiple comparison procedure.

Topography index	**Gradient**	**AGB**	**AGB Recruitment**	**AGB Increment**	**AGB loss**	**AGB Change**
		(Mg ha^{-1})	(Mg ha^{-1}year^{-1})	(Mg ha^{-1}year^{-1})	(Mg ha^{-1}year^{-1})	(Mg ha^{-1}year^{-1})
	High	352.40 ±14.67b	0.043 ±0.005a	7.076 ±0.241a	4.889 ±1.137	2.230 ±1.164
Elevation	Middle	416.16 ±19.83a	0.022 ±0.002b	5.319 ±0.261b	4.843 ±1.512	0.498 ±1.526
	low	349.52 ±16.73b	0.015 ±0.001b	5.991 ±0.320b	2.973 ±0.722	3.034 ±0.817
	F-test	4.791**	19.88***	10.3***	0.874^{ns}	1.158 ^{ns}
	East	396.07 ±19.89	0.043 ±0.005a	6.415 ±0.318	7.211 ±1.777a	-0.753 ±1.814b
Slope aspect	North-South	352.96 ±16.73	0.020 ±0.001b	5.955 ±0.263	3.349 ±0.745b	2.626 ±0.789ab
	West	369.06 ±15.11	0.018 ±0.001b	6.016 ±0.264	2.145 ±0.542b	3.889 ±0.611a
	F-test	1.575 ^{ns}	18.33***	0.779 ^{ns}	5.243***	4.032*
	steep	368.50 ±15.09	0.018 ±0.001b	6.074 ±0.268	3.046 ±0.583	3.046 ±0.673
Slope inclination	Moderate	402.69 ±19.56	0.041 ±0.005a	6.300 ±0.286	6.579 ±1.798	-0.238 ±1.817
	Gentle	346.90 ±16.97	0.022 ±0.002b	6.012 ±0.296	3.080 ±0.693	2.954 ±0.753
	F-test	2.643 ^{ns}	14.55***	0.285 ^{ns}	3.05*	2.428 ^{ns}
	Convex	399.16 ±16.87	0.025 ±0.003b	7.075 ±0.258a	5.437 ±1.714	1.663 ±1.742
IC	Rectilinear	371.50 ±17.01	0.041 ±0.005a	6.388 ±0.269a	4.998 ±0.924	1.431 ±0.976
	Concave	347.62 ±18.06	0.015 ±0.001b	4.935 ±0.289b	2.291 ±0.536	2.659 ±0.625
	F-test	2.225 ^{ns}	16.1***	16.19***	2.147 ^{ns}	0.293 ^{ns}

Remarks: * $P<0.05$; ** $P<0.01$; *** $P<0.001$; ns= Not significantly different

± 0.611 Mg $ha^{-1}y^{-1}$) and a negative value on the east slope aspect (–0.753 ± 1.814 Mg $ha^{-1}y^{-1}$).

Based on the results, the largest total AGB at moderate elevation in the 15 ha permanent plot was mostly due to the abundance of larger trees (DBH > 60 cm) with high species wood density (> 0.615 g cm^{-3}), such as *Betula alnoides*, *Chionanthus ramiflorus*, *Lithocarpus aggregatus*, *L. echinops*, *L. vestitus*, *Persea duthiei*, *Persea. sp.*, *Quercus brevicalyx*, *Q. eumorpha*, *Syzygium angkae* and *S. tetragonum* (Sungpalee *et al.*, 2009). However, huge specimens (DBH > 100 cm) of *Mastixia euonymoides* were also abundant at the moderate elevation, though this species had relatively light wood density. Brown and Lugo (1992) and Clark and Clark (1996) pointed out that even a few large individuals can account for and represent a large portion of a plot's total AGB. Moderate slope inclination produced a larger total AGB. Slope was negatively associated with the total AGB estimates of emergent trees (DBH≥ 70 cm) in Manaus, Central Amazonas, but was positively associated with understory and subcanopy trees (1cm ≤ DBH < 10 cm) (De Castilho *et al*., 2006).

The relationship between the spatial distribution of AGB and topography in this study contrasted with that in the Yasuni forest in Ecuador where on a 25 ha plot, ridges (higher elevation sites) had larger biomass density than valleys (lower elevation sites) (Valencia *et al.*, 2009). These differences were probably due to the differences in the relationship between topography and mean wood density at a very local scale, which was related to the local species composition of high and low wood densities. The mean wood density was larger on the ridges in Yasuni, while it was smaller on the ridges in Doi Inthanon. This was probably due to the effect of strong wind on the stand dynamics at Doi Inthanon, as was discussed by Noguchi *et al*. (2007). The ridges in Doi Inthanon are subjected to strong winds and are more favorable to species with light wood, which can grow more rapidly than in the valleys. A similar trend in stand dynamics was reported in a montane forest of north Queensland, Australia; trees with DHB ≥ 30 cm had a higher turnover rate and growth on the ridge top (Herwitz and Young, 1994). On the other hand, in Yasuni, the bottom valley had higher growth and mortality rates than on the ridge top (Valencia *et al.*, 2009).

According to Laurance *et al*. (1999), slope inclination had a negative effect on AGB in central Amazonian forests. Slope inclination had an important effect on soil physical and chemical properties; flatter areas had a high concentration of clay, silt, organic C, total N, total exchangeable base, K^+, Mg^{2+}, Fe and Mn^{2+}, while steeper areas had more sand and high aluminum saturation. AGB was correlated positively with total N, total exchangeable base, K^+, Mg^{2+}, clay and organic C, and negatively associated with Zn^+, aluminum saturation and fine sand. Therefore, flatter areas had larger AGB than steeper ones (Laurance *et al*., 1999). The largest biomass on moderate elevation and inclination in this study plot might be not only because of the abundance of larger trees but also because these topographic conditions may induce more litter and hence richer soil nutrients (De Castilho *et al*., 2006). There is some evidence that topography influences nitrogen cycling (Zak *et al*., 1991). A significant difference was reported between soil total nitrogen and nitrogen leaf concentration and the topographic position in the central Amazon (Luizao *et al*., 2004) due to the water potential gradient along slopes (Baker *et al.*, 1988; Ochiai *et al.*, 1994). On the other hand, Gale and Barfod (1999) reported that slope position affected the mortality of trees and a palm (*Iriartea deltoidea*). The proportion of trees that died standing increased moving from valleys to ridges and plateaus. The proportion of uprooted trees declined from the valleys up to the ridges. The proportion was three times larger in the valleys than on the ridges. Therefore, stands on ridges were more dynamic than those in the valleys.

Change in species diversity at spatial level

On average, species diversity from each subplot was 3.1359 from the first census and 3.1738 from the second census. The spatial distribution of change in species diversity ($\mathrm{D}H'$) is illustrated in Figure 1. Based on the analysis, there was a significantly different ($F= 10.1$, $P<0.001$) change in species diversity inter-census between high and low elevation. Slope aspect had no effect on species diversity, while gentle slopes had significantly higher changes in species diversity than moderate and steep slopes (Table 4). Considering microsite as an index of convexity, the ANOVA results showed significantly different changes in diversity, with convex having higher change in diversity than concave.

In this study, a similar relation between wood density and topography was found with wood densities being larger on windward, western slopes than on leeward, eastern ones and this was supported by the higher mortality rates and light wood density observed on the higher-elevation sites as previous studied by Sungpalee *et al*. (2009). Severe disturbance by wind on the ridges may lead to low stand-level wood densities because fast-growing, light-wooded trees have advantages on highly disturbed sites (Suzuki, 1999). Although we have discussed the results of spatial distribution only from the viewpoint of wind stress, the observed associations between topography and biomass dynamics, species diversity and partly wood density might be explained by other environmental factors related to topography. For example, we would expect a similar relationship if soils on western slopes were less fertile than those on eastern slopes. Low soil fertility slows tree growth and thus may favor better-surviving, shade-tolerant species, which have relatively high-density wood (Muller-Landau, 2004). Furthermore, the results of a study in a 20 ha forest dynamics plot in Xishuangbanna, southern Yunnan, found that species composition and diversity changed significantly along the topographical gradient (Liu *et al*., 2014). However, it is difficult to compare the effect of topography on diversity in Xishuangbanna because that study did not emphasize the dynamics of species diversity as in the current study. At present, however, we cannot evaluate this possibility because we do not have detailed soil distribution data although there are no field observations suggesting that soils on west and east slopes differed significantly or that soils on high, middle and low elevation were different.

Table 4 Results of one-way ANOVA for change in species diversity index $(\Delta H')$ among three classes of four topography variables. Different letters indicate significantly different values among three classes of each topography variable using Tukey's multiple comparison procedure.

Topography index	**Gradient**	$\Delta H'$		
		Max	**Min**	**Mean ± SE**
Elevation	High	0.113	–0.461	–0.049 ± 0.008b
	Middle	0.143	–0.141	0.003 ± 0.004a
	low	0.206	–0.986	–0.066 ± 0.017b
	F-test	–	–	10.1***
Slope aspect	East	0.206	–0.485	–0.052 ± 0.012
	North-South	0.112	–0.984	–0.039 ± 0.011
	West	0.143	–0.986	–0.022 ± 0.011
	F-test	–	–	1.62^{ns}
Slope inclination	steep	0.143	–0.230	0.001 ± 0.005a
	Moderate	0.113	–0.575	–0.033 ± 0.008a
	Gentle	0.206	–0.986	–0.082 ± 0.016b
	F-test	–	–	13.59***
IC	Convex	0.115	–0.986	–0.061 ± 0.017b
	Rectilinear	0.206	–0.461	–0.036 ± 0.008ab
	Concave	0.127	–0.166	–0.015 ± 0.058a
	F-test	–	–	3.774*

Remarks: * $P<0.05$; ** $P<0.01$; *** $P<0.001$; ns= Not significantly different

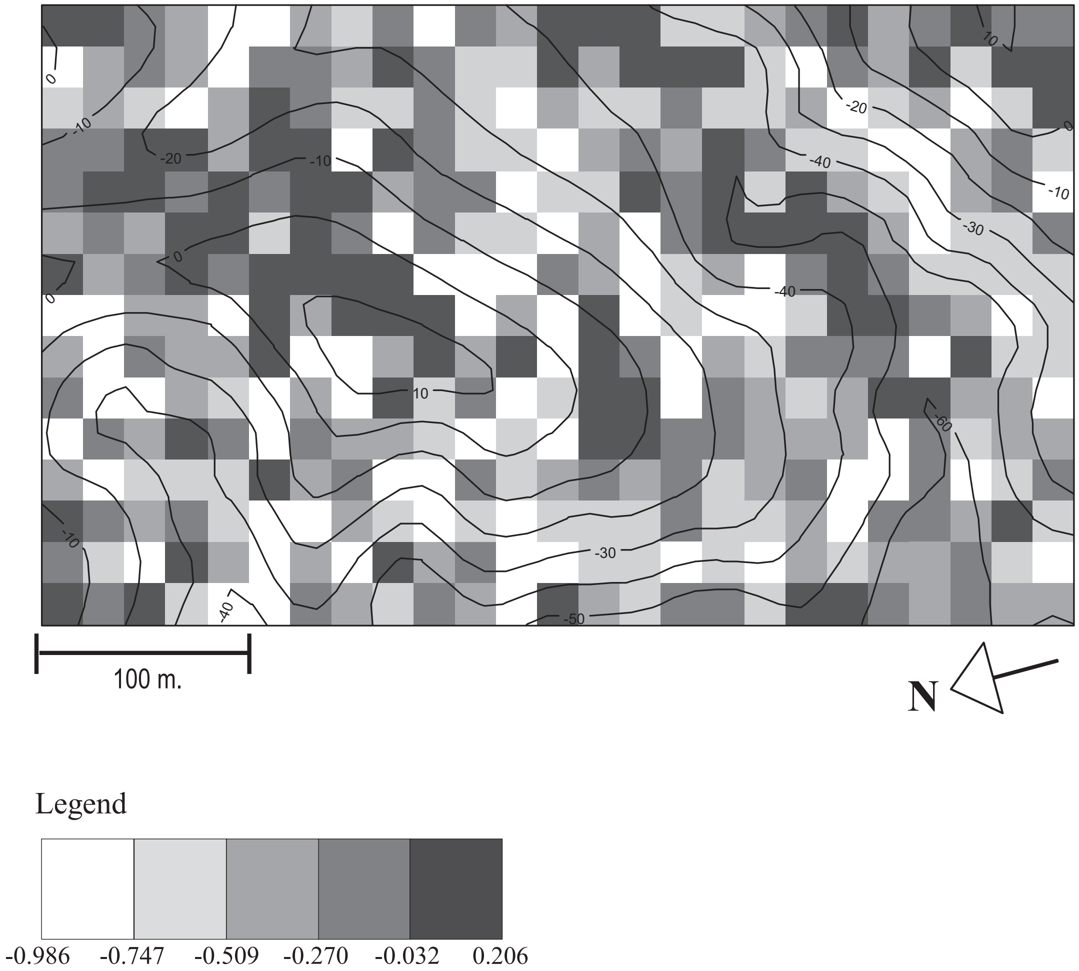

Figure 1 Spatial distribution of change in species diversity $\left(\Delta H'\right)$ in a 15 ha plot in Doi Inthanon National Park, northern Thailand. Shaded squares indicate $\Delta H'$ value of each 20×20 m. area. Different $\Delta H'$ values are indicated by different shades as shown. Topographic contours are shown at a 10 m interval..

CONCLUSION

This study showed that fine-scale, spatial distribution of AGB and species diversity are related to topography. Mean AGB and the forest change in dynamics based on AGB growth, AGB increment, AGB recruitment, AGB loss and species diversity showed statistically strongly significant differences among the topographic classes, indicating that biomass estimation and the biomass dynamics monitoring of the tropical lower montane forest should be based on data from various topographic sites. The relationship between AGB, species diversity and topography may be mediated by differences in stand turnover rates, which must be related to topography. However, more field data are necessary to be able to draw a more general conclusion on the relationships in various tropical forests.

ACKNOWLEDGEMENTS

We wish to thank the superintendent of Doi Inthanon and forest officers for their support. This study was partly supported by the Japan Society for the Promotion of Science: Grant-in-aid 20405008.

REFERENCES

Baker, P., P. E. Rabenold, J. R. Idol and A. P. Smith. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. **Journal of Tropical Ecology** 4 (2): 173-184.

Balvanera, P., S. Quijas and A. Perez-Jimenez. 2011. Distribution of tropical dry forest trees along a mesoscale water availability gradient. **Biotropica** 43 (4): 414-422.

Bellingham, P. J. and E. V. J. Tanner. 2000. The influence of topography on tree growth, mortality, and recruitment in a tropical montane forest. **Biotropica** 32 (3): 378-384.

Bohlman, S. A., W. F. Laurance, S. G. Laurance, H. E. Nascimento, P. M. Fearnside and A. Andrade. 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree community. **Journal of Vegetation Science** 19 (6): 863-874.

Brown, S. and A. E., Lugo. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. **Interciencia** 17 (1): 8-18.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Fölster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riéra and T. Yamakura. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. **Oecologia** 145 (1): 87-99.

Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easedale, H. Ter Steege and C. O. Webb. 2006. Regional and phylogenetic variation of wood density across 2,456 neotropical tree species. **Ecological Application** 16 (6): 2356-2367.

Chave, J., R. Condit, H. C. Muller-Landau, S. C. Thomas, P. S. Ashton, S. Bunyavejchewin, L. L. Co, H. S. Dattaraja, S. J. Davies, S. Esufali, C. E. N. Ewango, K. J. Feeley, R. B. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, T. B. Hart, C. Hernandez, S. P. Hubbell, A. Itoh, S. Kiratiprayoon, J. V. Lafrankie, S. Loo De Lao, J. R. Makana, M. N. S. Noor, A. R. Kassim, C. Samper, R. Sukumar, H. S. Suresh, S. Tan, J. Thompson, M. D. C. Tongco, R. Valencia, M. Vallejo, G. Villa, T. Yamakura, J. K. Zimmerman and E. C. Losos. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. **Plos Biology** 6 (3): 455-462.

Chave, J., R. Condit, S. Lao, J. P. Caspersen, R. B. Foster and S. P. Hubbell. 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. **Journal of Ecology** 91 (2): 240-252.

Clark, D. B. and D. A. Clark. 1996. Abundance, growth and mortality of very large tree in neotropical lowland rain forest. **Forest Ecology and Management** 80 (1-3): 235-244.

_____. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. **Forest Ecology and Management** 137 (1-3): 185-198.

De Castilho, C. V., W. E. Magnusson, N. O. De Araujo, R. C. C. Luizao, F. J. Luizao, A. P. Lima and N. Higuchi. 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. **Forest Ecology and Management** 234 (1-3): 85-96.

Fearnside, P. M. 1996. Amazonian deforestation and global warming: carbon stocks in vegetation replacing Brazil's Amazon forests. **Forest Ecology and Management** 80 (1-3): 21-34.

Gale, N. and A.S. Barfod. 1999. Canopy tree mode of death in a western Ecuadorian rain forest. **Journal of Tropical Ecology** 15 (4): 415-436.

Gibbons, J. M. and D. M. Newbery. 2003. Drought avoidance and the effect of local topography on trees in the understory of Bornean lowland rain forest. **Plant Ecology** 164 (1): 1-18.

Herwitz, S. R. and S. S. Young. 1994. Mortality, recruitment, and growth rates of montane tropical rain forest canopy trees on Mount Bellenden-Ker, Northeast Queensland, Australia. **Biotropica** 26 (4): 350-361.

Houghton, R. A. 2005. Aboveground forest biomass and the global carbon balance. **Global Change Biology** 11 (6): 945-958.

Houghton, R. A., K. T. Lawrence, J. L. Hackler and S. Brown. 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. **Global Change Biology** 7 (7): 731-746.

Kent, M. and P. Coker. 1992. **Vegetation description and analysis: A practical approach**. John Wiley & Sons.

Laurance, W. F., P. M. Fearnside, S. G. Laurance, P. Delamonica, T. E. Lovejoy, J. M. Rankin-De-Merona, J. Chambers and C. Gasccon. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. **Forest Ecology and Management** 118 (1-3): 127-138.

Liu, J., T. Yunhong and J. W. F. Slik. 2014. Topography related habitat association of tree species traits composition and diversity in a Chinese tropical forest. **Forest Ecology and Management** 330 (10): 75-81.

Luizao, R. C. C., F. J. Luizao, R. Q. Paiva, T. F. Monterio, L. S. Sousa and B. Kruijt. 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. **Global Change Biology** 10 (5): 592-600.

Malhi, Y. and J. Grace. 2000. Tropical forests and atmospheric carbon dioxide. **Trend in Ecology & Evolution** 15 (8): 332-337.

Muller-Landau, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. **Biotropica** 36 (1): 20-32.

Noguchi, H., A. Itoh, T. Mizuno, K. Sri-Ngernyuang, M. Kanzaki, S. Teejuntuk, W. Sungpalee, M. Hara, T. Ohkubo, P. Sahunalu, P. Dhanmmanonda and T. Yamakura. 2007. Habitat divergence in sympatric Fagaceae tree species of a tropical montane forest in northern Thailand. **Journal of Tropical Ecology** 23 (5): 549-558.

Ochiai, Y., S. Okuda and A. Sato. 1994. The influence of canopy gap size on soil water conditions in a deciduous broad-leaved secondary forest in Japan. **Journal of the Japanese Forestry Society** 76 (4): 308-314.

Ounkerd, K., P. Sunthornhao and L. Puangchit. 2015. Valuation of carbon stock in trees at Khao Wong community forest, Chaiyaphum province. **Thai Journal of Forestry** 34 (1): 29-38. (in Thai)

Punchi-Manage, R., S. Getzin, T. Wiegand, R. Kanagarai, C. V. S. Gunatilleke, I. A. U. N. Gunatilleke, K. Wiegand and A. Huth. 2013. Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. **Journal of Ecology** 101 (1): 149-160.

Slik, J. W. F. 2006. Estimating species-specific wood density from the genus average in Indonesian trees. **Journal of Tropical Ecology** 22 (4): 481-482.

Sungpalee, W., A. Itoh, , M. Kanzaki, K. Sri-Ngernyuang, H. Noguchi, T. Mizuno, S. Teejuntuk, M. Hara, K. Chai-Udom, T. Ohkubo, P. Sahunalu, P. Dhanmmanonda, S. Nanami, T. Yamakura and A. Sorn-Ngai. 2009. Intra- and interspecific variation in wood density and fine-scale spatial distribution of stand-level wood density in a northern Thai tropical montane forest. **Journal of Tropical Ecology** 25 (4): 359-370.

Suzuki, E. 1999. Diversity in specific gravity and water content of wood among Bornean tropical rain forest trees. **Ecological Research** 14 (3): 211-224.

Valencia, R., R. Condit, H. C. Muller-Landau, C. Hernandez and H. Navarrete. 2009. Dissecting biomass dynamics in a large Amazonian forest plot. **Journal of Tropical Ecology** 25 (5): 473-482.

Zak, R. D., A. Hairston and D. F. Grigal. 1991. Topographic influences on nitrogen cycling within an upland pin oak Ecosystem. **Forest Science** 37 (1): 45-53.