

Aboveground biomass and tree species diversity along altitudinal gradient in Central Highland, Vietnam

TRAN VAN DO^{1,2,3*}, TAMOTSU SATO³, VO DAI HAI⁴, NGUYEN TOAN THANG¹, NGUYEN TRONG BINH⁵, NGUYEN HUY SON¹, DANG VAN THUYET¹, BUI THE DOI⁵, HOANG VAN THANG⁴, TRIEU THAI HUNG^{1,6}, TRAN VAN CON¹, OSAMU KOZAN², LE VAN THANH⁴, NGO VAN CAM⁷

¹*Silviculture Research Institute, Vietnamese Academy of Forest Sciences, Hanoi, Vietnam*

²*Center for Southeast Asian Studies, Kyoto University, Kyoto, Japan*

³*Department of Forest Vegetation, Forestry and Forest Products Research Institute, Tsukuba, Japan*

⁴*Vietnamese Academy of Forest Sciences, Hanoi, Vietnam*

⁵*Vietnam Forestry University, Xuan Mai, Hanoi, Vietnam*

⁶*Tasmanian Institute of Agriculture/School of Agricultural Science, University of Tasmania, Hobart, Australia*

⁷*Tropical Forest Research Centre, Vietnamese Academy of Forest Sciences, Gia Lai, Vietnam*

Abstract: Central Highlands in Vietnam supports a very high forest cover and high tree species diversity. However, there are no quantitative studies that deal with altitudinal changes in aboveground biomass (AGB) and tree species diversity. Therefore, in this study we tested patterns of AGB, stem density, species diversity and canopy height along increasing altitude. A total of 49 temporary 50 m x 50 m plots were established in lower lowland (< 500 m), upper lowland (500–1000 m), sub-montane (1000–1500 m), and montane (1500–1800 m) zones. All individuals having stem diameter at breast height (dbh) ≥ 10 cm were identified to species and measured for dbh. AGB ($R^2 = 0.67$) and stem density ($R^2 = 0.39$) significantly increased with increasing altitude, while top canopy height ($R^2 = 0.78$) decreased. Species density ($R^2 = 0.52$) and diversity Shannon-Weiner index ($R^2 = 0.31$) significantly decreased towards higher altitude. Diameter at breast height showed a significant ($R^2 = 0.26$), but small, increase with increasing altitude. Cluster analysis indicated that there are two significant vegetation zones of different stand structures and tree species diversity in the Central Highlands of Vietnam, viz., lowland forests below 1000 m, and lower montane forests between 1000–1800 m elevation. This study found an increasing trends in AGB and stem density with increasing altitude.

Key words: Aboveground biomass, altitudinal zones, cluster analysis, forest structure, tree species richness, tropical forests

Handling Editor: G. S. Rawat

Introduction

Aboveground biomass (AGB) in tropical forests varies widely due to regional differences in climate, species diversity, stem density, stem size distribution, edaphic conditions, topography and disturbance history (Con *et al.* 2013; Do. *et al.*

2010; Mohandass *et al.* 2016; Ngo *et al.* 2013; Urquiza-Haas *et al.* 2007). In addition, variations in canopy height and wood density may also be responsible for variations in AGB (Chave *et al.* 2005; Nogueira *et al.* 2008; Slik *et al.* 2013).

Various templates depicting vegetation structure (e.g. community structure and tree

*Corresponding Author; e-mail: dotran@cseas.kyoto-u.ac.jp; dotranvan@hotmail.com

species composition) have been proposed to understand the interrelationships between ecosystem types and environmental factors (Holdridge 1967; Troll 1948; Whittaker 1975). Of these, the most notable and useful one for understanding the pattern of mountain vegetation is Troll's diagram (Troll 1948), which helps to establish the relationship between leaf-type and eco-climatic zones *vis-a-vis* major forest types such as conifer forests in the temperate zone and tropical evergreen forests. Basing on Troll's diagram, Ohsawa (1990) further explained the range of mean annual temperature along altitudinal gradient in Southeast Asian forests and found “the annual temperature sum” of months with temperature $> 5^{\circ}\text{C}$ as the controlling factor on altitudinal changes of vegetation. According to him, mean annual temperature reduces with increasing altitude from 22°C at 1200 m to 12°C at 2500 m and to 6°C at 3500 m elevation. These lead to “the annual temperature sum” to 15°C at 3500 m elevation and to 85°C at 2500 m elevation in Southeast Asian region (Ohsawa 1995).

On the basis of these facts, Ohsawa (1995) proposed a mountain-vegetation zonation, that include lowland forest (Mesophyll) distributed below 1000 m elevation, lower montane forests (Notophyll) between 1000–2500 m elevation and upper montane forests (evergreen trees with microphyllous leaves) between 2500–3800 m elevation. Edaphic conditions such as soil pH and litter decomposition decrease with increasing altitude while organic carbon and total nitrogen increase with increasing altitude as a result of decreasing temperature at higher altitudes (Kitayama & Aiba 2002). In addition, altitude governs several factors such as solar radiation which increases at higher altitude and atmospheric pressure which decreases by 11% with a gain in 1000 m (Korner 2007), especially in the tropics due to steep topography (Aiba *et al.* 2004; Daws *et al.* 2002; Ohsawa 1990).

The species composition and vegetation structure vary greatly with altitude (Bruijnzeel 2002; Ohsawa 1995), latitude (Barthelemy *et al.* 2015), and environment (Javaid & Zafar 2015; Sarker *et al.* 2014). The decrease in canopy height with increasing elevation and the increase of stem density with increasing elevation have been reported in tropical forests (Lieberman *et al.* 1996; Takyu *et al.* 2003). Similarly, decrease in species richness with increasing altitude is pronounced in tropical montane forests (Aiba & Kitayama 1999; Lieberman *et al.* 1996; Slik *et al.* 2009; Takyu *et al.*

2003). The general trend in AGB and/or total basal area shows an increase with increasing altitude in southwestern Mexico (Vazquez & Givnish 1998) and in Atlantic forest, Brazil (Luciana *et al.* 2010). However, decrease in AGB with increasing altitude has also been found in tropical forests in Mount Kinabalu Borneo (Kitayama & Aiba 2002), which has elevation of 4095 m and temperature of 24°C at 500 m elevation, reducing to 8°C at 3100 m elevation. While, Culmsee *et al.* (2010) found no clear change of AGB with altitude in tropical forests of Sulawesi Indonesia.

The objective of this study was to analyze the altitudinal changes in AGB, stand structures, and tree species diversity in evergreen broadleaf forests in Central Highland, Vietnam. We hypothesized that forests distributed at higher altitudes would have higher stem density and AGB but lower tree species diversity and canopy height.

Materials and methods

Study area and data collection

This study was conducted in Central Highland evergreen broadleaf forests of Vietnam between $11^{\circ}12' - 15^{\circ}27'\text{N}$ and $107^{\circ}12' - 108^{\circ}59'\text{E}$ (Fig. 1). The study area has high forest cover (55%) and rich biodiversity (FIPS 2011). Of a total of 2.6 million ha natural forests, 1.6 million ha is covered by tropical evergreen broadleaf forests, which is

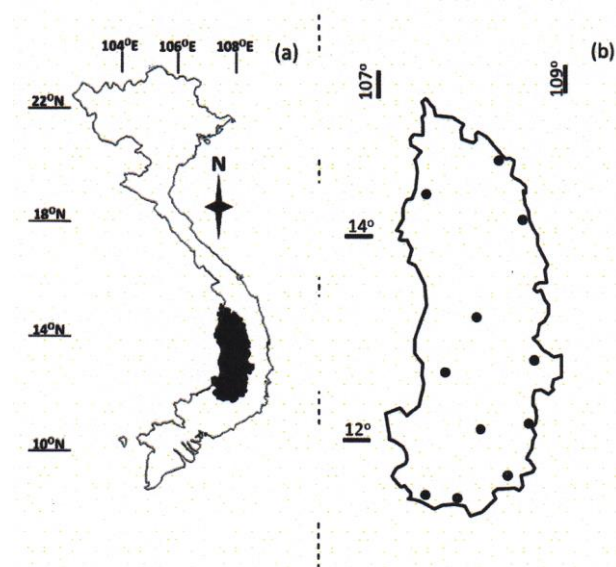


Fig. 1. Map of Vietnam and study area (Central Highland) in black (a), survey sites indicated as black dots (b).

distributed between 200 to 1800 m elevation (Con *et al.* 2013). Ferralsol is the predominant soil type, in which Xanthic Ferralsol dominate the 1000–1800 m altitudinal zones. While, Rhodic Ferralsols are dominant below 1000 m altitudinal zones (Hai *et al.* 2013). Mean annual temperature ranges from 18 to 24 °C, while maximum and minimum mean annual temperatures range between 28–30 °C and 15–20 °C, respectively. There are two distinct seasons, viz., rainy season from June to October and dry season from November to May. Mean annual precipitation is about 1900 mm and the variation of annual precipitation with altitude is not pronounced (Hai *et al.* 2013). Wide variation in geological, topographic, climatic, and edaphic conditions have led to high species diversity and varied forest structure as compared to other parts of Vietnam (Thai 1978). There is a considerable variation in forest structure and species diversity locally due to sharp altitudinal and micro-topographic differences (Thai 1978). To capture such variability we stratified the study area into four altitudinal zones: (1) lower lowland (200–500 m), (2) upper lowland (500–1000 m), (3) sub-montane (1000–1500 m), and (4) montane (1500–1800 m).

Most of the sampling was done in natural, undisturbed old growth forests (Hai *et al.* 2013) located in remote areas. Areas disturbed due to selective logging in the past were excluded from present survey. Survey plots were established at 11 undisturbed sites (Fig.1) which represented old-growth forests and showed no signs of human disturbances as indicated by absence of logged stumps. Plots of 50 × 50 m were set up for enumeration of trees and diameter at breast height (dbh). Plot elevation was measured using portable GARMIN-GPS. All stems ≥ 10 cm were identified to species and measured for diameter at breast height (dbh). Herbarium specimens (any available; leaves, bark, flower, fruit) and photos of unidentified tree species were taken for further identification by the taxonomists at Vietnamese Academy of Forest Sciences in Hanoi, Vietnam. In each plot, 20 stems of different species in different diameter classes were measured for tree height (H) using HAGLOF Vertex IV. H-measured stems in each plot included two tallest stems and two smallest dbh stems and other stems were equally distributed in all diameter classes. In total 49 plots were established covering upper lowland (14), sub-montane (14) and montane (14), and lower lowland (7). The lower plot number in lower lowland is because of less availability of undisturbed/old-

growth forests in this altitudinal zone (Hai *et al.* 2013). There were a total of 154 H-measured stems (dbh range of 10–88.2 cm) belonging to 112 of 163 species found in lower lowland. In upper lowland, 278 stems were measured for H (dbh range of 10–101.3 cm) belonging to 132 of 158 species. In sub-montane, 260 stems were measured for H (dbh range of 10–95.5 cm) belonging to 95 of 108 species found. While, 259 stems were measured for H (dbh range of 10–89.1 cm) belonging to 69 of 70 species found in montane belt.

Aboveground biomass estimation

Aboveground biomass (AGB; Mg ha⁻¹) of each tree stem was estimated using the allometric equation for moist tropical forest from Chave *et al.* (2005):

$$AGB = \rho * \exp(-1.499 + 2.148 \ln(dbh) + 0.207 (\ln(dbh))^2 - 0.028 (\ln(dbh))^3) \quad (1)$$

Where ρ is wood specific gravity, dbh is diameter at breast height in cm. The generic moist tropical forest equation was used because the annual precipitation of study area falls within the range 1500–3500 mm. Wood specific gravities of concerned species were obtained from a worldwide database (Chave *et al.* 2005). Then, AGB of a plot was calculated as the sum of the biomass of the individual tree stems in plot.

Tree species diversity

Species density (S) is number of species found in a plot (2500 m²) and species richness is total species found in all plots of each altitudinal zone. The diversity Shannon-Weiner index (H' , Magurran 1988) was applied to estimate diversity index for each plot as follows:

$$H' = - \sum_{i=1}^S p_i \ln(p_i) \quad (2)$$

Where p_i is the stem proportion of species i^{th} in survey plot.

Similarity index (SI) between altitudinal zones was calculated as

$$SI = \frac{\text{no. of species shared by two altitudinal zones}}{\text{total species found in two altitudinal zones}} \quad (3)$$

Statistical analyses

Stand parameters including stem density, species density, species diversity (Shannon-Weiner index), AGB, and mean dbh are calculated for each survey plot separately. ANOVA (single factor) is adopted to analyze the significant effect of elevations on stand parameters. Pair-wise comparison is then applied using *t*-test ($P = 0.05$) to find out elevation having highest stand parameter. Regression analyses are applied to identify significant relationship between elevations as an independent variable and stand parameters. For fitting elevation/top canopy height relationship, a tallest H-measured stem and elevation (m) of each survey plot are used (a total of 49 survey plots, $n = 49$ for regression). While stem density, mean dbh, AGB, species density, and elevation (m) of each survey plot are used to fit elevation/ stem density, elevation/dbh, elevation/AGB, elevation/species density, and elevation/diversity relationships (a total of 49 survey plots, $n = 49$ for regression). All H-measured stems are used to fit dbh/H relationship for each altitudinal zone using logarithmic form. Percent of > 70 cm dbh stems and that of AGB of > 70 cm dbh stems are estimated, since 70 cm dbh is known as the threshold in tropical lowland forest (Slik *et al.* 2013).

Cluster analysis using Ward's method (Ward 1963) with Euclidean distances is applied to group four altitudinal zones into similarity zones basing on altitudinal means of stem density, species density, species diversity, AGB, and dbh. Ward's method averages all distances between pairs of object in different clusters, with adjustments for covariance, to decide how far apart the clusters are. Euclidean distance is computed using normalized root mean squared distances.

Results

Aboveground biomass and stand structure

ANOVA indicated that elevation had significant effects on stem density ($df = 3$ and 45 , $F = 8.85$, $F_{crit} = 2.81$, $P < 0.001$) and AGB ($df = 3$ and 45 , $F = 116.01$, $F_{crit} = 2.81$, $P < 0.001$). The highest mean stem density per 50 m \times 50 m plot was found in the montane zone (185 stems) and was significantly higher ($P < 0.004$) compared to three other altitudinal zones. While there was no significant difference ($P > 0.22$) of mean stem density among lower lowland (129 stems), upper

lowland (130 stems), and sub-montane (138 stems, Table 1). Exponential curve significantly fitted for elevation/stem density relationship ($R^2 = 0.39$, $P < 0.001$, Fig. 2a), indicating increase of stem density with increasing altitude. The mean AGB per 50 m \times 50 m plot was significantly different ($P < 0.01$) among four altitudinal zones. The highest AGB was found in montane (93.2 Mg), following sub-montane (66.7 Mg), upper lowland (60.5 Mg), and lower lowland (53.3 Mg, Table 1). Increase of AGB with increasing altitude was significantly fitted by positive exponential ($R^2 = 0.67$, $P < 0.001$, Fig. 2b). The percent of stems in dbh > 70 cm was highest in sub-montane (1.4%), following montane (1.0%), upper lowland (0.9%), and lower lowland (0.7%, Table 2). The percent of AGB of stems in dbh > 70 cm was highest in sub-montane forest (24.6%), declining to 17.3% in upper lowland, 15.2% in montane, and 13.0% in lower lowland forests (Table 2).

The largest stems measured in lower lowland and upper lowland forests were 108.2 cm and 101.3 cm dbh (*Craibiodendron scleranthum*) in both the strata. In other strata the largest stems were 95.5 cm (*Castanopsis chinensis*) in sub-montane, and 89.1 cm (*Rhodoleia championii*) in montane forest. The top canopy heights were 41.0 m (*C. scleranthum*), 40.0 m (*Dialium cochinchinense*), 36.0 m (*R. championii*), and 31.0 m (*C. chinensis*) in lower lowland, upper lowland, sub-montane and montane forest, respectively. Linear form was well fitted for elevation/top canopy height relationship ($R^2 = 0.91$, $P < 0.001$, Fig. 2c), indicating the decrease of top canopy height with increasing altitude. ANOVA analysis indicated that elevations had significant effects on mean stem dbh ($df = 3$ and 45 , $F = 2.95$, $F_{crit} = 2.81$, $P = 0.04$). Mean dbh was lowest in lower lowland (26.3 cm) and was significant ($P < 0.05$) lower than that of three other altitudinal zones. The difference of mean dbh in upper lowland (27.2 cm), sub-montane (27.5 cm), and montane (28.0 cm) was not significant ($P > 0.23$, Table 1). There was a weak positive correlation ($R^2 = 0.26$, $P < 0.001$) between elevation and dbh indicating small increase of dbh with increasing altitude (Fig. 2d).

Logarithmic form (Fig. 3) was well fitted for dbh/H relationships in lower lowland ($R^2 = 0.77$, $P < 0.001$), upper lowland ($R^2 = 0.73$, $P < 0.001$), sub-montane ($R^2 = 0.68$, $P < 0.001$), and montane ($R^2 = 0.71$, $P < 0.001$). There were reverse J-shapes of the dbh/stem abundance relationships for all altitudinal zones, while no clear patterns were found for the dbh/AGB relationships (Fig. 4). Fifty

Table 1. Means (\pm SE per 50×50 m plot) of stem density, aboveground biomass (AGB), species density, diversity Shannon-Weiner index (H'), and dbh along the altitudinal zones of evergreen broadleaf forests (Central Highland, Vietnam).

Altitudinal zones	Stem density	AGB	Species density	H'	dbh
Lower lowland	129 ± 6.6^a	53.3 ± 1.4^a	46 ± 2.7^a	4.11 ± 0.11^a	26.3 ± 0.4^a
Upper lowland	130 ± 4.9^a	60.5 ± 0.9^b	45 ± 2.2^a	4.01 ± 0.09^a	27.2 ± 0.4^b
Sub-montane	138 ± 4.3^a	66.7 ± 1.7^c	37 ± 1.9^b	3.86 ± 0.07^a	27.5 ± 0.5^b
Montane	185 ± 6.2^b	93.2 ± 1.7^d	21 ± 1.3^c	3.44 ± 0.15^b	28.0 ± 0.5^b

^{a,b}Different letters in a column indicate significant difference of means by *t*-test at $P < 0.05$.

Table 2. Number of survey plots and stand parameters along the altitudinal zones of evergreen broadleaf forests (Central Highland, Vietnam).

Altitudinal zones	Number of survey plots	Species richness*	Density (stems ha ⁻¹)	AGB (Mg ha ⁻¹)	Stems of > 70 cm dbh (%)	AGB of stems of > 70 cm dbh (%)
Lower lowland	7	163	516	221.3	0.7	13.0
Upper lowland	14	158	520	242.0	0.9	17.3
Sub-montane	14	108	552	266.9	1.4	24.6
Montane	14	70	740	372.8	1.0	15.2

*Species richness is total species found in each altitudinal zones.

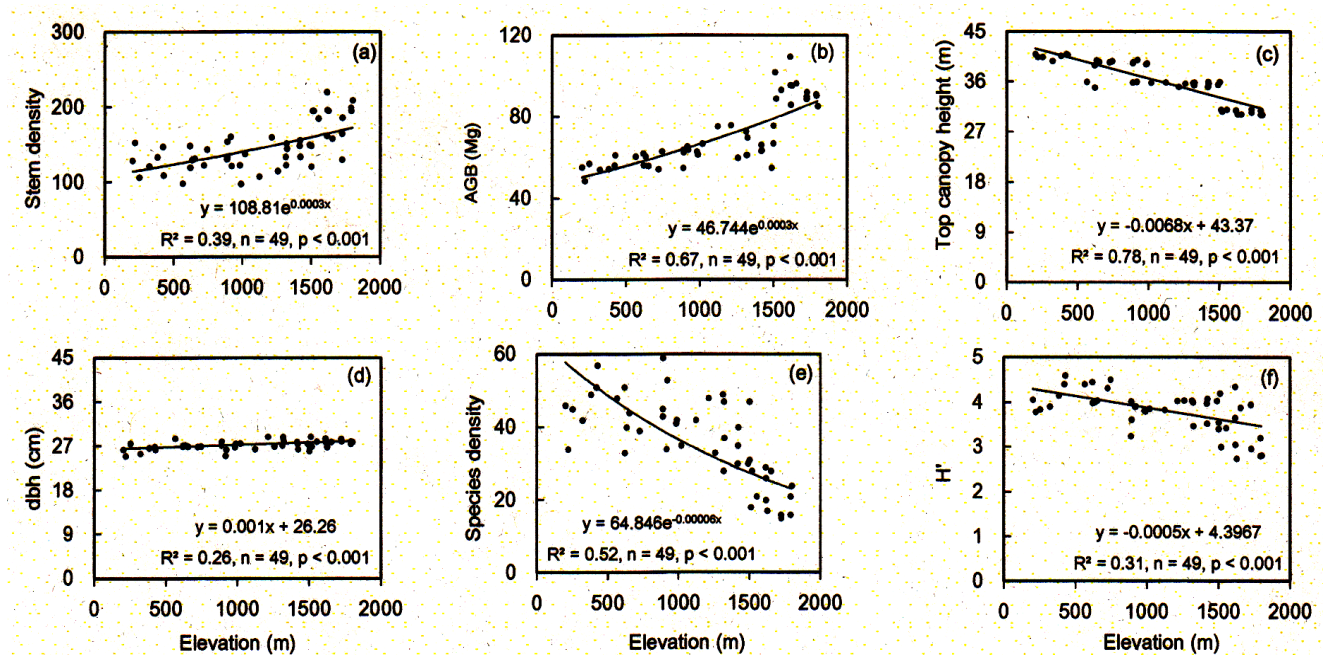


Fig. 2. Relationships between elevation and stem density (a), elevation and AGB/aboveground biomass (b), elevation and top canopy height (c), elevation and mean dbh (d), elevation and species density (e), elevation and diversity Shannon-Weiner index/ H' (f), and along the altitudinal zones of evergreen broadleaf forests (Central Highland, Vietnam).

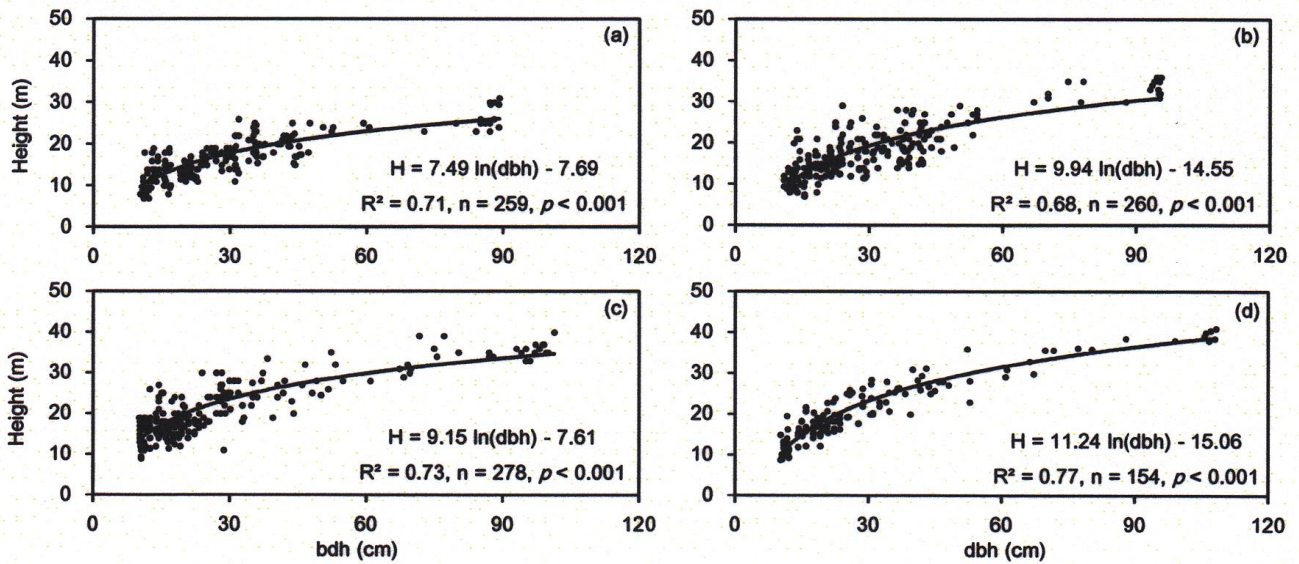


Fig. 3. Log-fitted relationships between dbh and height for montane (a), sub-montane (b), upper lowland (c), and lower lowland (d) evergreen broadleaf forests (Central Highland, Vietnam).

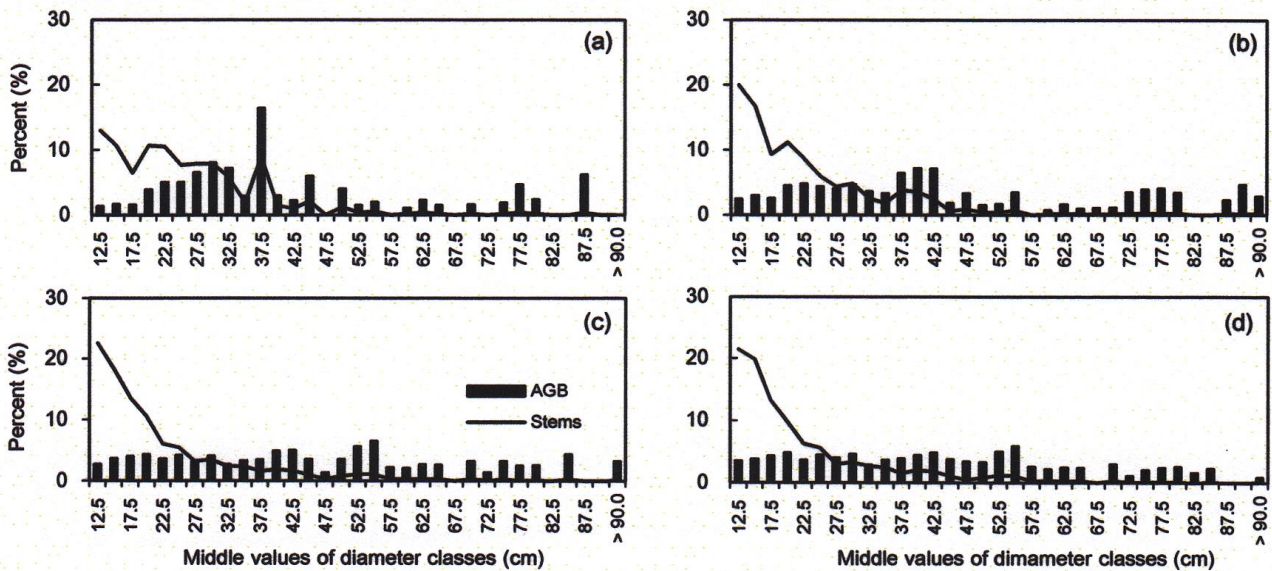


Fig. 4. Structure of stems and AGB/aboveground biomass for montane (a), sub-montane (b), upper lowland (c), and lower lowland (d) evergreen broadleaf forests (Central Highland, Vietnam). Diameter classes of 5 cm interval were used.

in lower lowland, 9.2% in upper lowland, 7.0% in sub-montane, and 11.1% in montane forest (Fig. 4).

Diversity

A total of 163 tree species were recorded in lower lowland, 158 species in upper lowland, 108 species in sub-montane, and 70 species in montane

(Table 2). ANOVA indicated that elevations had significant effects on species density ($df = 3$ and 45 ; $F = 33.44$; $F_{crit} = 2.81$; $P < 0.0001$) and diversity ($df = 3$ and 45 ; $F = 6.84$; $F_{crit} = 2.81$; $P = 0.0006$). Species density in montane zone was lowest (21 species per $50 \text{ m} \times 50 \text{ m}$) and was significantly lower ($P < 0.0002$) than that of other three altitudinal zones, followed by sub-montane (37

species, $P < 0.03$), upper lowland (45 species), and lower lowland (46 species). The difference of species density between lower lowland and upper lowland was not significant ($P = 0.8$, Table 1). Negative exponential was moderately fitted elevation/ species density relationship ($R^2 = 0.52$, $P < 0.001$, Fig. 2e). Montane zone had significant lower ($P < 0.02$) diversity compared to other three altitudinal zones (Table 1). While the difference of diversity index among sub-montane, upper lowland, and lower lowland was not significant ($P > 0.08$, Table 1). Negative linear was weakly fitted elevation/diversity Shannon-Weiner index relationship ($R^2 = 0.31$, $P < 0.001$, Fig. 2f).

A total of 239 tree species (dbh ≥ 10 cm) were found in forty nine 50 m x 50 m plots in four altitudinal zones. Of these, 124 species (51.9%) appeared in only one zone, 77 species (32.2%) appeared in two zones, 30 species (12.5%) appeared in three zones, and eight species (3.3%) appeared in all four zones. Generally, neighboring altitudinal zones had higher species similarity compared to disjunct zones. Pair of lower lowland had highest species similarity (0.79), followed by sub-montane and montane (0.32), upper lowland and sub-montane (0.25), lower lowland and sub-montane (0.14), upper lowland and montane (0.09), and pair of lower lowland and montane (0.06).

Vegetation zonation

Cluster analysis indicated that the vegetation in the present study area was discernible into two different altitudinal zones. Lower zone (below 1000 m elevation) was formed by a combination of lower lowland and upper lowland with linkage distance of 0.001 and upper zone (1000–1800 m) was formed by a combination of sub-montane and montane with linkage distance of 0.005 (Fig. 5).

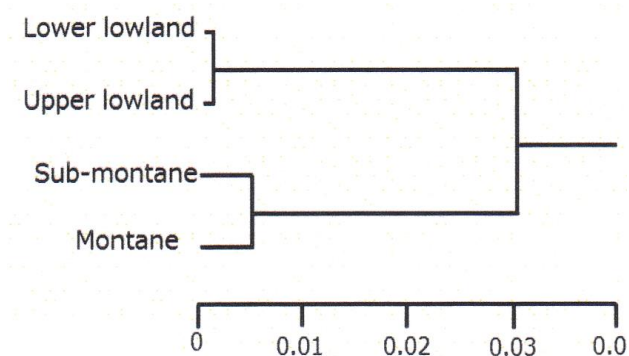


Fig. 5. Dendrogram (Ward linkage, Pearson distance).

Discussion

Aboveground biomass and stand structure

The patterns of increase of stem density, dbh, and AGB with increasing altitude (Fig. 2a,b,d) were found in the present study. This is consistent with studies in tropical forests, Malaysia (Takyu *et al.* 2003) and tropical Atlantic moist forests, Brazil (Luciana *et al.* 2010). However, other studies found the decreasing patterns of AGB with increasing altitude as limitation of soil nutrient supply at higher and cooler sites (Aiba & Kitayama 1999; Kitayama & Aiba 2002; Moser *et al.* 2007; Moser *et al.* 2011; Ohsawa 1995) or no clear pattern of elevation / AGB relationship (Unger *et al.* 2012). The shorter altitudinal zones included in the present study area (under 1800 m elevation), compared to Mount Kinabalu, Borneo (under 4095 m elevation; Aiba & Kitayama 1999 & Kitayama & Aiba 2002;) and the South Ecuadorian Andes (under 3060 m elevation, Moser *et al.* 2007) may explain such difference. Generally, it becomes cooler at higher altitudes and temperature drops faster at elevations higher than 2000 m in the tropics (Kitayama & Aiba 2002; Ohsawa 1995). As a result of lower temperatures, litter decomposition becomes slower leading to limitation of soil nutrient supply at higher altitudes (Kitayama & Aiba 2002; Takyu *et al.* 2003; Zhu *et al.* 2010). However, the present study focused on the altitudinal zones under 1800 m, therefore altitudinal climate shift is not very significant (Kira 1991) and should not lead to major differences in soil nutrient availability (Hai *et al.* 2013) between the four classified altitudinal zones. In addition, the present site is relatively free from clouds and fog (Hai *et al.* 2013) indicating greater availability of solar and UV-B radiation (Brunijnzeel 2002; Korner 2007), which may promote photosynthetic process and biomass accumulation in montane zone (1500–1800 m). Therefore, results in the present study provide a notable exception to the pattern of increases of AGB and stem density with increasing altitude. Montane forests distributed along 1500–1800 m elevation in the present study area is found to have highest AGB compared to other previously studied forests in Vietnam (Con *et al.* 2013; Do *et al.* 2010), but similar to that in other southeast Asian forests (Ngo *et al.* 2013; Takyu *et al.* 2003). This indicated the importance of forest carbon storage in 1500–1800 m elevation in the present

study area compared to other regions in the world (Keeling & Phillips 2007).

The decrease of top canopy height with increasing altitude in the present study (Fig. 2c) was consistent with other tropical evergreen broadleaf forests in Southeast Asian (Kitayama & Aiba 2002; Takyu *et al.* 2003) where at 700 m altitude top canopy height was 46.8 m, declining to 30.0 m at 1700 m altitude, and in Ecuadorian tropical forests (Moser *et al.* 2007) where at 1050 m altitude top canopy height was 31.8 m, declining to 18.9 at 1890 m altitude. The decline of soil fertility (Kitayama & Aiba 2002; Unger *et al.* 2012), limitation of energy (Ohsawa 1995), less competition for sunlight from increasing radiation (Korner 2007), and probably wind velocity increase (Bruijnzeel & Veneklaas 1998; Jones 1992; Lawton 1982; Lieberman *et al.* 1996) are known to be responsible for stem height decline at higher altitude.

Diversity

Decrease in species richness with increasing altitude was found in the present study site (Table 2). This pattern is consistent with other studies (Aiba & Kitayama 1999; Hernandez *et al.* 2012; Lieberman *et al.* 1996; Slik *et al.* 2009). Species density exponentially decreased with increasing altitude (Fig 2d) indicating the higher species holding capacity (number of species appears in a unit of area) of lower altitudinal zones. The more diverse topographies, sunlight availability (Korner 2007), and soil fertility (Hai *et al.* 2013) in lower altitudinal zones encourage the co-existence of more species (Hobbie 1992). In addition, at the local scale the area at higher altitude is smaller and more isolated from similar habitats than those at lower altitude, leading to a lower equilibrium species richness and species density (Ohsawa 2006). The lower diversity in montane forests compared to other three altitudinal zones (Table 1) may result from nutrient availability (Ashton 2003), energy shortage (Ohsawa 1995), and stressful environment such as low temperatures and atmospheric pressure (Aiba & Kitayama 1999; Ryan & Yoder 1997). In addition species density, which was significantly lower in montane than other altitudinal zones (Table 1), is a function (Eq. 2; Magurran 1988) of diversity Shannon-Weiner index. Therefore, lower diversity Shannon-Weiner index in montane was evident.

One hundred forty two of the 163 species found in lower lowland shared with upper lowland,

indicating highest species similarity (0.79) among all pairs of altitudinal zones. The species similarity between upper lowland and sub-montane (0.25) and sub-montane and montane (0.32) were quite low, indicating stronger discontinuity of species distributions with increasing altitude. There may be differences in habitat heterogeneities (Ohsawa 1995) between upper lowland (1000 m) and sub-montane (1500 m) that are stronger than those between sub-montane and montane (1800 m), leading to higher species similarity of latter pair (0.32) compared to former one (0.25). Such pattern was found in other tropical forests in Southeast Asian region (Ashton 2003; Teejuntuk *et al.* 2002).

Vegetation zonation

Template for mountain vegetation (Troll 1948) and/or mountain vegetation zonation (Oshawa 1993, 1995) were developed basing on changes in leaf-type from changes of temperature sum ($^{\circ}\text{C month}^{-1}$). While in the present study, parameters of stand structure and species diversity of different altitudinal zones were used to generate mountain vegetation zonation. The stand parameters (stem density, dbh, AGB, species density, species richness, and diversity) are climatic-, topographical-, and edaphic-dependent. Therefore, it may represent integrated impacts of environment on vegetation differentiation with altitude. Lower lowland (< 500 m) and upper lowland (500–1000 m) were combined to form lowland forest, and sub-montane and montane were combined to form low montane forest, which is consistent with other mountain vegetation zonation in Southeast Asian region (Oshawa 1993, 1995).

In conclusion, the study led to acceptance of hypothesis, i.e. stem density and AGB increase with increasing altitude at present study site. While, tree species diversity (species density and diversity) and canopy height decrease with increasing altitude in evergreen broadleaf forests of Central Highland Vietnam.

Acknowledgements

This research is funded by Vietnam National Foundation for Science and Technology Development (NAFOSTED) under grant number 106-NN.06-2016.10. We thank Dr. Slik J. W. F., and anonymous reviewers for comments on an earlier version of this manuscript.

References

- Aiba, S. & K. Kitayama. 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology* **140**: 139–157.
- Aiba, S., K. Kitayama & M. Takyu. 2004. Habitat associations with topography and canopy structure of tree species in a tropical montane forest on Mount Kinabalu, Borneo. *Plant Ecology* **174**: 147–161.
- Ashton, P. S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 87–104.
- Barthelemy, Y., S. Partrice, T. Salifou, M. Jeanne & H. Victor. 2015. Floristic diversity of *Piliostigma* associations in relation to latitudinal gradient, soil and climate variables in Burkina Faso, West Africa. *Tropical Ecology* **56**: 57–76.
- Bruijnzeel, L. A & E. J. Veneklaas. 1998. Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Ecology* **79**: 3–9.
- Bruijnzeel, L. A. 2002. Hydrology of tropical montane cloud forests: a reassessment. pp. 353–383. In: *Proceedings of the Second International Colloquium on Hydrology and Water Management in the Humid Tropics. Technical Documents in Hydrology* **52**. UNESCO, Paris.
- Chave, J., C. Andalo, S. Brown, M. A. Cairns, *et al.* 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**: 87–99.
- Con, T. V., N. T. Thang, D. T. T. Ha, C. C. Khiem, T. H. Quy, V. T. Lam, T. V. Do & S. Tamotsu. 2013. Relationship between aboveground biomass and measures of structure and species diversity in tropical forests of Vietnam. *Forest Ecology and Management* **310**: 213–218.
- Culmsee, H., G. Moser, C. H. Leuschner & R. Pitopang. 2010. Forest aboveground biomass along an altitudinal transect in Sulawesi, Indonesia, and the role of extra-tropical Fagaceae. *Journal of Biogeography* **37**: 960–974.
- Daws, M. I., C. E. Mullins, D. F. R. P. Burslem, S. R. Paton & J. W. Dalling. 2002. Topographic position affects the water regime in a semi-deciduous tropical forest in Panama. *Plant and Soil* **238**: 79–90.
- Do, T. V., A. Osawa & N. T. Thang. 2010. Recovery process of a mountain forest after shifting cultivation in Northwestern Vietnam. *Forest Ecology and Management* **259**: 1650–1659.
- FIPS. 2011. *Scientific Research Report on Central Highland*. Forest Inventory and Planning Sub-Institute in the Southern part of Central Vietnam and Central Highland. Hanoi.
- Hai, V. D, T. T. Dang, N. V. Cam, N. V. Bich, L. T. Hanh, T. A. Hai & D. Q. Trung. 2013. *Research on Carbon Sequestration Ability of Different Forest Types in Central Highland, Vietnam*. Scientific report. Vietnamese Academy of Forest Science. Hanoi.
- Hernandez, L., N. Dezzeo, E. Sanoja, L. Salazar & H. Castellanos. 2012. Changes in structure and composition of evergreen forests on an altitudinal gradient in the Venezuelan Guayana Shield. *Revista Biología Tropical* **60**: 11–33.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution* **7**: 336–339.
- Holdridge, L. R. 1967. *Life Zone Ecology*. Revised edition. Tropical Science Center, San Jose, Costa Rica.
- Javaid, M & A. R. Zafar. 2015. Influence of environmental and anthropogenic factors on the species distribution in alpine rangelands of Gurez valley, Kashmir, India. *Tropical Ecology* **56**: 335–346.
- Jones, H. G. 1992. *Plants and Microclimate: a Quantitative Approach to Environmental Plant Physiology*. Cambridge University Press, Cambridge.
- Keeling, H. C & O. L. Phillips. 2007. The global relationship between forest productivity and biomass. *Global Ecology Biogeography* **16**: 618–631.
- Kira, T. 1991. Forest ecosystems of east and Southeast Asia in global perspective. *Ecological Research* **6**: 185–200.
- Kitayama, K & S. Aiba. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology* **90**: 37–51.
- Korner, C. 2007. The use of “altitude” in ecological research. *Trends in Ecology & Evolution* **22**: 569–574.
- Lawton, R.O. 1982. Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. *American Journal of Botany* **69**: 1224–1230.
- Lieberman, D., M. Lieberman, R. Peralta & G. S. Hartshorn. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* **84**: 137–152.

- Luciana, F. A., A. V. Simone, A. S. Marcos, B. C. Plinio, A. M. S. Flavio, A. J. Carlos & A. M. Luiz. 2010. Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecology and Management* **260**: 679–691.
- Magurran, A. E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- Mohandass, D., A. C. Hughes, B. Mackay, P. Davidar & T. Chhabra. 2016. Floristic species composition and structure of a mid-elevation tropical montane evergreen forests (sholas) of the western ghats, southern India. *Tropical Ecology* **57**: 533–543.
- Moser, G., D. Hertel & C. Moser. 2007. Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pantropical meta-analysis. *Ecosystems* **10**: 924–935.
- Moser, R., C. Leuschner, D. Hertel, A. Graefe, N. Soethe & A. Iost. 2011. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology* **17**: 2211–2226.
- Ngo, K. M., B. L. Turner, H. C. Muller-Landau, S. J. Davies, M. Larjavaara, N. F bin N. Hassan & S. Lum. 2013. Carbon stocks in primary and secondary tropical forests in Singapore. *Forest Ecology and Management* **296**: 81–89.
- Nogueira, E. M., P. M. Fearnside, B. W. Nelson, M. B. Franc & A. C. A. Oliveira. 2008. Tree height in Brazil's 'arc of deforestation': shorter trees in south and southwest Amazonia imply lower biomass. *Forest Ecology and Management* **255**: 2963–2972.
- Ohsawa, M. 2006. Climate change impacts on vegetation in humid Asian mountains. *Global Environmental Research* **10**: 13–20.
- Ohsawa M. 1995. Latitudinal comparison of altitudinal changes in forest structure, leaf-type, and species richness in humid monsoon Asia. *Vegetatio* **121**: 3–10.
- Ohsawa, M. 1993. Latitudinal pattern of mountain vegetation zonation in southern and eastern Asia. *Journal of Vegetation Science* **4**: 13–18.
- Ohsawa, M. 1990. An interpretation of latitudinal patterns of forest limits in South and East Asian mountains. *Journal of Ecology* **78**: 326–339.
- Ryan, M. G & B. Yoder. 1997. Hydraulic limits to tree height and tree growth. *BioScience* **47**: 235–242.
- Sarker, S. K., S. Rashid, M. Sharmin, M. M. Haque, S. S. Sonet & M. Nur-Un-Nabi. 2014. Environmental correlates of vegetation distribution in tropical Juri forest, Bangladesh. *Tropical Ecology* **55**: 177–193.
- Slik, J. W. F., P. Gary, M. Krista, A. Shin-Ichiro, *et al.* 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecology and Biogeography* **22**: 1261–1271.
- Slik, J. W. F., N. Raes, S. I. Aiba, F. Q. Brearley *et al.* 2009. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Diversity and Distribution* **15**: 523–532.
- Takyu, M., S. Aiba & K. Kitayama. 2003. Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia* **134**: 397–404.
- Teejuntuk, S., P. Sahulanu, K. Sakurai & W. Sungpalee. 2002. Forest structure and tree species diversity along an altitudinal gradient in Doi Inthanon National Park, Northern Thailand. *Tropics* **12**: 85–101.
- Thai, V. T. 1978. *Forest Flora in Vietnam*. Science and Technology Publishing House, Hanoi.
- Troll, C. 1948. Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen an der Nord- und SUDHALBKAGEL. *Jahresbericht des Geobotanischen Forschungsinstituts Rubel for 1947* (Zurich), 46–83.
- Unger, M., J. Homeier & C. Leuschner. 2012. Effects of soil chemistry on tropical forest biomass and productivity at different elevations in the equatorial Andes. *Oecologia* **170**: 263–274.
- Urquiza-Haas, T., P. M. Dolman & C. A. Peres. 2007. Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: effects of forest disturbance. *Forest Ecology and Management* **247**: 80–90.
- Vazquez, G. J. A & T. G. Givnish. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlán. *Journal of Ecology* **86**: 999–1020.
- Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58**: 236–244.
- Whittaker, R. 1975. *Communities and Ecosystems*. 2nd ed. MacMillan, New York, USA.
- Zhu, B., X. Wang, J. Fang, S. Piao, H. Shen & S. Zhao. 2010. Altitudinal changes in carbon storage of temperate forests on Mt Changbai, Northeast China. *Journal of Plant Research* **123**: 439–452.