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Altitude-dependent variation in biomass and wood production of subalpine *Abies spectabilis* forest in eastern Himalaya

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Abstract

Himalayan subalpine forests with a wide altitudinal range of distribution are ideal target for quantifying the change in biomass dynamics along altitude. We estimated aboveground biomass and coarse wood production rate of subalpine *Abies spectabilis* forest on a north-facing slope in Langtang National Park, Nepal, over the entire altitudinal range from 3170 to 3820 m a.s.l. We established 36 plots (3251 m^2 in total) for closed-canopy stands, and additional sapling plots in open-canopy sites (772 m^2) in October 2015. We recorded stem diameter at breast height D and top height H for all trees ($H \geq 2.0$ m) and saplings ($2.0 > H \geq 0.2$ m). We measured recent five-year radial growth in D for all canopy trees in the plots from stem-core samples and recorded recent three-year height growth of all saplings by annual bud scars on leader shoot. We quantified altitude-dependent change in D-H relationship, by extended allometric equation with asymptotic H. We estimated aboveground biomass (AGB) using an allometric equation between D^2H and aboveground tree biomass W. For canopy trees with past D estimates in 2010, we estimated past H from D-H allometry, and past W as well. Based on the change in W, we estimated aboveground coarse wood production rate (CWP) as the annualized increment of AGB for surviving trees. Tree height H of *Abies spectabilis* at any given D decreased with altitude. Relative growth rate (RGR) of W decreased with W and altitude. RGR of sapling height increased with altitude for taller saplings (> 0.5 m), whereas it decreased with altitude for shorter ones. AGB of *Abies* trees in 36 plots was 489 Mg ha^{-1} and CWP was 4.88 Mg ha^{-1} $year^{-1}$, indicating relatively slow biomass turnover rate by tree growth (CWP/AGB) at 1% per year. AGB and CWP decreased with altitude. CWP relative to AGB also decreased with altitude. Altitude-dependent decline in canopy height, AGB and CWP/AGB suggests adaptation to ambient conditions for the maintenance of forest structure.

Key words: allometry, coarse wood production, height, stem diameter.

Introduction

In subtropical mountains, intra-annual thermal variation is small compared to those in temperate regions (Ohsawa 1990, 1993; Cogbill and White 1991). Therefore, in Himalayas, there occurs no summer-green deciduous broadleaved forest, and evergreen broadleaved forests are replaced with altitude by evergreen coniferous forests. On moist north-facing slopes, *Abies spectabilis* forest is superseded by deciduous *Betula utilis* forest near the forest line. In contrast, on the southern slopes, subalpine zone is usually dominated by *Juniperus recurva*, suggesting that *Abies spectabilis* is less tolerant to drought than *Juniperus recurva*. Dwarf scrub of *Rhododendron* spp. are dominant in alpine zone (Stainton 1972).

Coniferous forests in the high elevation are strongly influenced by climatic conditions changing with altitude (Wang *et al.* 2006; Dang *et al.* 2007; Liang *et al.* 2010). The climatic conditions of Himalayan subalpine forests are harsh due to low temperature, cold wind and snow deposition. Ground surface of subalpine forests receive low light resource under dense canopy cover, whereas tree density and canopy closure tend to decrease with altitude (Liu 1997). Tree architecture and height distribution of saplings in Himalayan forests are variable and change with altitude. In mountains, tree shapes quantified by tree height and stem diameter vary with altitude (Aiba and Kitayama 1999; Wang *et al.* 2006; Miyajima and Takahashi 2007; Liang *et al.* 2010). Biomass increment rate is low in higher elevation due to cool conditions (Yoda 1968; Tadaki *et al.* 1970).

In this study, we examined the variation in aboveground biomass and coarse wood production rate along elevational gradient in *Abies spectabilis* forest in eastern Himalaya. Coarse wood production rate is defined to be annual biomass growth of survived trees and biomass gain by recruited trees, and it is the part of aboveground net primary production rate together with the production of high-turnover components of leaves, twigs and reproductive organs (Kira and Shidei 1967; Clark *et al.* 2001).

Yoda (1967, 1968) estimated biomass and net primary production rate along altitudinal gradient from tropical to subalpine forest zones in East Asian subtropical region including Nepal Himalaya and reported extremely high coverage in basal area and

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biomass storage, as compared to montane and subalpine forests in cool-temperate regions. So far, change in net production rate along elevation gradient is not yet fully demonstrated in high altitude Himalayan forests with large biomass storage. Tadaki *et al.* (1967, 1970) reported total biomass and primary production rate of *Abies veitchii* forest in the subalpine zone of Mt. Fuji, central Japan. Although there are many studies of stand-level biomass (Yoda 1968; Tadaki *et al.* 1970; Adhikari *et al.* 1995; Aiba and Kitayama 1999; Binkley *et al.* 2003), only a few studies mention about the change in biomass and turnover rate along altitudinal gradients in subalpine forests (Tadaki *et al.* 1970).

The purpose of this article is to examine the variation of *Abies spectabilis* forest in the Langtang National Park in tree architecture, growth rate of trees and saplings, stand-level above-ground biomass and coarse wood production rate along altitudinal gradient. This study was designed to address the following questions. (1) How does tree architecture in stem diameter-height allometry changes with altitude? (2) How is the change in aboveground biomass and coarse wood production rate with altitude in relation to tree architectural change? (3) How does regeneration from sapling pool change with altitude? To answer these questions, we developed a simple assessment procedure using radial growth data (by stem core samples) and sapling height growth (by annual bud scars) for survivors at single-time census, with an appropriate allometric equation for biomass estimation and statistical models for testing questions.

Study Area

The study was carried out in Langtang National Park, Nepal Himalaya (85º15′– 86º00′E, 28º00′–28º20′N, 3100–3900 m a.s.l.) (Figure 1). Forest limit was around 3900 m a.s.l., above which *Abies* forest is replaced by *Rhododendron* scrubs. Below around 3100 m a.s.l. was covered by mixed evergreen forest dominated by *Quercus semecarpifolia*. Based on the data of the nearest weather station, Dhunche, at 1982 m a.s.l., the mean annual rainfall for 1999-2008 was 2038 mm, mean annual temperature was 15.5°C with highest monthly mean temperature in July at 20.2°C and lowest in January at 8.8°C (Tiwari *et al.* 2017). Further description of the study area is in Tiwari *et al.* (2017).

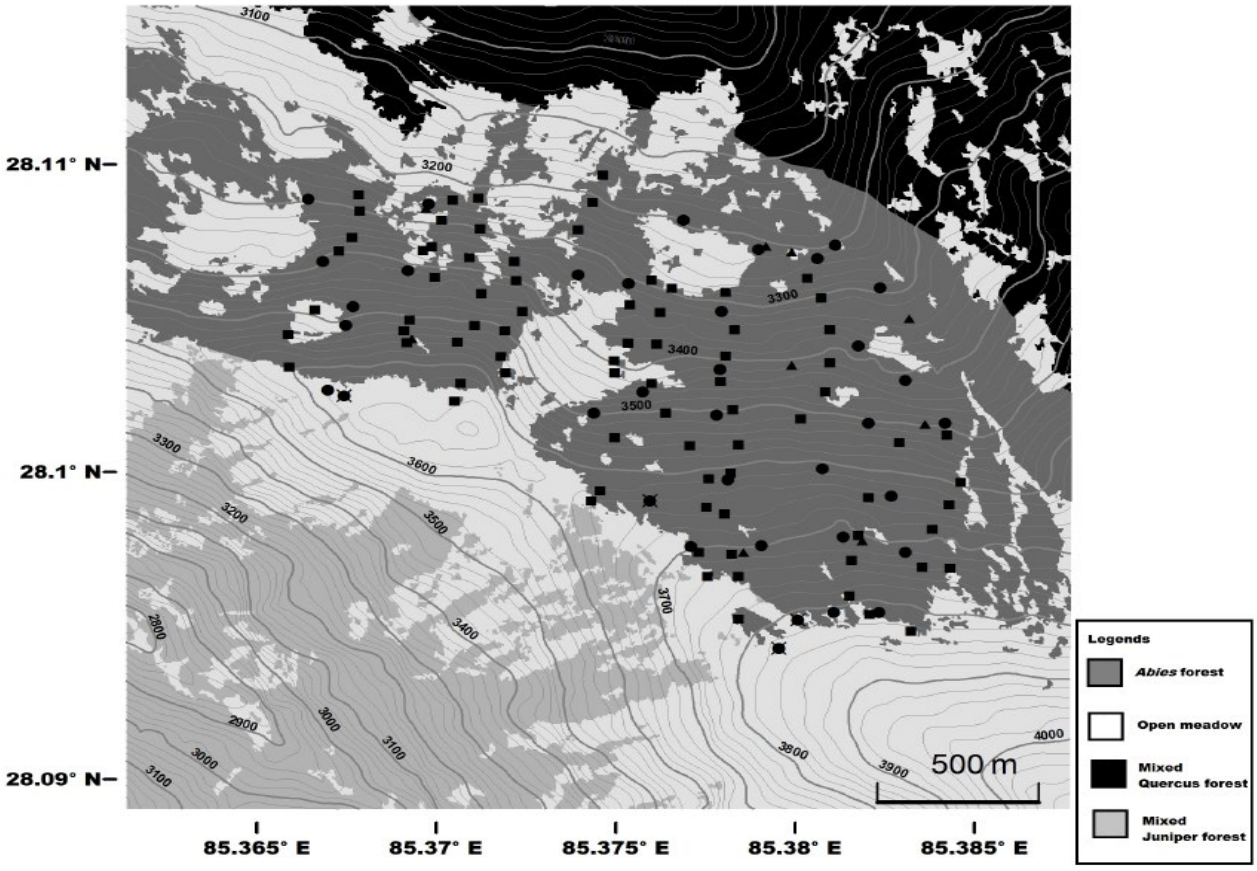

Figure 1. Vegetation distribution and sampling plot locations in Langtang National Park, eastern Himalaya. Filled squares for forest stands established in 2008; filled circles for those in 2015; crosses (with circles) for tree and sapling plots in 2015; triangles for sapling plots in open canopy stand margins in 2015. Vegetation classification by Stainton (1972) with the satellite image from Google Map (RgoogleMaps) (http://www.jstatsoft.org/v63/i04), Esri World Imagery and SRTM 1 Arc-Second Global elevation data using ArcGIS 10.2 for Desktop.

Methods

Field census

During 1 and 13 October 2015, we established 36 plots of 10-by-10 m in slope surface area on canopy-closed forest stands that scatter over the entire altitudinal range of *Abies spectabilis* forest (Figure 1; filled circles). In these plots we recorded all trees with stem diameter at breast height, *D,* to be 1.0 cm or larger. Because saplings of *Abies spectabilis* (with $D < 1$ cm and top height $H \geq 0.20$ m) were only sparsely distributed in closed-canopy plots and they were often abundant in forest edges, we monitored saplings in only four out of these 36 closed-canopy plots (circles-with-cross in Figure 1), and additionally set nine stand-edge plots for sapling sampling (triangles in Figure 1). Besides our 2015 census data, we also used *Abies* tree records in 80 plots set in 2008 (Tiwari *et al.* 2017) to predict aboveground biomass (Figure 1, filled squares). Using average slope inclination of each plot, we estimated horizontal area of each plot for density calculation. For trees ($H \geq 2.0$ m), stem girth was measured to the nearest 0.1 cm at 1.3 m above the ground surface, from which we obtained stem diameter at breast height, D (cm). We measured tree height with a measurement pole for trees with $H \leq 15$ m, and Vertex IV (Haglöf Sweden AB) for those taller than 15 m. We sampled wood cores using a core borer (Haglöf Sweden). Using annual rings, we recorded radial increment in the recent five years, 2010–2015 to the nearest 0.01 mm with a digital caliper, for all canopy trees ($H \geq 10$ m) in 36 plots (1 to 7 canopy tree(s) per plot). For saplings, we measured their top height in 2015 and that three-years ago (in 2012), judged by scars of winter buds on the leader shoot. We used shorter period for sapling shoot elongation than tree-stem radial growth to avoid the influence of size dependence for small-sized saplings, while to keep measurement accuracy for the period longer than one year.

Allometry between stem diameter and tree height

We employed the extended allometric equation (Ogawa *et al.* 1965) to fit asymptotic tree height H against stem diameter D (cm):

$$h = h_{\max} AD^b/(AD^b + h_{\max}), \quad (1)$$

where h (m) is H minus 1.3 (the breast height), b is allometric coefficient, A (cm^{-1}) is allometric constant, and $h_{\max}$ (m) is asymptotic height minus 1.3 for infinite D. To estimate three parameters of eqn (1), we took logarithm of eqn (1) such that

$$\ln h = \ln h_{\max} + \ln A + b \ln D - \ln (AD^b + h_{\max}). \quad (2)$$

We examined whether allometric coefficient $b = 1$ (H is proportional to D for small trees) or $b \neq 1$, and whether each of parameters (A, b, $h_{\max}$) are dependent on the altitude of plots or not. We used NLS on R (R core team 2013) for non-linear regression of parameter estimation (Bates and Watts 1988). To select the best model, we compared all possible models by means of AICc using R package MuMIn (Burnham and Anderson 2002).

Estimation of aboveground biomass

We estimated oven-dry aboveground biomass of a tree, W (kg), from D^2H (cm^2 m) of the tree based on the tree biomass data of *Abies spectabilis* by Yoda (1968) taken in Tumbu District and southern foot of Mt. Numbur, East Nepal:

$$W = \exp(-3.11) (D^2H)^{0.906} \quad (3)$$

Yoda (1968) provided allometric equations that estimate biomass of main stem, branches, and leaves separately. However, we added all of them to estimate aboveground tree biomass to reduce uncertainty in biomass estimation. We summed up W for all trees within each plot and obtained the estimate of aboveground biomass per stand area, AGB (kg m^{-2}).

Estimation of biomass gain

We recorded stem radial increment from core samples but not tree height increment. To estimate biomass gain by tree growth, we need to estimate height growth from stem radial growth. We developed a novel procedure to estimate past height and height growth by stem growth and diameter-height relationship. As we measured five-year radial increment of stem wood at breast height, Δr (cm), for all canopy trees, we obtained stem diameter in 2010 to be $D_{2010} = D_{2015} - 2\Delta r$ (cm), assuming that the bark thickness did not change during the recent five years. Relative growth rate of stem diameter, RGR_D (year^{-1}), during 2010 and 2015 can be defined as

$$\mathrm{RGR}_D = (\ln D_{2015} - \ln D_{2010})/5. \quad (4)$$

To estimate the top height of a tree in 2010 (H_{2010}) from the measured height of that tree in 2015 (H_{2015}), we employed the assumption that the D-H allometry in 2015 is also held in 2010. By differentiating the both sides of eqn (2) with respect to time t, we have

$$(\mathrm{d}h/\mathrm{d}t)/h = [bh_{\max}/(AD^b + h_{\max})](\mathrm{d}D/\mathrm{d}t)/D \quad (5)$$

or, by denoting the relative growth rate of h (= H–1.3) as RGR_h (year^{-1}),

$$\mathrm{RGR}_h/\mathrm{RGR}_D = bh_{\max}/(AD^b + h_{\max}). \quad (6)$$

Assuming that the height h of a tree changed on the ln h/ ln D slope of allometry at its diameter in 2015, D_{2015}, and that $\mathrm{RGR}_h = (\ln h_{2015} - \ln h_{2010})/5$, we have

$$(\ln h_{2015} - \ln h_{2010})/(\ln D_{2015} - \ln D_{2010}) = bh_{\max}/(AD_{2015}{}^b + h_{\max}). \quad (7)$$

(cf. eqn (1)). Therefore, we estimated the past height, $H_{2010} = h_{2010} + 1.3$ (m), using the equation

$$\ln h_{2010} = \ln h_{2015} - (\ln D_{2015} - \ln D_{2010})\, bh_{\max}/(AD_{2015}{}^b + h_{\max}). \quad (8)$$

By using eqn (3) with D_{2010} and H_{2010}, we obtained total aboveground tree biomass, W_{2010} (kg) for every canopy tree.

Tree and sapling growth dependence on altitude

We calculated RGR (year^{-1}) in tree biomass W by,

$$RGR_W = (\ln W_{2015} - \ln W_{2010})/5. \quad (9)$$

We examined altitude dependence of RGR_W by using log-linear regression model (Chambers 1992): ln RGR_W ~ alt * ln$W$, using glm of R, where 'alt' is the plot altitude minus 3.5 (km) as the reference midpoint of the observed altitudinal range. For saplings, we obtained relative growth rate of top height from 3-year elongation record as

$$RGR_H = (\ln H_{2015} - \ln H_{2012})/3, \quad (10)$$

and examined RGR_H dependence on sapling height and altitude by using the model: ln RGR_H ~ alt * ln H_{2015}. We used gamma distribution for RGR error distributions. In best models, size and altitude dependence was judged using AICc.

Estimation of coarse wood production rate

Increment rate of aboveground biomass for survivors (year^{-1}), sometimes called 'coarse wood production rate' (CWP) (Malhi *et al.* 2004), is obtained to be the sum of biomass increment of all stems survived during the census period standardized by the period length and target plot area. The coarse wood production rate plus the production rate of short-lived components (foliage leaves, twigs and reproductive organs) gives an estimate of aboveground net primary production rate (ANPP); CWP contributes to roughly 40% of ANPP (e.g. Malhi *et al.* 2004; Takyu *et al.* 2005).

We estimated annual rate of tree biomass increment, based on canopy-tree biomass W in 2010 and 2015. We employed the procedure of estimating annual increment rate from longer census interval by Sheil (1999), which is originally proposed for estimating per-capita recruitment rate of population size. Let W_t be total aboveground biomass of a given tree at year t. Annual time-step approximation of tree biomass increment can be

$$(1 - \delta)W_{t+1} = W_t, \quad (11)$$

where δ (year^{-1}) is specific annual growth rate based on the final tree mass at t+1 (Sheil 1999). To solve equation (11) over the period 2010–2015,

$$\delta = 1 - (W_{2010}/W_{2015})^{1/5}, \quad (12)$$

and annual rate of aboveground coarse wood production of the tree is δW_{2015} (kg year^{-1}). We calculated δW_{2015} for every canopy tree, and obtained the plot-level coarse wood production rate, CWP (kg m^{-2} year^{-1}), by summing up each canopy tree in each plot with plot-level aboveground biomass, AGB, in 2015 (kg m^{-2}) for all stems including those without radial-growth records:

$$CWP = AGB_{2015}\,\Sigma(\delta W_{2015})/\Sigma W_{2015}, \quad (13)$$

Where CWP is defined for the period 2014–2015. Because there is difference in δ among trees within a plot, the present tree-based estimation of annual CWP is recommended. Otherwise if we sum up biomass at two times first and employ eqn (11) for total biomass, we have underestimation of CWP, as is known for cases of demographic rate estimation in heterogeneous populations (Sheil and May 1996).

We examined how CWP was related to AGB across plots by the model: ln CWP ~ alt * ln AGB with glm on R, as tree/sapling growth analysis.

We illustrated the change in AGB and CWP with altitude, by dividing 36 plots into six altitude classes, for the ease of capturing average aggregative pattern (otherwise, unit plot size of 10-by-10 m with 1 to 7 canopy trees was small). We also estimated AGB for 80 plots set in 2008 (Tiwari *et al.* 2017) using the altitude-dependent D-H allometry (eqn (1)) and D^2H-W allometry (eqn (3)). For them, we have divided 80 plots into 10 altitude classes to illustrate altitudinal change in basal area and AGB in those plots. We defined biomass turnover rate to be CWP/AGB (year^{-1}). Meantime, we illustrate altitude dependence of plot basal area and aboveground biomass for census plots in 2008 and in 2015 without aggregating plots in altitude classes.

Results

Allometry between stem diameter and tree height

Based on the allometric equation between stem diameter and tree height by eqn (2), the best allometric model was that $b \neq 1$ and that A,b and h_{max} were all dependent on altitude of the plot. Estimated parameters are

$$b = 1.22 + 1.83 \text{ alt},$$
$$A = \exp(-0.75 - 4.95 \text{ alt}), \text{ and} \quad (14)$$
$$h_{max} = \exp(3.95 - 3.23 \text{ alt}).$$

Tree height of *Abies spectabilis* at any given stem diameter decreased with altitude (Figure 2).

Growth rate dependence on tree size and altitude

Relative biomass growth rate, RGR_W, showed dependence on altitude and biomass of canopy trees. RGR_W decreased with increase in altitude (Figure 3):

$$\ln RGR_W = -1.34 + 2.73 \text{ alt} - 0.481 \ln W - 0.469 \text{ alt} (\ln W). \quad (15)$$

Relative height growth rate of saplings was dependent on height and altitude as

$$\ln RGR_H = 0.103 - 3.16 \text{ alt} - 0.524 \ln H + 0.788 \text{ alt} (\ln H) \quad (16)$$

For taller saplings (H>ca. 50 cm), RGR_H increased with altitude, whereas for shorter saplings, those decreased with altitude (Figure 4).

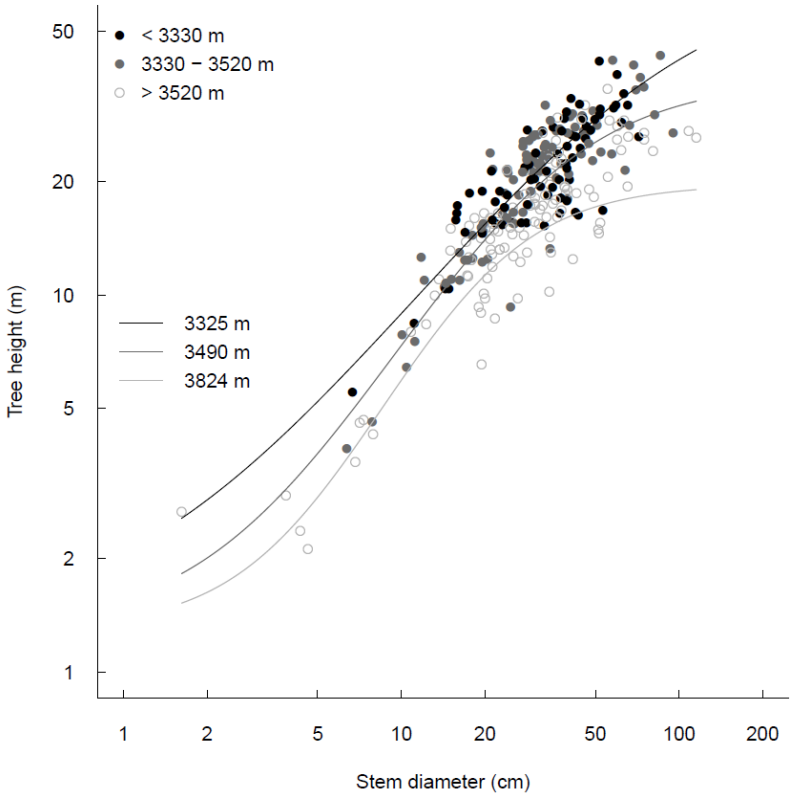

Figure 2. Tree height versus stem diameter relationship for *Abies spectabilis* trees in forest stand plots. Extended allometric equations with asymptotic height (eqn (2)) with altitude-dependent allometric parameters (eqn (14)). Trees are classified into three altitude classes of plots (by gray scales).

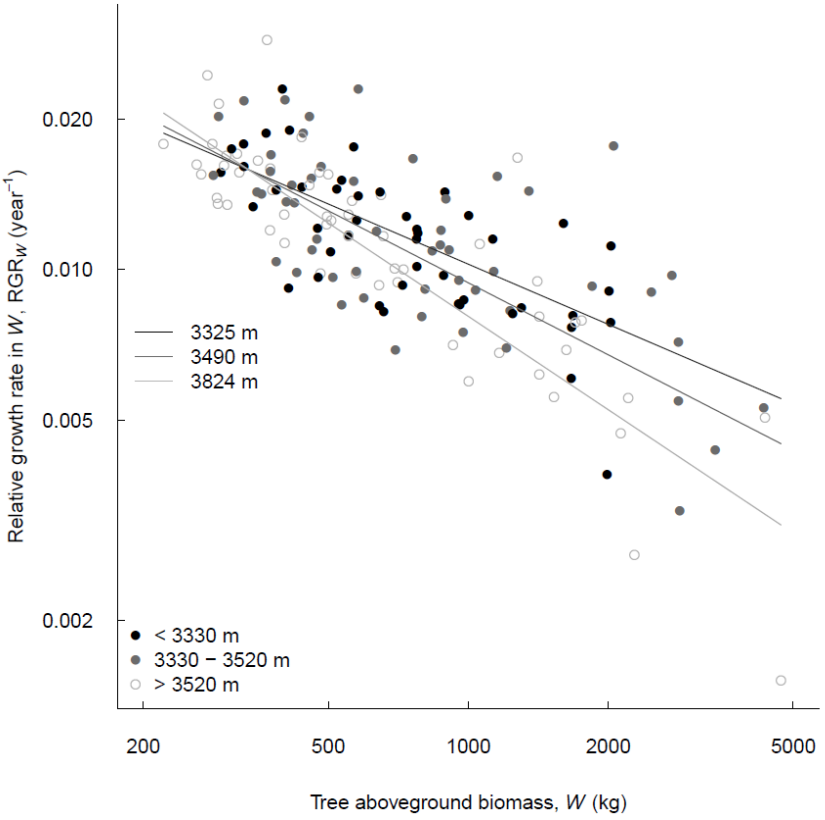

Figure 3. Relative biomass growth rate of trees over aboveground biomass of canopy trees of *Abies spectabilis*. Trees are classified into three altitude classes of plots (by gray scales).

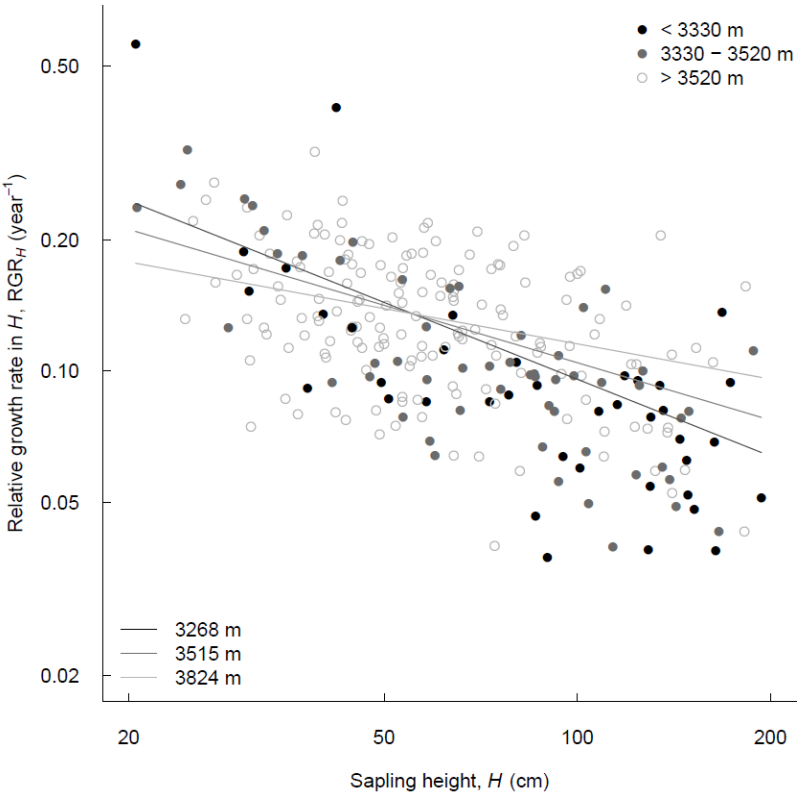

Figure 4. Sapling-height H and altitude dependence of relative growth rate in height of *Abies spectabilis* saplings ($H \leq 2.0$ m). Saplings are classified into three altitude classes of plots (by gray scales).

Table 1. Aboveground biomass and production rates of subalpine *Abies* forests across regions

Region	Latitude	Longitude	Altitude (m)	Canopy height (m)	Basal Area ($cm^2\ m^{-2}$)	Aboveground biomass ($kg\ m^{-2}$)	Net primary production rate ($kg\ m^{-2}\ year^{-1}$)	Coarse wood production rate ($kg\ m^{-2}\ year^{-1}$)	Source
Eastern Nepal	27°30′-27°45′N	84°40′-86°20′E	2920	23.6	72.5	41.8			Yoda (1967, 1968)
Eastern Nepal	27°30′-27°45′N	84°40′-86°20′E	3120	23.1	73.3	40.1			Yoda (1967, 1968)
Eastern Nepal	27°30′-27°45′N	84°40′-86°20′E	3280	22.1	59.6	32.5			Yoda (1967, 1968)
Eastern Nepal	27°30′-27°45′N	84°40′-86°20′E	3420		59.6	34.2			Yoda (1967, 1968)
Eastern Nepal	27°30′-27°45′N	84°40′-86°20′E	3530	21.9	49.9	27.1			Yoda (1967, 1968)
Eastern Nepal	27°30′-27°45′N	84°40′-86°20′E	3680	11.6	44.6	15.9			Yoda (1967, 1968)
Mt.Fuji, Japan	35°21′N	138°43′E	1640	14.9	64.7	22.3	1.88	0.86	Tadaki *et al.* (1970)
Mt.Fuji, Japan	35°21′N	138°43′E	1660	18.6	63.4	25.7	1.39	0.68	Tadaki *et al.* (1970)
Mt.Fuji, Japan	35°21′N	138°43′E	1700	12.4	58.0	15.9	1.06	0.55	Tadaki *et al.* (1970)
Hokkaido, Japan	43°13′N	138°22′E	230	11.7	32.6	9.41	1.47		Satoo (1973)
Central, Japan	35°59′N	142°23′E	2300-2500		63.6	20.3	1.11	0.55	Kimura (1963)
Washington, USA	47°19′N	122°42′W	1140	24.3	74.3	38.9	1.68	0.23	Grier *et al.* (1981)
(young stand)	47°19′N	122°42′W	1140		45.7	44.5	1.83	0.43	Grier *et al.* (1981)
Central Himalaya	30°5′-30°10′N	79°45′-79°57′E	2500		106.0	45.5	1.89		Adhikari *et al.* (1995)
Rocky Mountains	40° 20′ N	105° 41′ W	3180-3400		63.0	25.3	0.37		Binkley *et al.* (2003)
Langtang National Park, Nepal	28°00′-28°20′N	85°15′-86°00′E	3100-3900		74.9	37.1			Present study (2008)
Langtang National Park, Nepal	28°00′-28°20′N	85°15′-86°00′E	3100-3900	24.3	97.6	48.9		0.48	Present study (2015)

Altitude dependence of biomass and wood production

The basal area of trees for plots set in 2015 was 97.6 $cm^2\ m^{-2}$. The basal area is fairly high as compared to those in other subalpine forests in Himalayas (Table 1). The tree basal area for plots in 2008, 74.9 $cm^2\ m^{-2}$. Tree basal area for 2008 plots showed decrease with altitude (ln BA_{08}= 4.29 – 0.701 alt), whereas basal area for 2015 plots showed no clear altitude dependence (ln BA_{15}= 4.58 + 0.00029 alt) (Figure 5). Up to mid-elevation (<3500 m), basal area did not show clear change with altitude, while above 3500 m a.s.l., it showed sharp decline (Figure 5).

The total aboveground biomass, AGB, estimated for the year 2015 was 48.9 kg m^{-2} (= 489 Mg ha^{-1}) as the average of 36 plots. AGB showed sharp decline in higher elevation with both 2008 and 2015 data (ln AGB_{08}= 3.57– 1.37 alt; ln AGB_{15} = 3.88 – 0.48 alt) (Figure 5). In contrast, the aboveground biomass estimates for plots in 2008 was 37.1 kg m^{-2} as the average of 80 plots. Relatively higher estimates of both basal area and aboveground biomass for 2015 plots can be caused by the fact that we established plots in 2015 in well closed-canopy stands with larger biomass, meantime plots in 2008 were set in quasi-even spatial intervals without sampling bias towards closed stands.

Estimated annual rate of coarse wood production (CWP) for 2014–2015 was 0.488 kg $m^{-2}\ year^{-1}$ (= 4.88 Mg $ha^{-1}\ year^{-1}$) as the average of 36 plots. The coarse wood production rate varied from 0.228 to 1.41 kg $m^{-2}\ year^{-1}$.

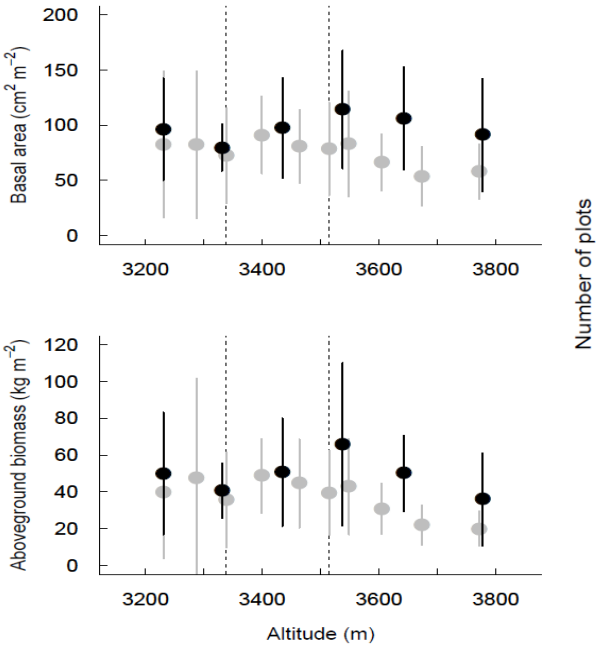

Figure 5. Altitude dependence of stand basal area and aboveground biomass of *Abies spectabilis* forest. Gray circles and bars for 80 forest plots in 2008 divided into 10 altitude groups (8 plots each); black circles and bars for 36 plots in 2015 divided into 6 groups (6 plots each). Dashed lines (3330 m and 3520 m) show boundaries of three altitude classes indicated in Figs. 2-4, 6 and 7.

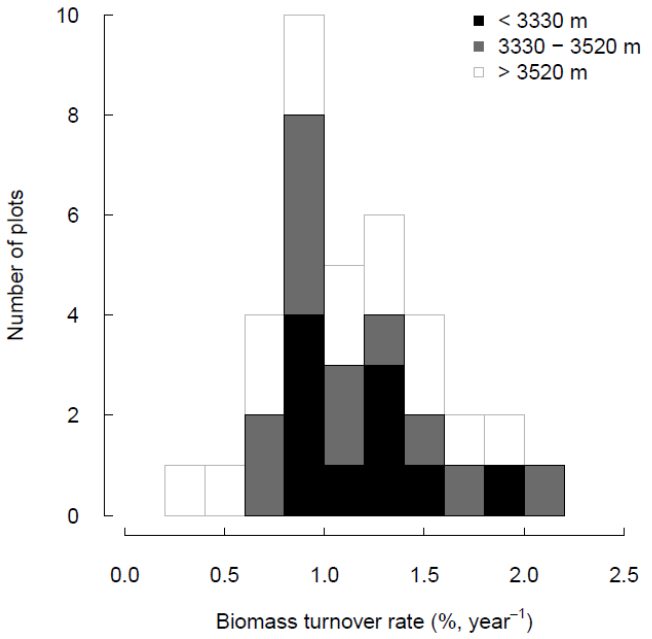

Figure 6. Distribution of biomass turnover rate (%, year^{-1}), i.e. coarse wood production rate divided by aboveground biomass of *Abies spectabilis* in each of 36 plots set in 2015. Plots are classified into three altitude classes (by gray scales).

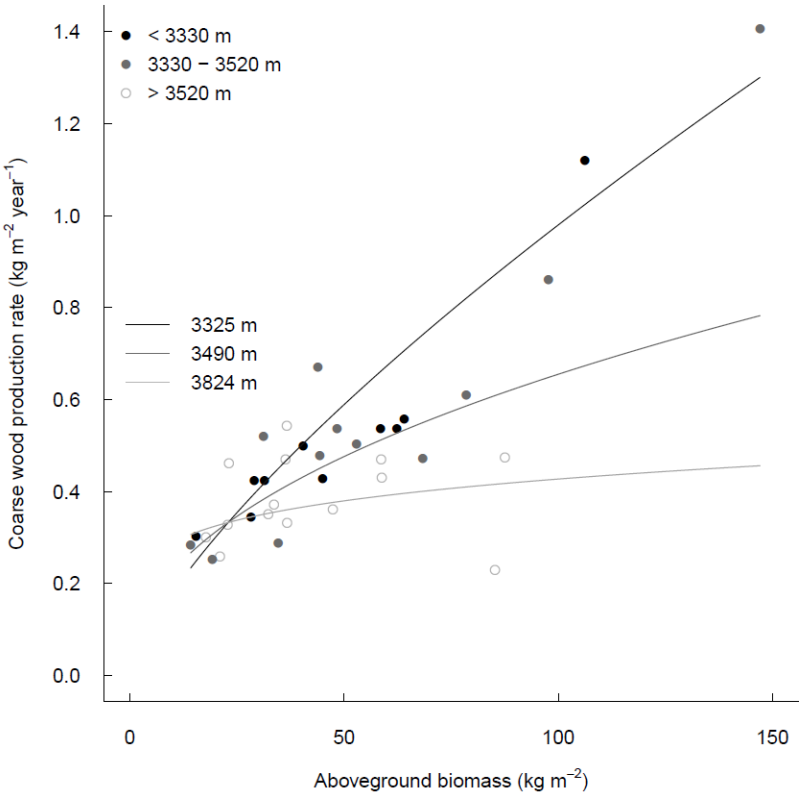

Figure 7. Coarse wood production rate against aboveground biomass in *Abies spectabilis* forest plots in 2015, and of which dependence on altitude. Plots are classified into three altitude classes (by gray scales).

Biomass turnover rate, defined here by CWP/AGB, varied, and was 1.1% year^{-1} in average (Figure 6). Biomass turnover rate decreased with altitude (Figure 7) as

$$\ln \mathrm{CWP} = -2.51 + 3.44\ \mathrm{alt} + 0.450 \ln \mathrm{AGB} - 1.09\ \mathrm{alt}\ (\ln \mathrm{AGB}). \quad (17)$$

Discussion

The present study estimated aboveground biomass of 48.9 kg m^{-2}, a higher end of those reported across subalpine forests in the Northern Hemisphere (Table 1). Adhikari *et al.* (1995) reported high aboveground biomass > 40 kg m^{-2} in a high-altitude mixed *Abies pindrow* forest in central Indian Himalaya. These are similar to the present study. Yoda (1968) reported aboveground biomass around 40 kg m^{-2} for *Abies spectabilis* forests in eastern Nepal. These are the largest biomass records as compared with other subalpine *Abies* forests (Table 1). It should be noted that we set plots with small size of 10 by 10 m in fully closed stands, which may cause overestimation of biomass storage. For 80 plots in 2008 census, estimated biomass was 37 kg m^{-2}, which is still comparable to the upper end of records (Table 1).

Our estimate of aboveground coarse wood production of about 0.5 kg m^{-2} year^{-1} is relatively low for the aboveground biomass of 50 kg m^{-2} (cf. Kimura 1963; Tadaki *et al*. 1970). Low rates of net primary production and coarse wood production relative to aboveground biomass were also recorded by Grier *et al.* (1981) in a mature *Abies* forest of Rocky Mountains. Meantime, higher coarse wood production rate was reported by Tadaki *et al.* (1970) in subalpine *Abies veitchii* forests on Mount Fuji, central Japan. It would reflect that the stage of stand maturation in stand development is associated with the high biomass storage and slow turnover, due to the decline of assimilative leaf mass relative to supportive woody mass.

The allometry between tree height and stem diameter, and biomass turnover of subalpine forests of Himalayas are expected to be influenced by environmental conditions (Yoda 1967,1968; Aiba and Kitayama 1999; Wang *et al.* 2006; Liang *et al.* 2010).The tree architecture and growth rates are variable because in higher elevation trees are mostly damaged due to environmental factors (Miyajima and Takahashi 2007).It is therefore, in the present study, we examined how *Abies spectabilis* forest on a north-facing mountain slope in the Langtang National Park showed variation in tree architecture, growth rate of trees and saplings, stand-level above-ground biomass and coarse wood production rate along altitudinal gradient. We found that the height of canopy trees decreased with altitude, in accordance with earlier studies (Yoda 1968; Wang *et al.* 2006; Miyajima and Takahashi 2007; Liang *et. al.* 2010), and so did the aboveground biomass (Yoda 1968) and coarse wood production rate.

Altitude is linked with temperature and precipitation: temperature decreases, and precipitation increases with altitude in subalpine zone (Cierjacks *et al.* 2008). There are several studies targeting on subalpine forests, which show growth of trees was mainly reduced by low temperature in high altitude (Wang *et al.* 2005; Liang *et al.* 2010; Zhang *et al.* 2010). *Abies spectabilis* population in the studied forest showed altitude dependence, where trees became less slender with altitude, which is in accordance with studies elsewhere (Yoda 1968; Aiba and Kitayama 1999; Wang *et al.* 2006; Miyajima and Takahashi 2007; Takahashi *et al.* 2012). Miyajima and Takahashi (2007) reported that tree growth rate was slower at higher elevation due to reduction in air temperature and increasing wind speed in a temperate forest in central Japan.

Taking into account that trees were shorter at the same stem diameter in higher elevation (Figure 2), growth rate in height and that in tree biomass are decreased with elevation. Takahashi *et al.* (2012) found increased growth rates for *Abies mariesii* in higher elevation, in a subalpine forest in central Japan. We found that relative growth rate of tree aboveground biomass, RGR_W, decreased with tree biomass W, and the degree of W-dependent decrease of RGR_W was larger in higher altitude (Figure 3). This shows that growth rate of *Abies spectabilis* in high altitude subalpine forests may be not only affected by reduction in temperature but also by precipitation, mechanical damage due to strong wind and snow deposition. Thus, tall trees may fail gaining their height at higher elevation, which results in decreasing canopy height with altitude (Figure 2).

Generally, plants grow slower at higher altitude since the environmental stress is severer at high altitude (Jobbagy and Jackson 2000). However, the growth rate in top height H of saplings of *A. spectabilis* did not simply decrease with altitude: relative growth rate in H for tall saplings increased with altitude, while that for short saplings decreased with altitude, at a given H (Figure 4). The height-dependent shift of growth response to altitude suggests that (1) depression in height gain as expected from the stem-shape change with altitude for trees is also the case for tall saplings, and meantime (2) relatively less crowded conditions in high-altitude stands may be favorable for height gain of tall saplings rather than in dense stands at lower elevation (Cunningham *et al.* 2006).Tiwari *et al.* (2017) showed that seedling/sapling density of *Abies spectabilis* in the same forest increased in higher elevation. Less shaded, under-canopy shelter of high-altitude stands would provide favorable conditions for *Abies* regeneration.

The basal area and aboveground biomass showed decreasing pattern from lower to higher altitude, which is comparable with Yoda (1968) who examined the biomass change from around 2000 to 4000 m in the eastern Nepalese Himalayas and found the maximum biomass at the lower boundary of subalpine forest at 2900–3100 m and it decreased towards higher altitude. The coarse wood production rate (CWP) in our studied plots decreased towards higher elevation. At the same aboveground biomass, CWP was smaller in higher elevation (Figure 7), suggesting slower biomass

turnover rate at higher elevation.

We have recorded low biomass turnover rate (1.1%, year^{-1}) in subalpine *A. spectabilis* forest (Figure 6), as compared to other studies on subalpine forests (Tadaki *et al.* 1970; Binkley *et al.* 2003). Biomass turnover rate of any forested ecosystem is regulated by environmental conditions and developmental stages of forest stands. Subalpine coniferous forests experience short growing season due to low temperature (Wang *et al.* 2006; Liang *et al.* 2010; Zhang *et al.* 2010). Reduced temperature at higher altitude can primarily be responsible to slow biomass turnover rate.

Subalpine *Abies* forest in high elevation Himalaya is strongly influenced by altitude in its structure and biomass storage. The present results indicate that *Abies spectabilis* forest has high coverage in stand basal area and aboveground biomass, even though studied plots are taken in closed-canopy stands, as compared to other subalpine forest ecosystems. Stem architecture showed clear change with altitude and so did above-ground biomass and its turnover rate. Aboveground biomass, particularly in higher altitude, is maintained by slow turnover rate relative to the usual forest ecosystems, which would be a key property of maintaining forest ecosystem near forest line in the highest elevation worldwide.

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References

Adhikari, B.S., Rawat, Y.S. and Singh, S.P. (1995) Structure and function of high altitude forests of Central Himalaya. I. Dry matter dynamics. Annals of Botany, 75: 237-248.

Aiba, S.I. and Kitayama, K. (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.

Bates, D.M. and Watts, D.G. (1988) Nonlinear Regression Analysis and Its Applications. Wiley, New York.

Binkley, D., Olsson, U., Rochelle, R., Stohlgren, T. and Nikolov, N. (2003) Structure, production and resource use in some old-growth spruce/fir forests in the Front Range of the Rocky Mountains, USA. Forest Ecology and Management, 172: 271- 279.

Burnham, K.P. and Anderson, D.R. (2002) Model Selection and Multimodel Inference: Practical Information-theoretic Approach, 2nd ed. Springer, New York.

Chambers, J.M. (1992) Linear models. In: Statistical Models in S (ed. T.J. Hastie), CRC Press, Boca Raton.

Cierjacks, A., Ruhr, N.K., Wesche, K. and Hensen, I. (2008) Effects of altitude and livestock on the regeneration of two treeline forming *Polylepsis* species in Ecuador. Plant Ecology, 194: 207- 221.

Clark, D.A., Brown, S., Kicklighter, D.W., Chamber, J.Q., Thomlison, J.R. and Jian, N. (2001) Measuring net primary production in forests: concepts and field methods. Ecological Application, 11: 356-370.

Cogbill, C.V. and White, P.S. (1991) The latitude-elevation relationship for spruce-fir forest and treeline along the Appalanchian mountain chain. Vegetatio, 94: 153-175.

Cunningham, C., Zimmermann, N.E., Stoeckli, V. and Bugmann, H. (2006) Growth of Norway spruce (*Picea abies* L.) saplings in subalpine forest in Switzerland: does spring climate matter? Forest Ecology and Management, 228: 19-32.

Dang, H., Jiang, M., Zhang, Q. and Zhang, Y. (2007) Growth responses of subalpine fir (*Abies fargesii*) to climate variability in the Qinling Mountain, China. Forest Ecology and Management, 240: 143-150.

Grier, C.C., Vogt, K.A., Keyes, M.R. and Edmonds, R.L. (1981) Biomass distribution and above-and belowground production in young and mature *Abies amabilis* zone ecosystems of Washington Cascades. Canadian Journal of Forest Research, 11: 155-167.

Jobbagy, E.G. and Jackson, R.B. (2000) Global controls of forest line elevation in the northern and southern hemispheres. Global Ecology and Biogeography, 9: 253-268.

Kira, T. and Shidei, T. (1967) Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. Japanese Journal of Ecology, 17: 70-87.

Kimura, M. (1963) Dynamics of vegetation in relation to soil development in Northern Yatsugatake Mountains. Japanese Journal of Botany,18: 255-287.

Liang, E., Wang, Y., Xu, Y., Liu, B. and Shao, X. (2010) Growth variation in *Abies georgei* var. *smithii* along altitudinal gradients in the Sygera Mountains, Southeastern Tibetan Plateau. Trees, 24: 363-373.

Liu, Q.J. (1997) Structure and dynamics of the subalpine coniferous forest on Changbai Mountain, China. Plant Ecology, 132: 97-105.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Fiore, A.D., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B. and Lloyd, J. (2004) Above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biology, 10, 563–591.

Miyajima, Y. and Takahashi, K. (2007) Changes with altitude of the stand structure of temperate forests on Mount Norikura, Central Japan. Journal of Forest Research, 12: 187-192.

Ogawa, H., Yoda, K., Ogino, K. and Kira, T. (1965) Comparative ecological studies on three main types

of forest vegetation in Thailand II. Plant biomass. Nature and Life in Southeast Asia, 4: 49-80.

Ohsawa, M. (1990) An interpretation of latitudinal patterns of forest limits in south and east Asian mountains. Journal of Ecology, 78: 326-339.

Ohsawa, M. (1993) Latitudinal pattern of mountain vegetation zonation in southern and eastern Asia. Journal of Vegetation Science, 4: 13-18.

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Satoo, T. (1973) Materials for the studies of growth of forest stands. XI. Primary production relations in a young plantation of *Abies sachalinensis* in Hokkaido. Bulletin of Tokyo University Forest, 66: 127- 137.

Sheil, D. and May, R.M. (1996) Mortality and recruitment rate evaluations in heterogeneous tropical forests. Journal of Ecology, 84: 91-100.

Sheil, D. (1999) Developing tests of successional hypothesis with size-structured populations, and an assessment using long-term data from a Ugandan rain forest. Plant Ecology, 140: 117- 127.

Stainton, J.D.A. (1972) Forests of Nepal. John Murray, London.

Tadaki, Y., Hatiya, K. and Miyauchi, H. (1967) Studies on the production structure of forest (XII). Primary productivity of *Abies veitchii* in the natural forests at Mt. Fuji. Journal of the Japanese Forestry Society, 49: 421-428.

Tadaki, Y., Hatiya, K., Tochiaki, K., Miyauchi, H. and Matsuda, U. (1970) Studies on the production structure of forest (XVI). Primary productivity of *Abies veitchii* forests in the subalpine zone of Mt. Fuji., Bulletin of the Government Forest Experiment Station, 229: 1-22.

Takahashi, K., Hirosawa,T. and Morishima, R. (2012) How the timberline formed: altitudinal changes in stand structure and dynamics around the timberline in central Japan. Annals of Botany, 109: 1165-1174.

Takyu, M., Kubota, Y., Aiba, S., Seino, T. and Nishimura, T. (2005) Pattern of changes in species diversity, structure and dynamics of forest ecosystems along latitudinal gradients in East Asia. Ecological Research, 20: 287-296.

Tiwari, R.M., Shrestha, B.B. and Kohyama, T.S. (2017) Topographic and anthropogenic factors shaping subalpine *Abies spectabilis* forest in Langtang National Park, Eastern Himalaya. Eurasian Journal of Forest Research, 20:1- 9.

Wang, T., Ren, H.B. and Ma, K.P. (2005) Climatic signals in tree ring of *Picea schrenkiana* along an altitudinal gradient in the Central Tianshan Mountains, Northwestern China. Trees, 19: 735-741.

Wang, X., Fang, J., Tang, Z. and Zhu, B. (2006) Climatic control of primary forest structure and DBH-height allometry in Northeast China. Forest Ecology and Management, 234: 264- 274.

Yoda, K. (1967) A preliminary survey of the forest vegetation of Eastern Nepal. II. General description, structure and floristic composition of the sample plots chosen from different vegetation zones. Journal of the College of Arts and Sciences, Chiba University, 5: 99-140.

Yoda, K. (1968) A preliminary survey of the forest vegetation of Eastern Nepal. III. Plant biomass in the sample plots chosen from different vegetation zones. Journal of the College of Arts and Sciences, Chiba University, 5: 277-302.

Zhang, L., Luo, T., Liu, X. and Kong, G. (2010) Altitudinal variations in seedling and sapling density and age structure of timberline tree species in the Sergyemla Mountains, Southeast Tibet. Acta Ecologica Sinica, 30: 76-80.