# Dynamic properties of subalpine coniferous forests in Nepal Himalaya and Hokkaido

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# Contents

## Summary

Subalpine forests form the highest forest ecosystems on mountains. Subalpine forests dominated by coniferous species are commonly observed in the northern Hemisphere, which provide a range of ecosystem services to not only local human communities but also those in downstream regions. In this study, I focused on two contrastive subalpine forests in East Asia, a high altitude subalpine forest in Nepal Himalaya under subtropical climate, and a low altitude forest in northern Hokkaido under cool-temperate climate. I examined how forest structure is determined by environmental factors and whether or not forests experience change in biomass dynamics in a subalpine forest dominated by *Abies spectabilis* in Langtang National Park, Nepal Himalaya and a subalpine forest co-dominated by *Abies sachalinensis* and *Picea glehnii* on Mount Oakan, northern Hokkaido so as to quantify the structure and dynamics of two subalpine coniferous forests.

In Chapter 1, I quantified the change in forest stand variables due to geographic and anthropogenic factors in *Abies spectabilis* forest of Langtang National Park. Woody species composition was changed with altitude and trampling intensity. The number of species decreased with altitude and increased with slope inclination and the number of cut stumps. Frequency distribution of tree size in stem diameter at breast height (*D*) showed monotonous decrease with *D*. Stands in higher altitude showed lower tree density, basal area and maximum *D*, while higher density of juvenile trees ($D < 1.0$ cm). Juvenile density of *A. spectabilis* was reduced in plots with high basal area. Stands on steeper slopes had higher tree density with smaller maximum *D* on poorer soil. With increasing cut stumps, basal area and soil carbon content decreased while

woody species richness and tree density increased. These results showed that *Abies* population is vulnerable to livestock trampling, and that altitude-dependent management is needed.

In Chapter 2, I estimated the aboveground biomass (AGB) developing an allometric equation between stem diameter $D$ and tree height $H$ of which change with altitude, and $D^2H$ versus aboveground total tree mass $W$ using the data of *Abies spectabilis* in eastern Nepal (Yoda 1968). For canopy trees with records of present $D$ in 2015 and past $D$ estimates in 2010, I estimated past $H$ employing $D$-$H$ allometry, and past $W$ as well. Based on the change in $W$ for canopy trees per plot, I estimated aboveground coarse wood production rate (CWP) for each plot, as the annualized increment of AGB for survived trees. Tree height of *Abies spectabilis* at any given diameter was increased with altitude. Growth rate of sapling height was increased with altitude for taller saplings (> 50 cm). AGB and CWP tended to be decreased with altitude. CWP relative to AGB was also decreased with altitude, suggesting slower turnover in high altitude. These results showed that there is huge biomass storage in subalpine *Abies spectabilis* forest in eastern Himalaya, and that biomass is maintained by slow turnover rate (ca. 1% per annum in CWP/AGB) relative to usual forest ecosystems (1.5 to 2%). Altitude-dependent decline in canopy height, AGB and CWP/AGB suggests adaptation to ambient conditions for the maintenance of forest structure.

In Chapter 3, I quantified the species-dependent architectural and demographic properties of *Abies sachalinensis* and *Picea glehnii* populations using repeated census data of trees in a 1-ha plot in years 2004 and 2014. Based on $D$-$H$ allometry for the two species, I estimated AGB with allometry between $D^2H$ and $W$ using the data for subalpine *Abies veitchii* (Tadaki *et al.* 1970). Based on the change in $W$ over 10 years, I estimated CWP and annualized wood loss rate. At the same $D$, $H$ of *Abies sachalinensis* was larger for understory trees with $D <$ ca. 50 cm, while $H$ of

*Picea glehnii* was larger for canopy trees both in year 2004 and 2015. Growth rate of understory trees ($D$ < ca. 30 cm) was larger for *A. sachalinensis*, whereas that of canopy trees ($D$ > ca. 30 cm) was larger for *P. glehnii*. Mortality rate of understory trees ($D$ < ca. 30 cm) was lower in *A. sachalinensis*, whereas that of canopy trees was lower for *P. glehnii*. There was gradual change abundance from *P. glehnii* to *A. sachalinensis* on young volcanic substrate. AGB of ca. 13.9 kg $m^{-2}$ was maintained with a high demographic turnover rate of 3% per year with CWP of ca. 0.40 kg $m^{-2}$ $year^{-1}$, suggesting that stands of the 1-ha plot experienced high disturbance, and recovery enhancing the increasing abundance of *A. sachalinensis*.

The overall results suggest that relatively mild winter in Himalayan subalpine forests may bring about lower disturbance compared to chilly-winter in subalpine forest in Hokkaido. Relatively higher biomass turnover rate in Hokkaido forest can be attributed to the recovery from such frequent disturbances. Co-dominance of coniferous species is likely to be associated with high disturbance in severer climate, which enhance inter-specific differentiation in successional niche.

## General Introduction

Subalpine forest forms a transitional zone between alpine meadow and montane forest, and is often dominated by coniferous species belonging to such genera as *Abies*, *Picea*, *Juniperus*, *Tsuga*, *Larix* and *Pinus*, which are resistant to cold climate (Liu 1997). Subalpine coniferous forests form the highest altitude forest zone shaping forest line. They provide such services to local communities as tourism, water supply, timber, fuel wood, and livestock feeding sites. Due to the location in high elevation, their functions of water supply and erosion prevention provide benefits to remote downstream communities as well. Understanding of structural and dynamic properties of subalpine forests is therefore essential not only for ecology but for natural resource management.

The structure of forest in canopy architecture, species composition, is influenced by many factors including disturbance and competitive interactions in resource use between trees (North *et al.* 2004). Among regions in the Northern Hemisphere, there are varied environmental conditions that regulate subalpine forests. High altitude forests in the world-highest Himalayas located in low latitude, ca. 27–29°N, are regulated by a variation of climatic factors such as precipitation, temperature, wind, solar radiation (Ohsawa 1990; Kira 1991; Krauchi *et al.* 2000) together with low atmospheric pressure and high UV-B radiation (Sullivan 2005), and these forests are highly disturbed by human activities via livestock trampling and tree harvesting (Krauchi *et al.* 2000; Gairola *et al.* 2008, 2009, 2014). In contrast, subalpine forests in Hokkaido, northern Japan at ca. 43°N with large intra-annual variation in temperature (Ohsawa 1990) are characterized by severe winter, causing tree crown damage by snow and rime-ice deposition and stem breakage by freezing. Thus, severe winter brings about natural disturbances on subalpine forests in Hokkaido.

In comparison with Himalayan subalpine forests, the effect of direct human disturbance is almost negligible there.

By altering forest structure, disturbances directly affect stand dynamics and shape larger-scale forest landscape (Turner *et al.* 1994), Forest response to disturbances varies depending on the types, size, severity and frequency of disturbances (Taylor *et al.* 1996). Dynamic properties of plant community structure, tree populations and forest ecosystem processes are prone to disturbance regimes of the site (Taylor and Qin 1988; Taylor *et al.* 1996).

Tree population dynamics are quantified by demographic processes of recruitment, size growth and mortality. Quantifying demographic processes is also needed to predict ecosystem dynamics of the forest as an assembly of tree populations (Peet and Christensen 1980). Understanding the forest dynamics and development history of subalpine coniferous forests is of great importance of sustainable ecosystem management.

The aim of this study was to quantify the structure and dynamics of dominant coniferous species in two contrastive subalpine forests; *Abies spectabilis* dominated forest in the Langtang National Park, in eastern Himalaya, Nepal, and *Abies sachalinensis–Picea glehnii* co-dominated forest on Mount Oakan in the Akan National Park, eastern Hokkaido, Japan. This study is composed of three chapters. In Chapter 1, I examined the change in plant community structure and population structure of mono-dominant *Abies spectabilis* with topographic conditions and anthropogenic disturbances in subalpine forest of Langtang Himalaya. I employed a series of general linear models to evaluate which factors contributed to forest structure measures. In Chapter 2, I quantified tree growth rate, aboveground biomass and biomass turnover rate of *Abies spectabilis* along altitudinal gradient in Langtang Himalaya. In Chapter 3, I quantified structure and dynamics of Oakan forest, focusing on contrastive architectural and demographic properties between *Abies sahalinensis* and *Picea glehnii*. In Chapters 2 and 3, I developed a procedure of estimating coarse wood production rate, or demographic turnover rate of aboveground biomass. I discussed possible reasons of higher biomass storage in Langtang forest and similar coarse wood production rate in two forests, from the viewpoint of contrastive disturbance regimes and data sampling protocols.

# Chapter 1

# Topographic and anthropogenic factors shaping subalpine *Abies spectabilis* forest in Langtang National Park, eastern Himalaya

## 1.1 Introduction

Subalpine forests are prone to natural variation in climate (Kullman 1988), and we commonly observe a variety of disturbances and their influence on population structure of tree species in forest ecosystems (North *et al.* 2004). Population structure of dominant tree species reflects the regeneration/degradation status of the species (Gairola *et al.* 2014), which represents the forest structure (Zhang *et al.* 2007). Mountain forests have been described on the basis of altitudinal change. In high altitude, climatic factors such as temperature, precipitation, wind and solar radiation strongly influence the forest structure (Ohsawa 1990; Kira 1991; Krauchi *et al.* 2000). Besides, all these topography, soil condition and the degree of human disturbances modify the distribution and structure of mountain forests (Krauchi *et al.* 2000; Gairola *et al.* 2008, 2009, 2014). Subalpine forests of Nepal Himalaya are distributed at the highest altitude in the world, which provide opportunities to evaluate how disturbances impact the forest structure in such environment.

Subalpine forests in the Himalayas are often dominated by *Abies spectabilis* (D. Don) Mirb. *A. spectabilis* is a tall evergreen conifer occurring in high-altitude Himalayas from Afghanistan to Nepal (Stainton 1972). *Abies spectabilis* usually prefer moist northern slopes (Tabata 2004; Ghimire and Lekhak 2007). On the northern slopes at altitude above 3000 m, it tends to dominate the forest. At moist sites, *A. spectabilis* forest is superseded by *Betula utilis* forest near the forest line. On the southern slopes, in contrast, subalpine zone is often dominated by *Juniperus recurva* forest from 3000 to 3600 m, and by dwarf scrub in alpine zone (Stainton 1972).

Subalpine forests in Himalayas are prone to anthropogenic disturbances due to severe climatic conditions and high-altitude residence of local people (Gairola *et al.* 2014). There are some studies that examine the role of disturbances on the plant species composition in subalpine forests (Taylor *et al.* 1996; Kumar and Ram 2005; Gairola *et al.* 2009; Zhang *et al.* 2010; Rai *et al.* 2012). However, the question how topographic and anthropogenic factors jointly affect tree community and stand structure is not yet fully understood in subalpine forests of Himalayas (Qingshan *et al.* 2007; Gairola *et al.* 2008; Jiangming *et al.* 2008; Gairola *et al.* 2014). Regardless of high-elevation distribution, subalpine forests in the Himalayas have been experiencing strong human pressure through timber logging, livestock farming and tourism, and are facing the progress of degradation, deforestation, and the loss of ecological services for local residents (Stevens 2003; Garbarino *et al.* 2014). For the conservation of this unique vegetation and ecological services it provides, it is necessary to evaluate the present status of *A. spectabilis* population and forest-stand conditions over the entire range of subalpine forest in relation to natural and human disturbances. The present study was carried out in the *Abies spectabilis* forest in the Langtang National Park, Nepal Himalaya, so as to address two research questions: (1) by which environmental factors the population structure of *A. spectabilis* is regulated; and (2) how natural and/or anthropogenic disturbances bring about emerging effects on the forest structure at large-scale subalpine landscape. This study aims to contribute to the reduction of forest degradation based on ecological knowledge.

## 1.2 Study area and methods

The present study was carried out in a subalpine forest on north facing slope located around the trekking route passing Cholangpati (with hotels) in the Langtang National Park, Nepal Himalaya (85°15′–86°00′E 28°00′–28°20′N, 3100–3900 m a.s.l.) (Figures 1-1 and 1-2). The forest was exclusively dominated by *Abies spectabilis*. At lower elevation as well as higher up to 3500 m on northwestern slopes, evergreen oak forest dominated by *Quercus semecarpifolia* was located (Figure 1-1). Above the forest limit around 3900 m, shrub of *Rhododendron anthopogon* and *R. lepidotum* replaced *Abies* forest. *Abies spectabilis* in this area grew up to 43 m tall. Subalpine *Abies spectabilis* forest is often fragmented due to human impact in the Langtang National Park, whereas the study area represented subalpine *Abies* forest with high and continuous coverage, with the scatter of meadow patches as deforested gaps (Figure 1-1). The total area of subalpine forest in the frame of Figure 1-1 accounts for 2.23 km$^2$.

Based on the data of the nearest weather station in Dhunche at 28°7′N 85°17′E, 1982 m a.s.l. (Department of Hydrology and Meteorology, Kathmandu, 2010), mean annual rainfall over 1999-2008 was 2038 mm with the highest monthly rainfall in July at 568 mm, and the monthly mean temperature was highest at 20.2℃ in July and lowest in January at 8.8℃ (Figure 1-3). The warmth index (WI) and the coldness index (CI) (Kira 1991) were calculated for three reference altitudes; lower limit (3100 m), mid elevation (3500 m) and upper limit (3900 m) of subalpine *Abies spectabilis* forest in the study site, by assuming –0.6℃ lapse rate per 100 m from the Dhunche Station at 1982 m. WI were 51.5, 33.5 and 15.7℃ month at 3100, 3500 and 3900 m respectively. Meantime, CI were –5.0, –16.3 and –28.3℃ month at 3100, 3500 and 3900 m respectively. These suggest that the forest limit is determined by the growing-season temperature sum at WI =15℃ month (Kira 1991; Ohsawa 1990, 1993), and the limit of evergreen broad-leaved forest at CI = –10℃ month is around at 3500 m a.s.l., corresponding to the midst of the subalpine *Abies spectabilis* forest in northeast slopes, and to the upper limit of *Quercus semecarpifolia* forest in northwestern slopes (Figure 1-1), thus the luck of deciduous broadleaved forest between subalpine fir forest and montane evergreen oak forest can be explained by mild winter in the area.

In the target subalpine forest, there were grazing pressure by yaks (*Bos grunniens*), cows (*Bos taurus*), horses (*Equus caballus*) and sheep (*Ovis aries*), concentrated during July, August and September. Local people take their cows and sheep in the forest for grazing. The entire ground surface of the study area was covered with mosses, litter and humus layer, whereas sites with high trampling pressure disturbed the ground cover and humus layer, removed with the sign of hoof on the ground surface. I observed the ground surface inside the forest greatly affected by trampling. The ground surface was pressed down some 10 to 20 cm from the original surface level.

The forest has also been influenced by tourism, with Lake Gosainkund (4380 m a.s.l.) being the area attraction center for many tourists. Hoteliers inside the study site (Figures 1-1 and 1-2) cut down trees for firewood and timber. Cut stumps of *Abies spectabilis* and *Rhododendron* spp. were commonly observed inside forest stands. The hoteliers in the area got permission only to collect dry wood of dead trees from the forest for firewood and timber. Wood of *Abies spectabilis* is preferred as timber and wood of *Rhododendron* spp. is as firewood. In some instances, hoteliers removed the bark from the basal region to induce death, and used wood of dead stems. There were some open meadow and/or shrub lands within the subalpine forest zone (Figure 1-1) presumably due to past human impact.

In October 2008, I carried out vegetation censuses by setting nine transects along maximum slope angle across altitudinal ranges within the study area. Among these, four transects ended up at the ridge of the mountain slope forming topographic edge of fir forest, while the other five ended up at the forest line. I established 80 plots of 10-by-10 m in slope surface area (Figure 1-1); the number of plots in each transect ranged from 7 to 12. Using average inclination of slope, I obtained horizontal area of each plot for density calculation. I recorded the geographic location and elevation of each plot using a GPS (Garmin eTrex Vista).

In each of 80 plots, I recorded the number of individual stems of every tree and measured stem diameter at breast height (DBH) 1.37 m above ground level. I categorized individuals into three size categories, namely trees (DBH ≥ 1.0 cm), saplings (DBH < 1.0 cm and top height ≥ 20 cm) and seedlings (height < 20 cm). I define juveniles of *Abies spectabilis* to be individuals < 1 cm DBH (i.e. seedlings plus saplings). I recorded the presence of shrub species (shorter than 137 cm). Due to the variation in growth forms, some species were recorded in both tree and shrub categories. If the individual plant had no branch below the height of 137 cm, I recorded it a tree; otherwise the individual had profuse branching below 137 cm, I recorded it a shrub.

I divided each plot into four subplots of 5-by-5 m, and recorded the height of all seedlings and saplings of *Abies spectabilis* occurring only in two diagonal subplots. The degree of trampling intensity was categorized into three classes: category 'high' is for plots where more than 50% of ground surface was disturbed due to trampling with pressed surface to 10-20 cm; category 'middle' is for plots with 10-50% of surface disturbance by trampling; category 'low' is for plots where trampling disturbance was less than 10%. I recorded the geographic location and elevation of each plot using a GPS (Garmin eTrex Vista). Slope inclination and slope aspect were measured by using a clinometer. I counted in every plot the number of cut stumps (≥ 10 cm cross-section diameter) and fallen logs (≥ 20 cm in basal diameter). From each plot, a soil sample of ca. 200 g wet weight was collected at 15-cm deep from the ground surface. Soil samples were air dried in shade and packed in airtight plastic bags for laboratory analysis. From samples, carbon and nitrogen content was measured in the Ecology laboratory of Central Department of Botany, Tribhuvan University, following Gupta (2000). I made identification of plant species with herbarium specimens. Most of the specimens were identified in the field with the help of floristic references (Stainton and Polunin 1987; Stainton 1988), whereas identification of remaining were made in the Herbarium of Central Department of Botany in Tribhuvan University. Botanical nomenclature followed Press *et al.* (2000).

The statistical analysis was carried out using R (R core team 2013). For the ordination of species composition, Package Vegan (Oksanen *et.al.* 2013) was used. I examined how stand variables of each plot (tree density of *Abies spectabilis*, that of other species, juvenile density of *A. spectabilis*, total basal area and maximum DBH, species richness, soil C content and soil C/N ratio) were related to topographic and anthropogenic factors (altitude, slope inclination, slope aspect, number of fallen logs and cut stumps, and trampling intensity). Categorical variables (slope aspect and trampling intensity) were treated as factorial. For slope aspect, less than $180^{o}$ were defined northeast (default), and more than $180^{o}$ to be defined northwest. While analyzing the generalized linear model, altitude was in km and 3.5 km was taken as default mid elevation. In case of slope inclination, 16° (as average) was set default. For trampling, trampling intensity, 'low' was set default. Because saplings were rare compared to seedlings (saplings were present only in 33 plots and few in number), I examined seedlings and saplings of *Abies spectabilis* collectively, and called juveniles in this study. To examine the variation in composition of woody plant species across 80 plots, I used the detrended correspondence analysis (DCA) (Hill and Gauch 1980) based on the presence/absence records. I used the first axis value of DCA to quantify the community structure of each plot, and used it as the community variable to be related to environmental factors. The generalized linear models (Hastie and Tibshirani 1990) was applied to relate forest variables (response variables) and environmental factors (explanatory variables). I used Package MASS (Venables and Ripley 2002) to run negative binomial model for count data. The count-based response variables follow negative binomial (with log-link function), and continuous non-negative variables follow gamma distribution (with log-link function). For DCA, I assumed variation follows Gaussian distribution. The best models are selected by the lowest AIC.

### 1.3 Results

Altogether 25 species were recorded from 80 sampling plots (Table 1-1). Numbers of species (excluding *Abies spectabilis*) in each plot were few (Table 1-2). Detrended correspondence analysis (DCA) based on the presence of species abbreviated the observed variation in woody species composition with 0.16 and 0.08 by the first and second axes. These small contribution ratios of the two axes and the U-shaped dispersion of the second-axis values against the first-axis values are caused by opportunistic and low abundances of minor species. I therefore use the value of DCA first axis only. Species distributions along the first axis suggested no clear separation into groups. *Rhododendron. arboreum, R. barbatum, Jasminum humile, Rubus hypargyrus* and *Lyonia ovalifolia* with large values on DCA first axis were found only towards the lower altitude, whereas *Rhododendron anthopogon* with small value on the first axis was found only on higher altitude (Figure 1-4).

The height distribution of *Abies spectabilis* juveniles (Figure 1-5A) indicates abundant seedlings far more than saplings. Out of 80 plots *Abies spectabilis* seedlings were present in 72 plots and saplings were present only in 33 plots (Table 1-2). Frequency distribution of DBH showed inverse-J shape except for the smallest class of DBH < 10 cm (Figure 1-5B). The range of maximum DBH in each plot were between 14.5 to 167.5 cm (Table 1-2).

Pairwise correlations among environmental variables show no significant tendency (Table 1-3A), so that I carried out the examination of how forest variables are explained by the linear combination of environmental variables (as in Table 1-4). By contrast, forest stand variables were mutually interdependent (Table 1-3B). The most pronounced relationships were that juvenile density of *Abies spectabilis* and species richness was low in developed stands with high basal area and maximum stem size.

Table 1-4 shows environment dependence of forest variables. With altitude, tree densities of *Abies spectabilis* and other species, and basal area were decreased while juvenile density of *A. spectabilis* was increased (Table 1-4). Density of *Abies* juveniles was decreased with trampling intensity (Table 1-4), and with basal area (Table 1-3B, Figure 1-6). Soil carbon-to-nitrogen ratio was lower in higher altitude. Densities of *Abies spectabilis* trees and number of species were higher on steep slopes, while maximum DBH were smaller there (Table 1-4). The study area has steep slopes ranging from 14°–38° (Table 1-2). Increase in slopes brought about the decrease in soil organic carbon content. Soil C/N ratio was generally low across plots (Table 1-2), meanwhile it was relatively high on steep slopes. The study area was set on north-facing slope (Figure 1-1), where I distinguished slope aspect into northeast (NE) and northwest (NW). There was no clear relationship between forest stand variables and slope aspect, while soil C/N ratio were found lower on NW slope than on NE (Table 1-4).

Anthropogenic factors such as the density of man-cut stumps influenced tree population structure. There were only 26 plots without cut stumps (Table 1-2). The average cut stump density per plot (surface area of 100 m$^2$) was 2.3. Tree density was higher in plots with more cut stumps while basal area and maximum DBH were smaller in these plots (Table 1-4). Soil organic carbon content was decreased, and species number was increased with cut stump density (Table 1-4). Both the number of species and the value of DCA first axis were decreased with altitude, with the number of fallen logs, and with increasing trampling intensity. Meantime, they were increased on steep slopes.

## 1.4 Discussion

Altitude, topography and disturbance are the important determinants that characterize the structure and composition of subalpine forest (Liu 1997; Grytnes 2003; Gairola *et al.* 2008, 2009, 2014). The studied forest was poor in woody species diversity (Table 1-1), and there was no clear differentiation in species composition within the subalpine *Abies spectabilis* forest. This study suggested tree density, total basal area, and number of woody species were decreased with altitude, which agrees with the previous studies (Yoda 1967; Miyajima and Takahashi 2007; Dang *et al.* 2013; Gairola *et al.* 2014). Altitude is linked with climatic environments such as temperature and precipitation (Cierjacks *et al.* 2008). Low temperature in high-elevation subalpine zone influences tree growth (Zhang *et al.* 2010), which results in the reduction of density of trees, basal area and maximum tree size. Meantime, Takahashi *et al.* (2012) suggested the decrease in tree density at high altitude is mainly due to mechanical damage, strong winds and snow deposition, not to low temperature. Subalpine forests are also affected by topographic factors like slope inclination and aspect (Miller and Halpern 1998). The increase in tree density for both *Abies spectabilis* and other species and the decrease in maximum tree size on steep slopes suggest that trees cannot grow large due to unstable substrate stands. On steep slopes, species richness was higher, and species composition tended to be similar to that in lower elevation, which also suggests that there are higher opportunity to find more species in relatively short-statured stands with higher tree density per unit area.

Disturbances are common in subalpine forests (Taylor *et al.* 1996). High-altitude forests in Himalayas are affected by timber logging and trampling (Kreyling *et al.* 2008; Gairola *et al.* 2014; Garbarino *et al.* 2014). High anthropogenic disturbances via trampling intensity reduce the plant diversity in subalpine forests (Dang *et al.* 2009; Mingyu *et al.* 2009; Garbarino *et al.* 2014). Low- and moderate-class trampling showed less effect on forest-floor moss cover than high-class trampling (Mingyu *et al.* 2009). The present subalpine forest was highly disturbed by livestock trampling, and where sites with high trampling intensity showed removal of moss and litter cover and humus layer. *Abies spectabilis* juveniles and density of non-*Abies* trees were reduced by increased trampling intensity due to the loss of safe site for establishment, which is consistent with those reported elsewhere (Eilu and Obua 2005; Wehn *et al.* 2011; Garbarino *et al.* 2014). Zhang *et al.* (2010) found decline in seedling density due to trampling by yaks and human interference in southeast Tibet. In the present forest, species composition in plots with high trampling intensity was similar to that in high-altitude plots, and species richness was decreased with trampling intensity.

The studied forest also experienced logging of trees for timber and firewood. Increasing tourists cause demand for firewood and enhance illegal logging (Garbarino *et al.* 2014). Tree density of *Abies spectabilis* and species richness were higher in plots with more cut stumps, while basal area and maximum tree size were decreased there (Table 1-4). The removal of canopy trees may enhance replacement by small-sized trees. Selective removal of dominant and subordinate species, i.e. *Abies spectabilis* and *Rhododendron campanulatum* for timber and firewood respectively, may provide chance for other species to establish. This is a possible reason of higher species richness in plots with higher cut stump density.

Soil properties such as organic carbon and nitrogen content are interrelated with the structural properties of forest stands (Egnell *et al.* 2015). Topography is an important determinant for soil carbon and nitrogen content in subalpine coniferous forest (Garten 2000). In the study site, soil organic carbon content was found low on steep slopes. Due to direct solar radiation, soil in steeper slopes gets drier (Small and McCarthy 2005), which results in the fast decomposition of soil organic carbon. Meantime, soil C/N ratio was higher on steeper slopes, suggesting higher microbial activities due to increased radiation and soil temperature. Soil C/N ratio declines with increase in elevation (Table 1-4), which may be due to lower microbial activity in low temperature. Soil carbon and nitrogen content were also varied with disturbances.

In high elevation, forest stands showed sparse canopy layer and dense juvenile layer (Table 1-4). Even at the same basal area, density of *Abies* juveniles was increased with altitude (Figure 1-6). In higher elevation tall trees are damaged by wind and/or snow deposition (Qingshan *et al.* 2007), and where seedling regeneration is enhanced under better light conditions (Zhang *et al.* 2010). Similar results have been reported in other regions (Ghimire and Lekhak 2007; Gaire *et al.* 2010; Dang *et al.* 2013; Gairola *et al.* 2014).

Scattered non-forest gaps observed in the *Abies* forest zone (Figure 1-1) are likely caused by intensive pressure of livestock trampling and timber logging. As the present results indicated, *Abies* population is, to some extent, able to respond to such anthropogenic disturbances with enhanced regeneration. Selective logging indicated by cut stump density can enhance regrowth. It is needed to evaluate the types as well as the threshold intensities of human disturbances for sustainable management of subalpine *Abies* forests in high altitude Himalayas.

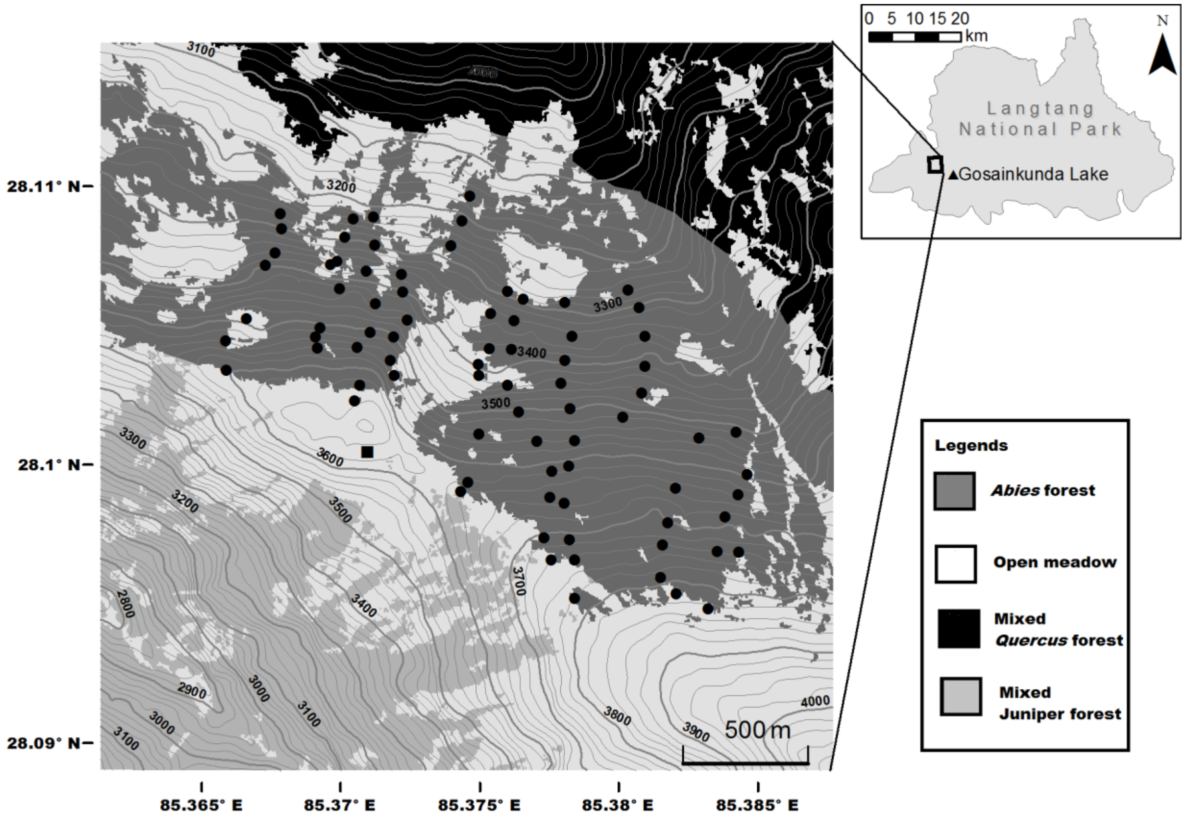

Figure 1-1. Vegetation distribution and sampling plot locations in Langtang National Park, eastern Himalaya. Plots of 10-by-10 m in surface area are shown by black circle (location based on GPS records) and the hotels at Cholangpati by filled square in vegetation map. Vegetation map is based on the vegetation 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. Langtang National Park map is based on IUCN and UNEP-WCMC (2016), the World Database on Protected Areas (WDPA) (on-line). [Downloaded Dec. 2016. Version 3.1], available at www.protected planet.net.

Figure 1-2. View of the study area on north facing slope covered by *Abies spectabilis* forest (left-hand side slope from the ridge); the construction on the ridge is hotels at Cholangpati at 3584 m a.s.l. Right-hand foreground tree crowns are *Juniperus recurva*.

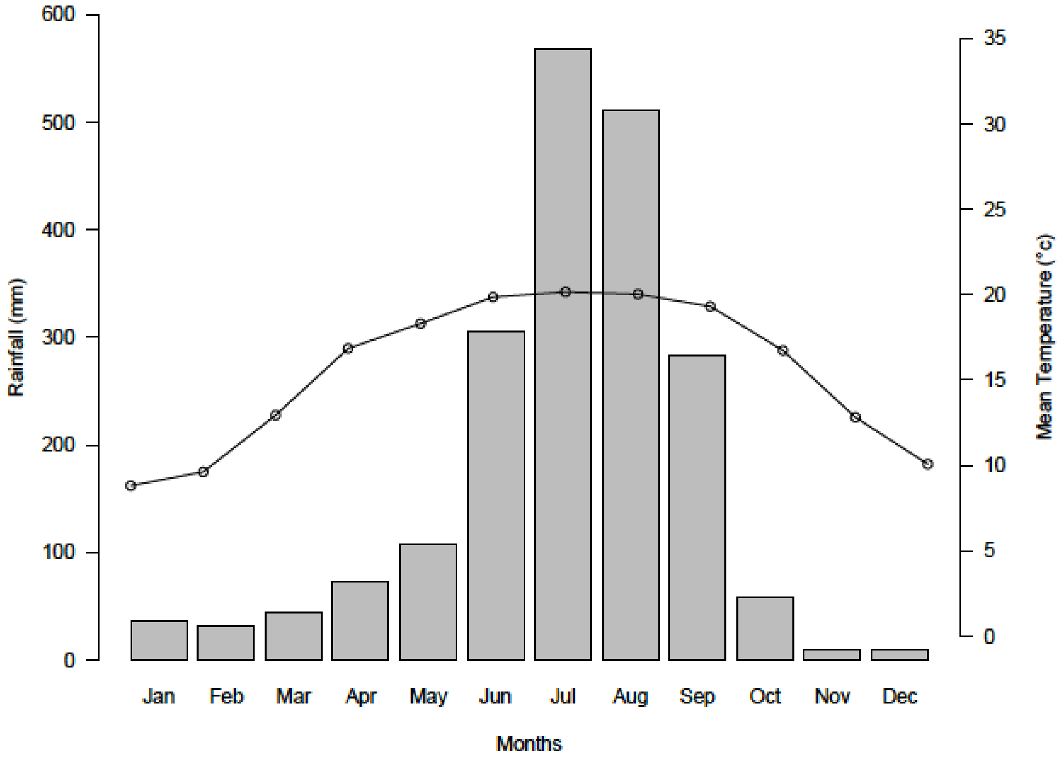

Figure 1-3. Average monthly temperature (℃) (circles with lines) and rainfall (mm) (barplot) at Dhunche Weather Station (85°18′E 28°06′N, 1982 m a.s.l.) for 1999–2008.

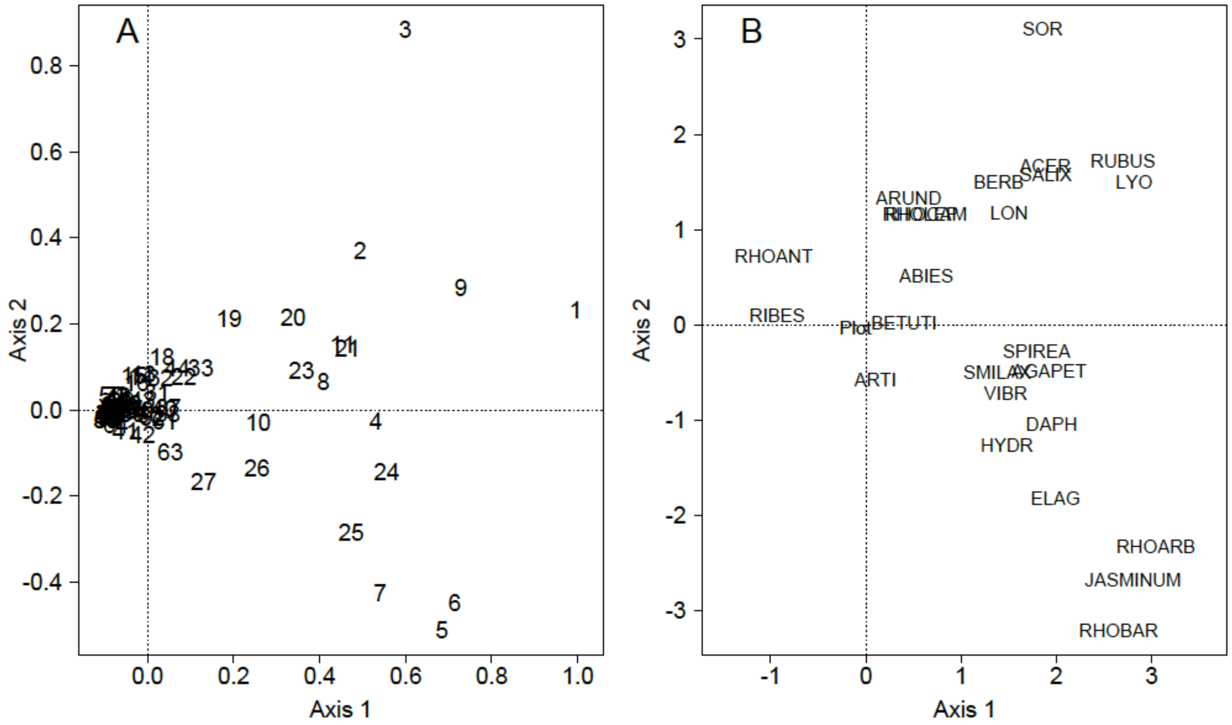

Figure 1-4. Results of the detrended correspondence analysis (DCA) based on the presence/absence of woody species in 80 plots. A, ordination of 80 plots; B, species scores on the coordinates of the first two axes. Species are shown by codes in Table 1.

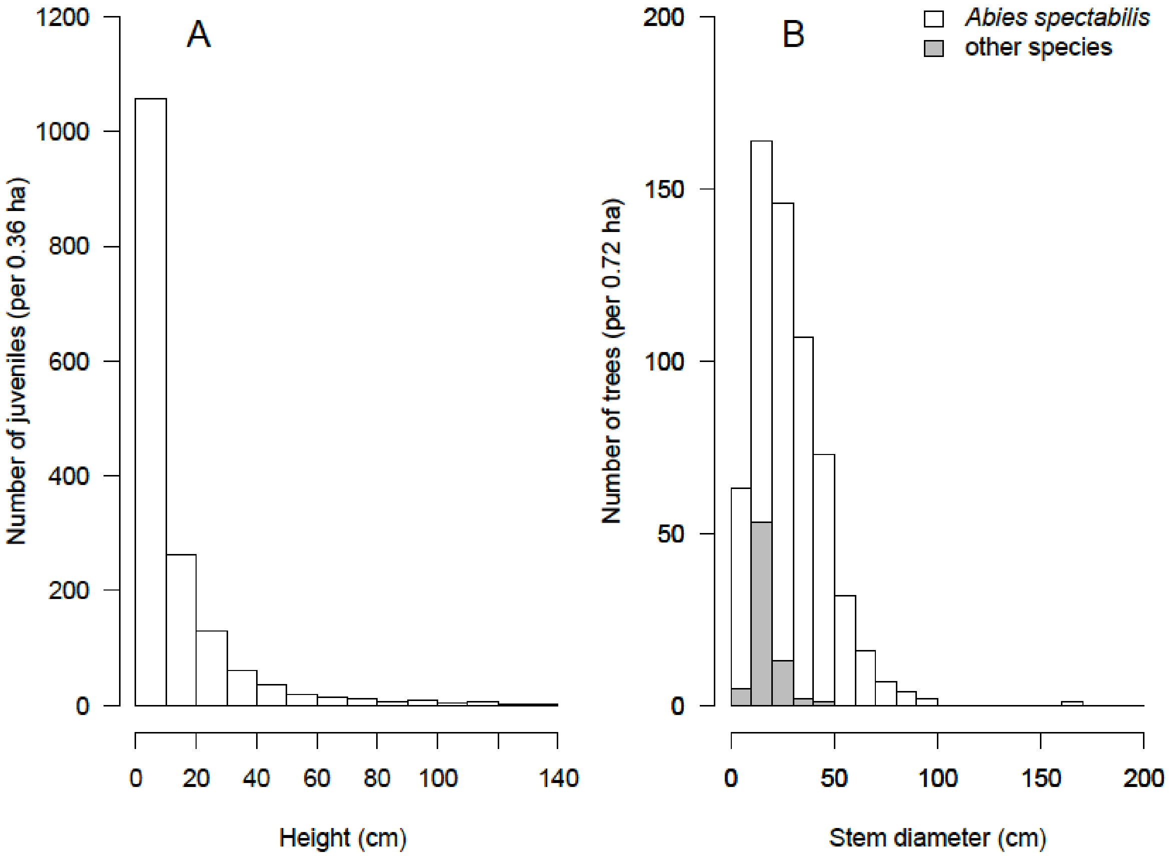

Figure 1-5A, Frequency distribution in top height of juveniles (< 1 cm DBH); B, frequency distribution in stem diameter at breast height (DBH) of trees (≥ 1 cm DBH); recorded in all 80 plots. Open, *Abies spectabilis*; shaded, other species.

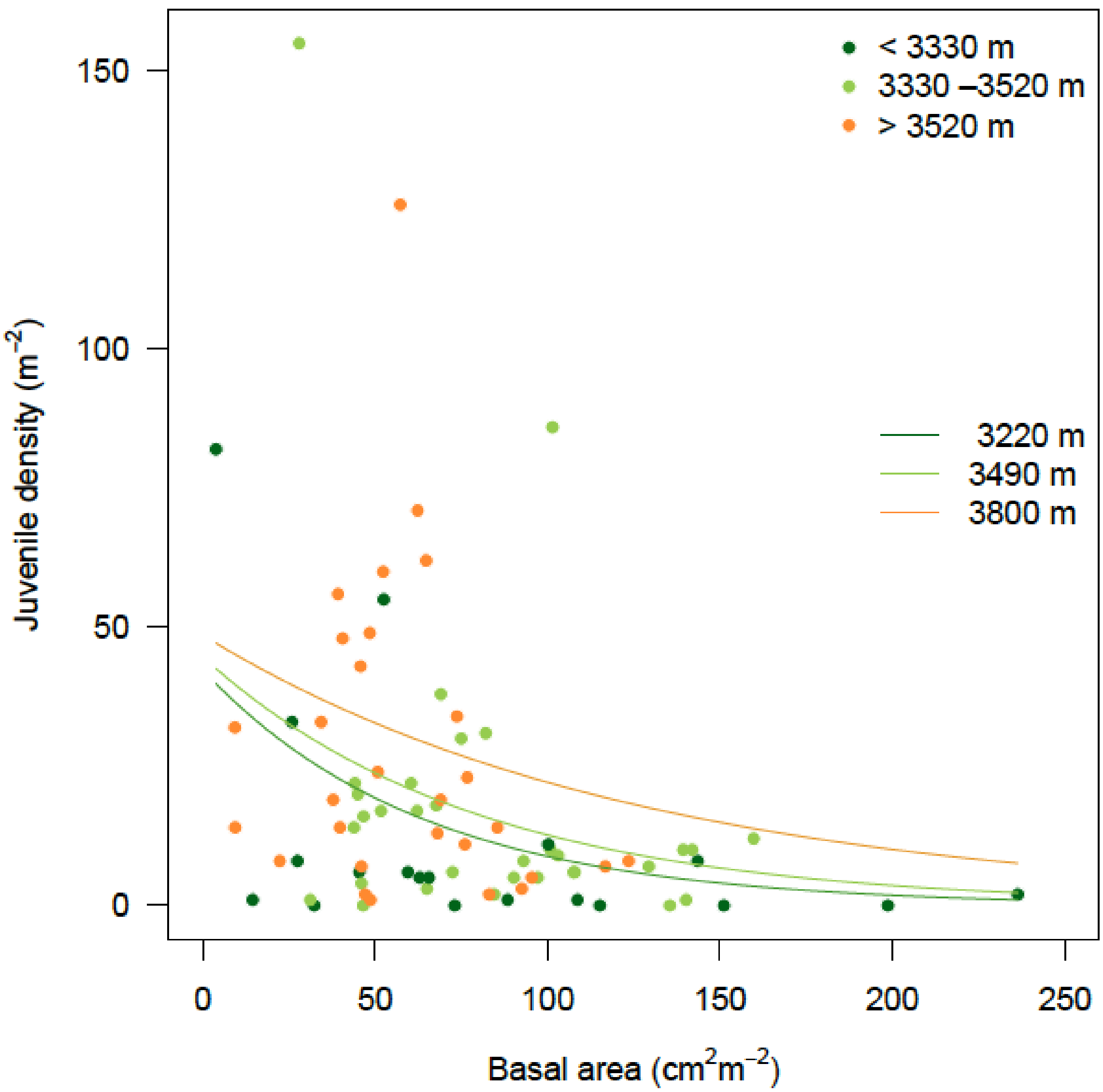

Figure 1-6. Density of *Abies spectabilis* juveniles plotted against basal area of all trees in 80 plots. Colors indicate altitude classes. The selected model of juvenile density with basal-area and altitude is: ln[juvenile density ($m^{-2}$)] = 1.34 – 0.012 BA + 0.36 alt + 0.021 alt BA, where BA is basal area ($cm^2m^{-2}$) and alt is altitude –3.5 km.

Table 1-1. Species and their abundance in 80 plots of subalpine *Abies spectabilis* forest.

| Code | Species | Abundance per 80 plots |
|---|---|---|
| ABIES | *Abies spectabilis* (D. Don) Mirb. | 80 |
| RHOCAM | *Rhododendron campanulatum* D. Don | 64 |
| VIBR | *Vibernum erubescens* Wall. ex. D. Don | 33 |
| DAPH | *Daphne bholua* Buch-Ham. ex. D. Don | 23 |
| BERB | *Berberis* sp. | 21 |
| SPIREA | *Spiraea bella* Sims. | 14 |
| BETUTI | *Betula utilis* D. Don | 12 |
| ARUND | *Arundinella* sp. | 12 |
| SMILAX | *Smilax aspera* L. | 10 |
| LON | *Lonicera acuminata* Wall. | 8 |
| RHOBAR | *Rhododendron barbatum* Wall. ex. D. Don | 7 |
| LYO | *Lyonia ovalifolia* (Wall.) Drude | 6 |
| SALIX | *Salix* sp. | 5 |
| ELAG | *Elaeagnus parvifolia* Wall. ex. Royle. | 4 |
| RHOLEP | *Rhododendron lepidotum* Wall. ex. D. Don | 3 |
| AGAPET | *Agapetes* sp. | 3 |
| RHOARB | *Rhododendron arboreum* Sm. | 2 |
| RHOANT | *Rhododendron anthopogon* D. Don | 2 |
| ARTI | *Artimisia* sp. | 2 |
| ACER | *Acer* sp. | 2 |
| SOR | *Sorbus microphylla* Wenz | 2 |
| HYDR | *Hydrangea aspera* Buch-Ham. ex. D. Don | 1 |
| JASMINUM | *Jasminum humile* L. | 1 |
| RUBUS | *Rubus hypargyrus.* Edgew. | 1 |
| RIBES | *Ribes orientale* Desf. | 1 |

Table 1-2. Forest-stand variable variations across 80 plots.

| Variables | Minimum | 2.5-% | Median | 97.5-% | Maximum |
|---|---|---|---|---|---|
| *Abies spectabilis* trees per plot | 1 | 1 | 6 | 16 | 25 |
| Trees other than *Abies* per plot | 0 | 0 | 0 | 7 | 14 |
| *A. spectabilis* seedlings per plot | 0 | 0 | 8 | 82 | 114 |
| *A. spectabilis* juveniles per plot | 0 | 0 | 10 | 87 | 155 |
| Basal area ($cm^2 m^{-2}$) | 3.9 | 9.5 | 66.7 | 161 | 236 |
| Maximum DBH (cm) | 14.5 | 18.9 | 47.0 | 94.5 | 167.5 |
| Soil C per dry mass (%) | 2.7 | 3.8 | 7.2 | 9.7 | 10.5 |
| Soil C/N ratio | 8 | 11.6 | 15.5 | 58.2 | 107 |
| Number of woody species per plot | 1 | 1 | 4 | 11 | 14 |
| Altitude (km) | 3.17 | 3.22 | 3.49 | 3.80 | 3.81 |
| Slope inclination (degree) | 14 | 16 | 25 | 36 | 38 |
| Number of fallen logs per plot | 0 | 0 | 1 | 6 | 7 |
| Number of cut stumps per plot | 0 | 0 | 1 | 14 | 19 |

Table 1-3. Pairwise Pearson correlation coefficients among environmental variables, and among forest stand variables.

(A) Environmental variables

| | Slope inclination | Slope aspect | Fallen logs | Trampling class | Cut stumps per plot |
|---|---|---|---|---|---|
| Altitude (km) | –0.063 | –0.039 | –0.101 | 0.101 | 0.149 |
| Slope inclination (°) | | 0.041 | –0.055 | 0.008 | –0.041 |
| Slope aspect | | | 0.085 | 0.121 | 0.017 |
| Fallen logs per plot | | | | 0.078 | –0.104 |
| Trampling class | | | | | 0.122 |

(B) Forest stand variables

| | Non-*Abies* tree density | *Abies* juvenile density | Maximum DBH | Basal area | Soil C per dry mass | Soil C/N ratio | DCA first axis | Species richness |
|---|---|---|---|---|---|---|---|---|
| *Abies* tree density ($m^{-2}$) | **–0.278** | –0.039 | **–0.271** | 0.052 | **–0.249** | –0.092 | **0.366** | **0.246** |
| Non-*Abies* tree density ($m^{-2}$) | | –0.115 | –0.083 | 0.004 | 0.155 | **0.409** | –0.019 | 0.167 |
| *Abies* juvenile density ($m^{-2}$) | | | **–0.431** | **–0.539** | **–0.233** | 0.014 | –0.208 | –0.035 |
| Maximum DBH (cm) | | | | **0.874** | **0.244** | –0.209 | **–0.258** | **–0.366** |
| Basal area ($cm^2$ $m^{-2}$) | | | | | 0.209 | –0.191 | –0.133 | **–0.386** |
| Soil C per dry mass (%) | | | | | | –0.176 | **–0.226** | –0.186 |
| Soil C/N ratio | | | | | | | 0.101 | **0.361** |
| DCA first axis | | | | | | | | **0.651** |

* All forest stand variables except DCA axis are log-transformed. Bold values are significant at P=0.05.

Table 1-4. Dependence of tree population, soil, and community properties on environmental variables; estimated parameters by generalized linear models.

| Objective variables* | Altitude (km) | Slope inclination (°) | Slope aspect (NW/NE) | Number of fallen logs | Number of cut stumps | Trampling intensity | | exp(constant) |
|---|---|---|---|---|---|---|---|---|
| | | | | | | middle/low | high/low | |
| *Population variables* | | | | | | | | |
| *Abies* tree density (m$^{-2}$) | –0.90 | 0.024 | | | 0.029 | | | 0.053 |
| Non-*Abies* tree density (m$^{-2}$) | –1.97 | 0.098 | | | | 1.01 | –0.61 | 0.0027 |
| *Abies* juvenile density (m$^{-2}$) | 2.3 | | | | | –0.74 | –0.90 | 0.85 |
| Basal area (cm$^2$ m$^{-2}$) | –0.57 | | | | –0.036 | | | 79.6 |
| Maximum stem diameter (cm) | | –0.012 | | | –0.036 | | | 63.9 |
| *Soil properties* | | | | | | | | |
| C per dry mass (%) | | –0.011 | | | –0.019 | | | 8.36 |
| C/N ratio | –0.51 | 0.021 | –0.21 | | | | | 17.3 |
| *Community attributes* | | | | | | | | |
| DCA axis-1 by species abundance | –0.67 | 0.0074 | | –0.022 | | –0.070 | –0.15 | |
| Number of species per plot (excl. *Abies*) | –2.7 | 0.018 | | –0.093 | 0.028 | –0.074 | –0.44 | 3.07 |

* Except DCA axis-1, all objective variables are log transformed; logarithmic horizontal plot area was set to be offset term for count-based density variables; negative binomial distributions were applied for count-based variables and gamma distribution for other variables except DCA axis-1, where normal distribution was applied.

# Chapter 2

## Aboveground biomass and turnover rate of subalpine *Abies spectabilis* forest in eastern Himalaya along altitudinal gradient

## 2.1 Introduction

In subtropical mountains, intra-annual thermal variation is small compared to those in temperate regions (Ohsawa 1990; Cogbill and White 1991; Ohsawa 1993). In Himalayas, there occurs no summer-green deciduous broadleaved forest, and where evergreen broadleaved forests are replaced with altitude by evergreen coniferous forests. On moist north-facing slopes, *A. 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*, and by dwarf scrub of *Rhododendron* spp. are dominated 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 in the 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). In mountains, tree shape quantified by tree height and stem diameter varies with altitude (Aiba and Kitayama 1999; Wang *et al.* 2006; Miyajima and Takahashi 2007; Liang *et al.* 2010). Biomass increment rate is also low in higher elevations due to cooler conditions (Tadaki *et al.* 1970).

In this study, I examined the variation in aboveground biomass and coarse wood production rate along elevation gradient in *Abies spectabilis* forest in eastern Himalaya. Coarse wood production rate per annum is defined to be annual biomass growth rate of survived trees, and it is the part of aboveground net primary production rate together with the production rate of fine, high-turnover components of leaves, twigs and reproductive organs (Kira and Shidei 1967; Clark *et al.* 2001). The coarse wood production rate can be estimated by recording radial stem increment of canopy trees from stem core samples and by projecting past tree height using allometric relationship between stem diameter and tree height.

Yoda (1967, 1968) estimated biomass and net primary production rate along altitudinal gradient from tropical to subalpine forest zones in subtropical region including Nepal Himalaya, and reported extremely high coverage in basal area and biomass storage, as compared to montane and subalpine forest in cool-temperate regions. So far, coarse wood production rate along elevation gradient is not yet fully examined in high altitude Himalayan forests with huge biomass storage. Tadaki *et al.* (1967,1970) reported total biomass and primary productivity of *A. veitchii* forest in the subalpine forest on 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 changes in biomass and turnover rate along altitudinal gradient in subalpine forests (Tadaki *et al.* 1970).

The purpose of this study is to describe the aboveground biomass and coarse wood production rate of mono-dominant *Abies spectabilis* trees along the entire range of subalpine *Abies* forest zone in Nepal Himalaya. This study was designed to address these research 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 related to tree architectural change? (3) How regeneration from sapling pool change with altitude? To evaluate these questions, I developed the simple assessment procedure using radial growth data (by stem core samples) and sampling height growth (by annual bud scars) for survivors at single-time census, with a set of appropriate statistical models.

## 2.2 Study area and methods

### *Study area description*

The study was carried out in Langtang National Park, Nepal Himalaya (85°15´– 86°00´E, 28°00´–28°20´N, 3100–3900 m a.s.l.) (Figure 2-1). Forest limit was around 3900 m, above which *Abies spectabilis* forest is replaced by *Rhododendron* scrubs. Below around 3100 m is 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℃ with highest monthly mean temperature in July at 20.2℃ and lowest in January at 8.8℃ (Figure 1-3, Chapter 1). Further description of the study area is in Chapter 1.

### *Field sampling and measurements*

During 1 and 13 October 2015, I established 36 plots of 10-by-10 m in slope surface area on canopy-closed forest stands that cover the entire altitudinal range of *Abies spectabilis* forest (Figure 2-1; filled circles), In these plots I 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 $H \geq 0.20$ m) were only occasionally observed in closed-canopy plots and because saplings were often abundant in forest edges, I monitored saplings in four of these plots and nine sampling plots set in forest margins. I also used *Abies* tree records in 80 plots set in 2008 (Chapter 1) to predict aboveground biomass (Figure 2-1, filled squares). Using average slope inclination, I obtained 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 I obtained stem diameter at breast height, $D$ (cm). I 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. I sampled wood cores using a core borer (Haglöf Sweden) to record radial wood increment in recent five years (to the nearest 0.01 mm with a digital caliper) judged from annual rings, for all canopy trees ($H \geq 10$ m, $D \geq 28.6$ cm) in 36 plots (1 to 7 canopy tree(s) per plot). For saplings, I measured their top height in 2015 and that three-years ago (in 2012), judged by scars of winter buds on the leader shoot.

*Allometry between stem diameter and tree height*

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

$$1/h = 1/AD^b + 1/h_{\max}, \text{ or}$$

$$h = h_{\max}\, AD^b/(AD^b + h_{\max}), \tag{2-1}$$

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 (2-1), I took logarithm of eqn (2-1) such that

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

I examined whether allometric coefficient $b = 1$ (proportional $H$: for small trees) or $b \neq 1$, and whether each of parameters ($A$, $b$, $h_{\max}$) are dependent on the altitude of plots. I used NLS on R (R core team 2013) for non-linear regression of parameter estimation (Bates and Watts 1988). To select the best model, I compared all possible models by means of AICc using R package MuMIn (Burnham and Anderson 2002).

### *Estimation of aboveground biomass*

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

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

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

### *Tree and sapling Growth*

As I measured five-year radial increment of stem wood at breast height, $\Delta r$ (cm), for all canopy trees, I estimated stem diameter in 2010 to be $D_{2010} = D_{2015} - 2\Delta r$ (cm), assuming that the bark thickness did not change during five years. Relative growth rate of stem diameter, $\mathrm{RGR}_D$ (year$^{-1}$), during 2010 and 2015 can be defined as

$$\mathrm{RGR}_D = (\ln D_{2015} - \ln D_{2010})/5. \tag{2-4}$$

I examined size and altitude dependence of $\mathrm{RGR}_D$ by using log-linear regression model (Chambers 1992): $\ln \mathrm{RGR}_D \sim \mathrm{alt} * \ln D_{2015}$, using glm of R, where ‘alt’ is the plot altitude minus

3.5 (km). Similarly for saplings, I obtained relative growth rate of sapling height from 3-year elongation record as,

$$\mathrm{RGR}_H = (\ln H_{2015} - \ln H_{2012})/3, \tag{2-5}$$

and examined how $\mathrm{RGR}_H$ was related to size and altitude by using the regression model: ln $\mathrm{RGR}_H$ ~ alt * ln $H_{2015}$, using glm of R. I used gamma distribution for RGR error distributions. Best model in size and altitude dependence was judged using AICc.

### *Estimation of past tree height and biomass*

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

$$(\mathrm{d}h/\mathrm{d}t)/h = [b\, h_{\max}/(AD^b + h_{\max})]\, (\mathrm{d}D/\mathrm{d}t)/D \tag{2-6}$$

or, by denoting the relative growth rate of $h$ (= $H$ –1.3) as $\mathrm{RGR}_h$ (year$^{-1}$),

$$\mathrm{RGR}_h / \mathrm{RGR}_D = b\, h_{\max} /(AD^b + h_{\max}). \tag{2-7}$$

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 $\mathrm{RGR}_h = (\ln h_{2015} - \ln h_{2010})/5$, I have

$$(\ln h_{2015} - \ln h_{2010}) / (\ln D_{2015} - \ln D_{2010}) = b\, h_{\max} / (AD_{2015}{}^{b} + h_{\max}). \qquad (2\text{-}8)$$

(cf. eqn (2-1)). Therefore, I estimated the past height, $H_{2010} = h_{2010} + 1.3$ (m), using the equation

$$\ln h_{2010} = \ln h_{2015} - (\ln D_{2015} - \ln D_{2010})\, b\, h_{\max}/(AD_{2015}{}^{b} + h_{\max}). \qquad (2\text{-}9)$$

By using eqn (2-3) with $D_{2010}$ and $H_{2010}$, I obtained total aboveground tree biomass, $W_{2010}$ (kg) for every canopy tree.

*Estimation of coarse wood production rate*

Increment rate of aboveground biomass for survivors (year$^{-1}$), sometimes called the 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 contribute to roughly half of ANPP (e.g. Malhi *et al.* 2004; Takyu *et al.* 2005).

I estimated annual rate of tree biomass increment, based on canopy-tree biomass $W$ in 2010 and 2015. I 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 mass of a given tree at year $t$. Annual time-step approximation of tree mass increment can be

$$(1 - \delta)\, W_{t+1} = W_t, \tag{2-10}$$

where $\delta$ (year$^{-1}$) is specific annual mass growth rate based on the final tree mass at year $t$+1 (Sheil 1999). To solve equation (2-10) over the period 2010–2015 (years),

$$\delta = 1 - (W_{2010}/W_{2015})^{1/5}, \tag{2-11}$$

and annual rate of aboveground coarse wood production of the tree is $\delta W_{2015}$ (kg year$^{-1}$). I calculated $\delta W_{2015}$ 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 with radial-growth record in each plot with plot-level aboveground biomass, AGB, in 2015 (kg m$^{-2}$) for all stems including those without radial-growth records:

$$\mathrm{CWP} = \mathrm{AGB}_{2015}\, \Sigma(\delta W_{2015})/\Sigma W_{2015}, \tag{2-12}$$

where CWP is defined for the period 2014 – 2015.

Because there is difference in $\delta$ among trees within a plot, the present tree-based estimation of annual CWP is recommended. Otherwise if I sum up biomass at two times first and employ eqn (2-10) for total biomass, I have underestimation of CWP, as is known for cases of demographic rate estimation in heterogeneous populations (Sheil and May, 1996).

I 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.

I showed the change in basal area, AGB and CWP with altitude, by dividing 36 plots into six altitude classes. I also estimated AGB for 80 plots set in 2008 (Chapter 1) using the altitude-dependent *D-H* allometry (eqn (2-1)) and $D^2H$-*W* allometry (eqn (2-3)). For them, I have divided 80 plots into 10 altitude classes to demonstrate altitudinal change in basal area and biomass in those plots. I defined biomass turnover rate to be CWP/AGB.

## 2.3 Results

*Allometry between stem diameter and tree height*

The best allometric model between stem diameter and tree height was that $b \neq 1$ and that *A*, *b* and $h_{\max}$ are all dependent on altitude of the plot. Estimated parameters were

$$b = 1.22 + 1.83\ \mathrm{alt}$$
$$A = \exp(-0.75 - 4.95\ \mathrm{alt}),\ \text{and} \qquad (2\text{-}13)$$
$$h_{\max} = \exp(3.95 - 3.23\ \mathrm{alt}).$$

Tree height of *Abies spectabilis* at any given stem diameter was decreased with altitude (Figure 2-3).

*Growth rate dependence on tree size and altitude*

I did not find the dependence of relative growth rate on altitude. Relative growth rate of stem decreases with stem diameter ($R^2 = 0.54$) of trees (Figure 2-4).

$\ln RGR_D = -1.53 - 1.01 \ln D.$

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

$$\ln \mathrm{RGR}_H = 0.103 - 3.16\ \mathrm{alt} - 0.524 \ln H + 0.788\ \mathrm{alt}\ (\ln H). \qquad (2\text{-}14)$$

(Figure 2-5). For taller saplings (> 50 cm), height growth rate increased with altitude, whereas for shorter saplings, those decreased with altitude.

*Altitude dependence of biomass and turnover rate*

The basal area for trees in 2015 was 97.6 $\mathrm{cm}^2\ \mathrm{m}^{-2}$. The basal area is fairly high as compared to those in other subalpine forests in Himalayas (Table 2-1). Tree basal area in 2008 was 74.9 $\mathrm{cm}^2\ \mathrm{m}^{-2}$. Tree basal area tended to decrease with altitude (Figure 2-6). Up to mid-elevation (< 3500 m), basal area did not show clear change with increase in altitude, while above 3500 m a.s.l., the tree basal area for *Abies* forest showed sharp decline ( Figure 2-6).

The total aboveground biomass estimated for the year 2015 was 48.9 kg $\mathrm{m}^{-2}$ as the average of 36 plots. The amount of aboveground biomass was high in comparison with those reported in subalpine coniferous forests (Table 2-1). AGB showed sharp decline in higher elevation (Figure 2-6). In contrast, the aboveground biomass estimates for 2008 was 37.1 kg $\mathrm{m}^{-2}$ as the average of 80 plots set at that time. Relatively higher estimate for 2015 biomass can be caused by the fact that I established plots in 2015 in well closed-canopy stands with larger biomass.

The coarse wood production rate (CWP) during 2014 and 2015 was estimated to be 0.488 kg $m^{-2}$ $year^{-1}$ as the average of 36 plots. CWP decreased with elevation (Figure 2-6). Biomass turnover rate (i.e. CWP/AGB) varied, and was 1.1% $year^{-1}$ in average (Figure 2-7). The coarse wood production rate varied from 0.228 to 1.41 kg $m^{-2}$ $year^{-1}$. CWP relative to aboveground biomass AGB tended to be decreased with altitude ($R^2 = 0.64$, Figure 2-8):

$$\ln \mathrm{CWP} = -2.51 + 3.44\,\mathrm{alt} + 0.450 \ln \mathrm{AGB} - 1.09\,\mathrm{alt}\,(\ln \mathrm{AGB}). \tag{2-15}$$

## 2.4 Discussion

Structure and biomass dynamics of subalpine forests of Himalayas are expected to be influenced by environmental conditions (Yoda 1967, 1968; Wang *et al.* 2006; Liang *et al.* 2010). In the present study, I 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 aboveground biomass and coarse wood production rate along altitudinal gradient. I 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; as 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 affected 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 is slower at higher elevation due to reduction in air temperature and increasing wind speed in a temperature forest in central Japan.

As I expected, the stem growth rate of *A. spectabilis* decreased with increase in altitude. However, the relative growth rate in stem diameter of canopy trees did not show altitude dependence in our study. Taking into account that trees were shorter at the same stem diameter in higher elevation (Figure 2-3), 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. This shows that growth rate of *Abies spp.* 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.

The growth rate in tip height of saplings of *A. spectabilis* did not simply decrease with altitude, but tall and short saplings showed different response to altitude (Figure 2-5). Generally plants grow slower at higher altitude since the environmental stress is severer at high altitude (Jobbagy and Jackson 2000). The present study found that growth rate for tall saplings was increased with altitude, but that growth rate for short saplings was decreased with altitude. 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 at lower elevation (Cunningham *et al.* 2006). Chapter 1 showed that seedling/sapling density of *Abies spectabilis* in the same forest was increased in higher elevation. Less shaded, under-canopy shelter of high-altitude stands provides favorable conditions for *Abies* regeneration.

The present study estimated high aboveground biomass of 48.9 kg $m^{-2}$ compared to those reported across subalpine forests in the Northern Hemisphere (Table 2-1). Adhikari *et al.* (1995) reported high basal area > 100 $cm^2$ $m^{-2}$ and 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) also reported basal area > 60 $cm^2$ $m^{-2}$ and 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 2-1). It should be also noted that I set plots with small size of 10 by 10 m in fully closed stands, and which may cause overestimation of biomass storage. In 2008, census in 80 plots with the same plot sizes, estimated biomass was ca. 37.1 kg $m^{-2}$, three quarter of the estimate for plots set in 2015.

My estimate of aboveground coarse wood production rate of about 0.5 kg $m^{-2}$ $year^{-1}$ is fairly low for the aboveground biomass of 50 kg $m^{-2}$. 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.

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 my studied plots was higher towards lower elevation and decreased towards higher elevation (Figure 2-6). At the same aboveground biomass, CWP was smaller in higher elevation (Figure 2-8), suggesting slower biomass turnover rate at higher elevation.

I have recorded low biomass turnover rate (1.1%, $\text{year}^{-1}$) in subalpine *A. spectabilis* forest (Figure 2-7), 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 have 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 be primarily responsible to the slower biomass turnover rate.

*Abies* forest zone is strongly influenced by altitude in its structure and biomass storage. The present results indicate that *Abies spectabilis* forest has high coverage in basal area and aboveground biomass as compared to other subalpine forest ecosystems. Stem architecture showed clear change with altitude and so did aboveground biomass and its turnover rate. Aboveground biomass is maintained by slow turnover rate relative to the usual forest ecosystems particularly in high altitude, which might be a key property of maintaining forest ecosystems near forest line in the highest elevation worldwide.

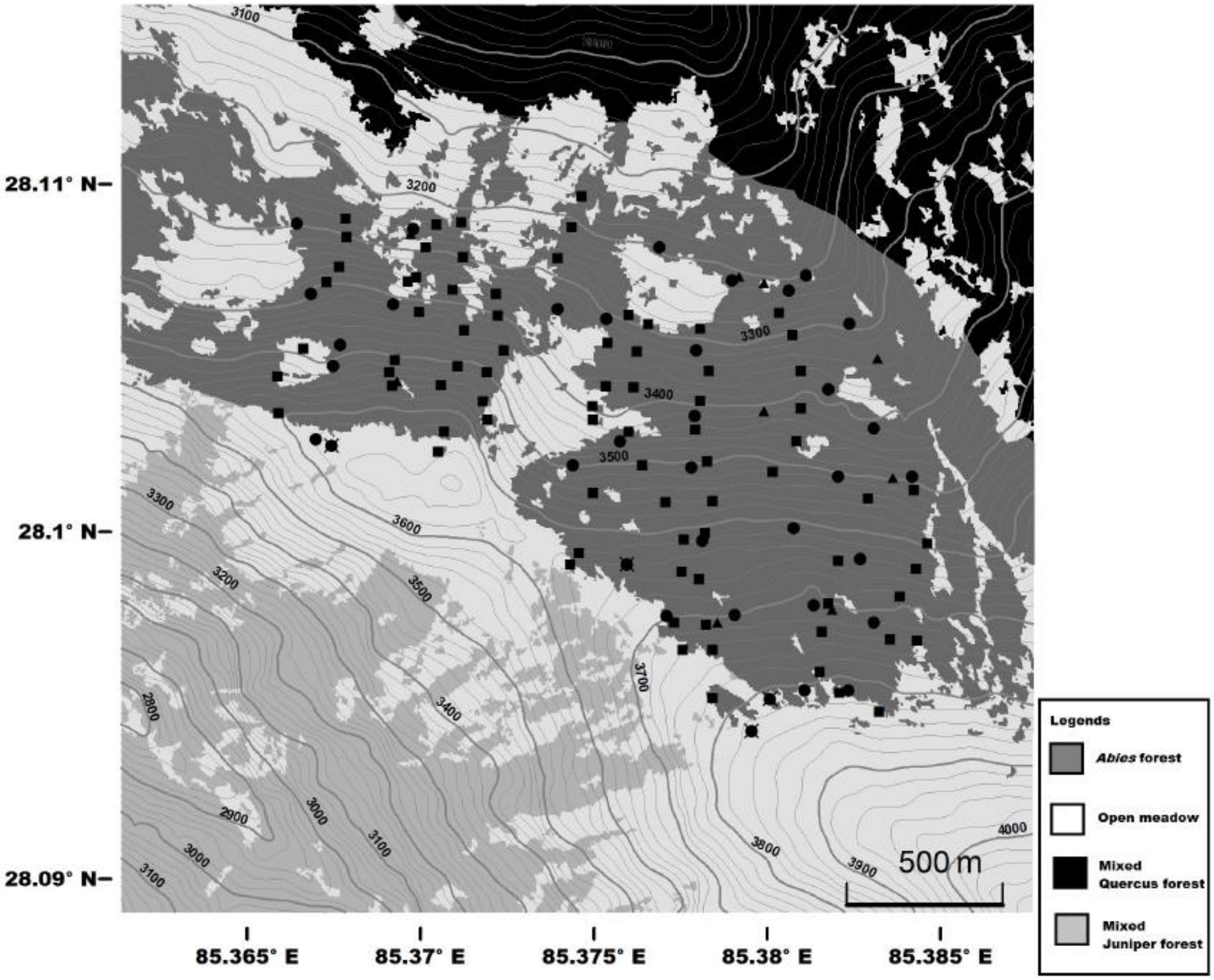

Figure 2-1. Vegetation distribution and sampling plot locations in Langtang National Park, eastern Himalaya. Plots of 10-by-10 m in surface area are shown by; filled square for tree sampling (2008); filled circle for tree sampling (2015); cross for sapling on same plots where trees were sampled (2015); triangle for sapling records (2015) (location based on GPS records). Vegetation map is based on the 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.

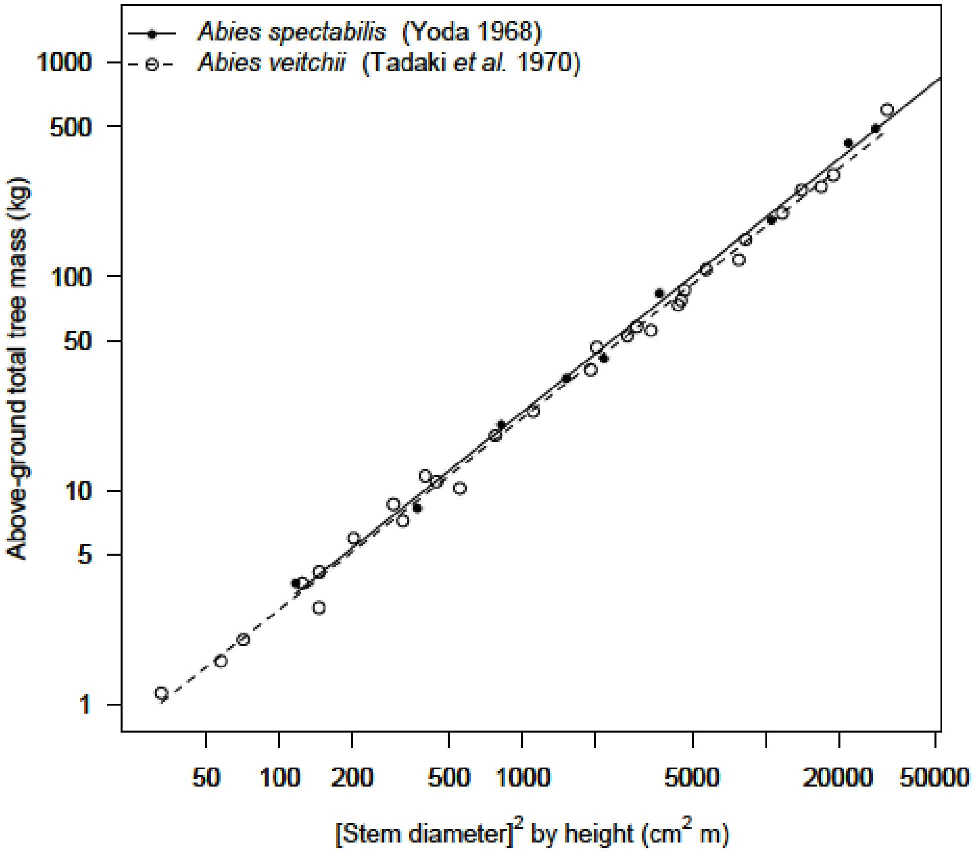

Figure 2-2. Allometry between aboveground tree biomass (*W*) versus squared stem diameter by tree height ($D^2H$). Closed circles, *Abies spectabilis* in eastern Nepal (Yoda 1968); open circles, *Abies veitchii* on Mt. Fuji, Japan (Tadaki *et al.* 1970).

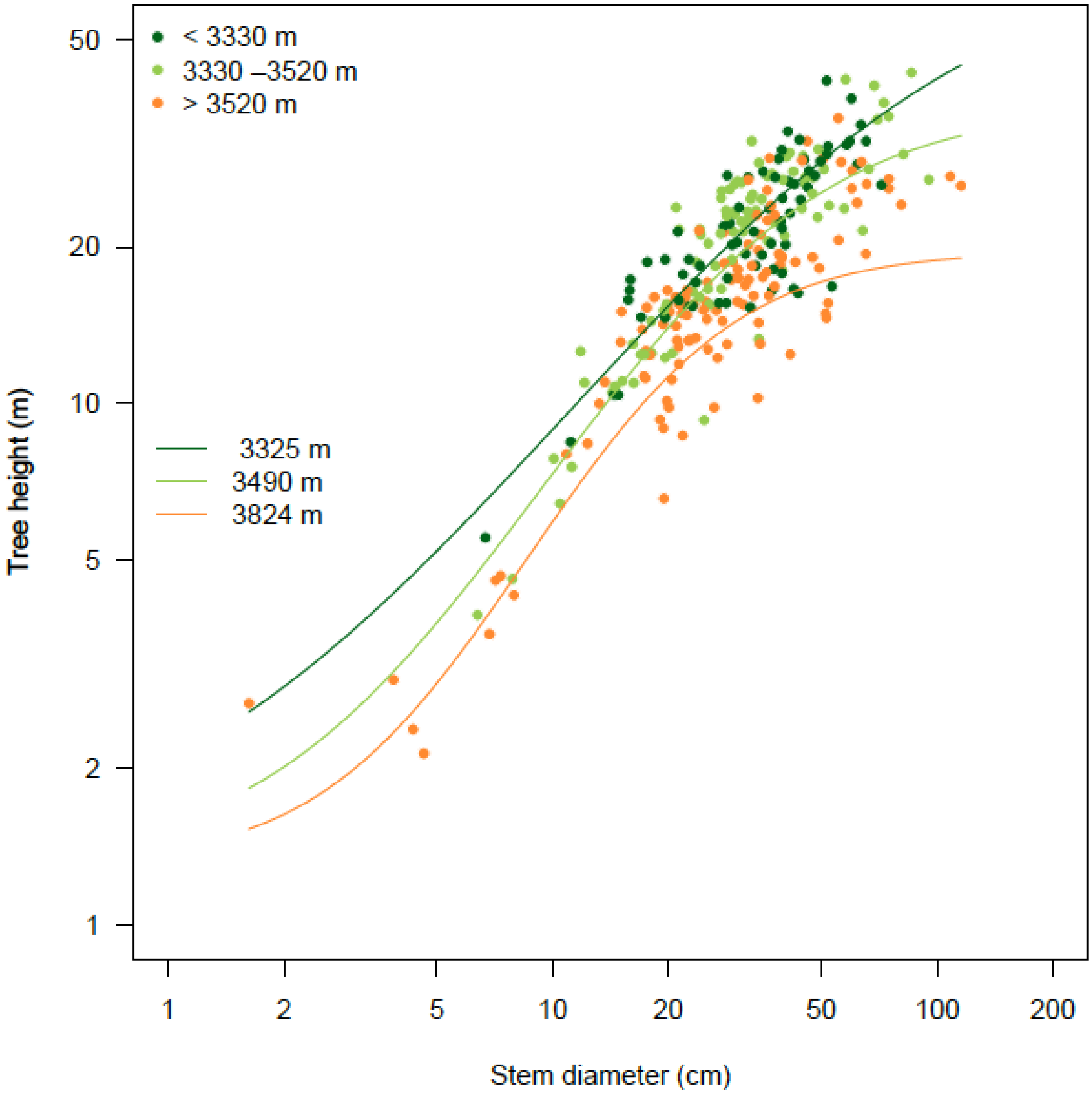

Figure 2-3. Tree height versus stem diameter relationship for *Abies spectabilis* trees in forest stand plots. Extended allometric equations with asymptotic height is applied, with the examination of the dependence on allometric parameters on plot altitude.

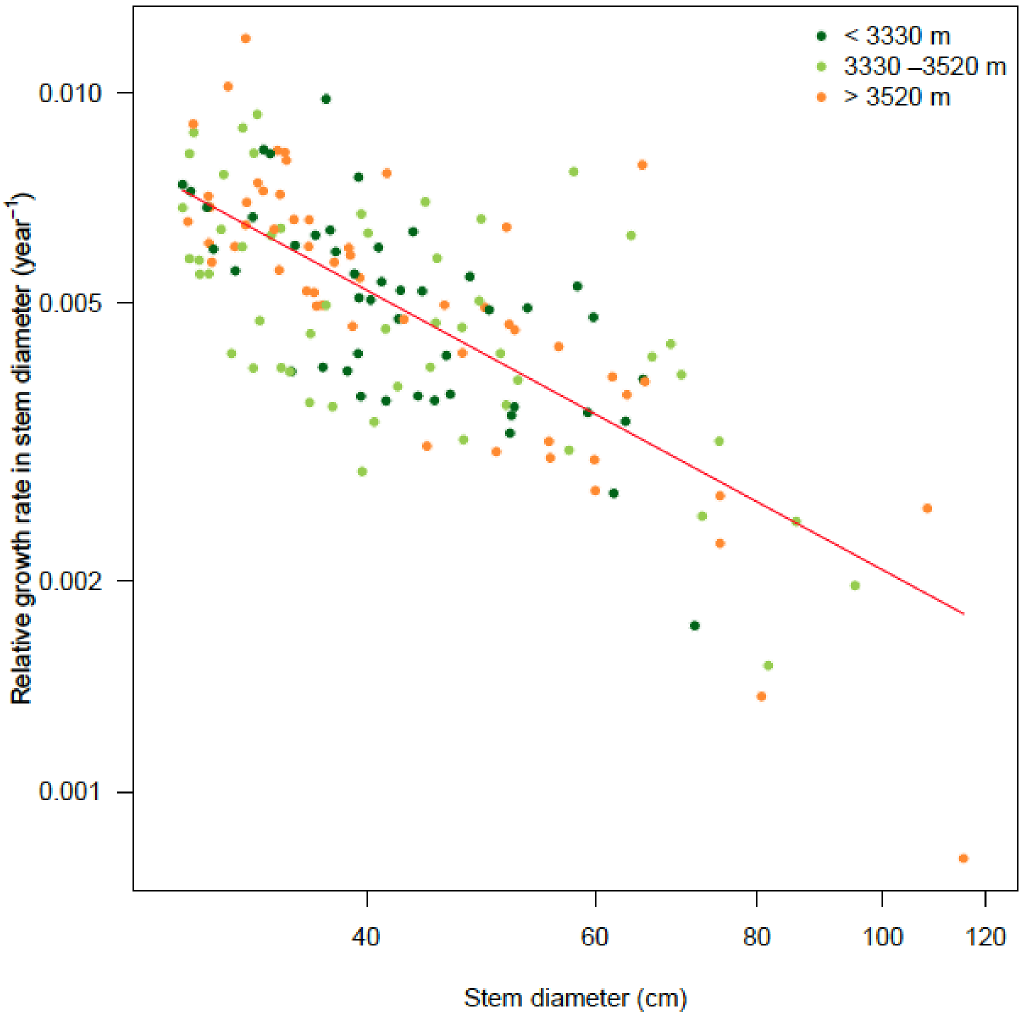

Figure 2-4. Stem-diameter dependence of relative growth rate in stem diameter of canopy trees of *Abies spectabilis*; no altitude dependence was found.

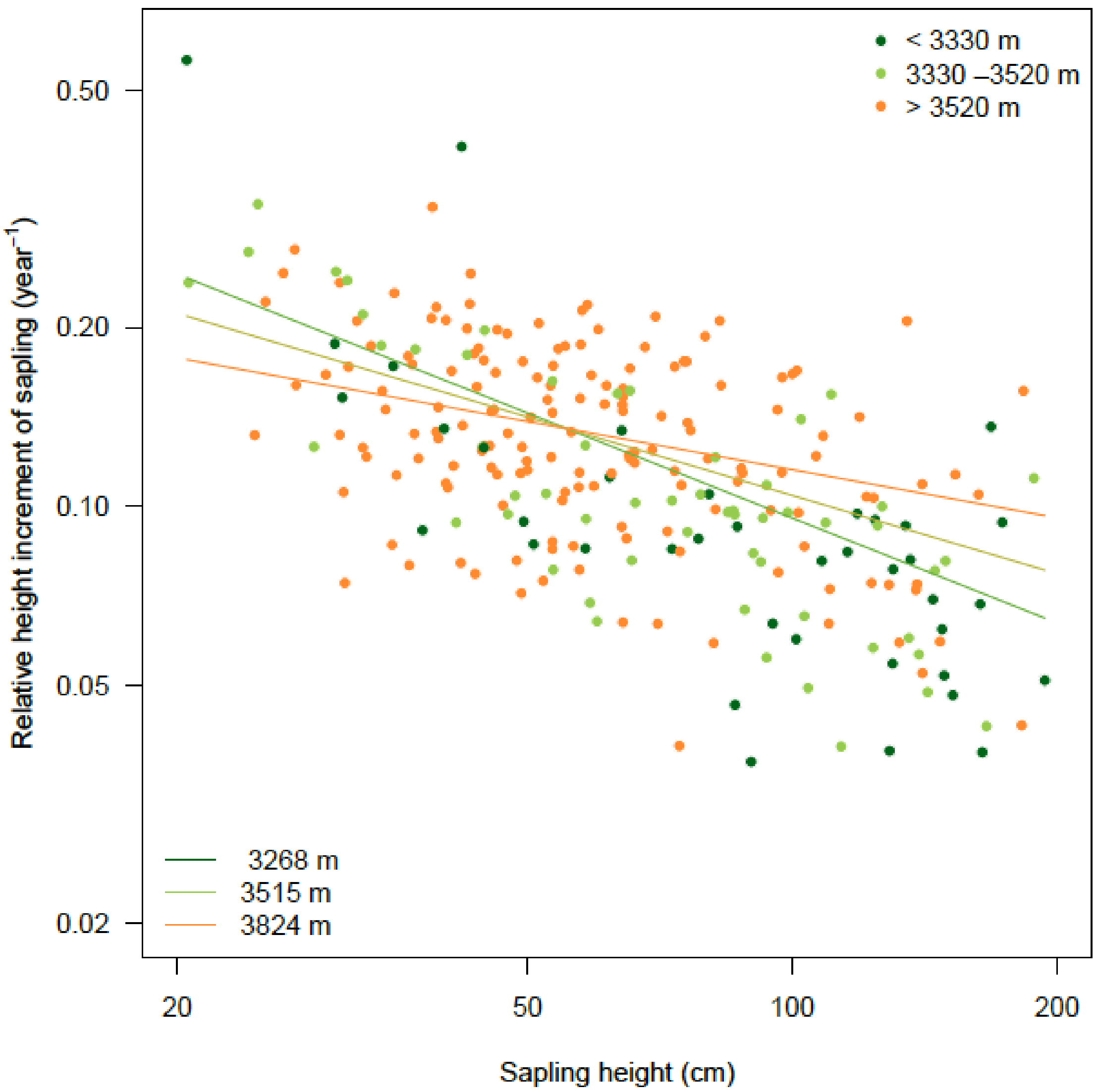

Figure 2-5. Sapling-height and altitude dependence of relative height increment over three years of *Abies spectabilis*.

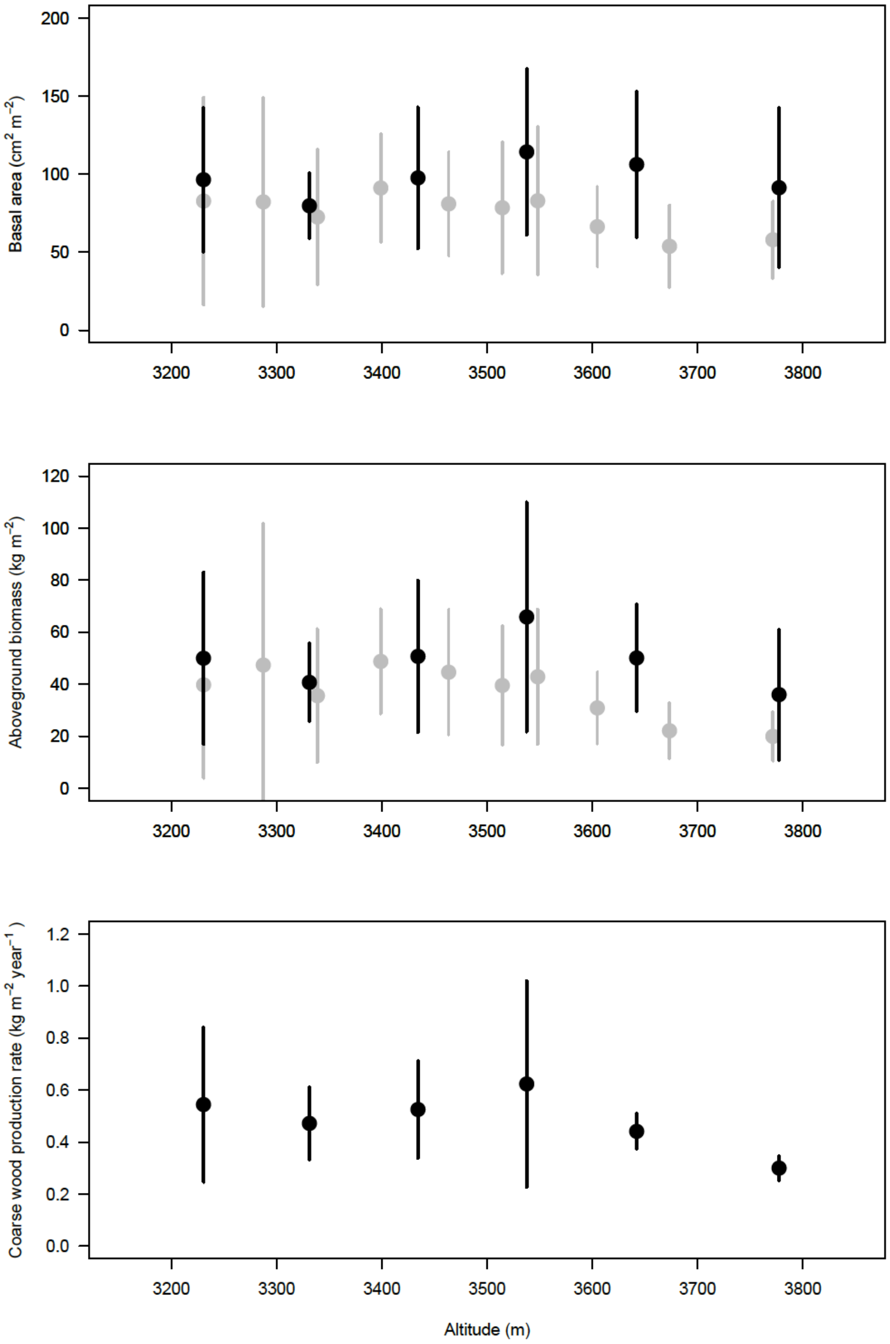

Figure 2-6. Altitude dependence of basal area, aboveground biomass and coarse wood production rate of *Abies spectabilis* forest. Gray circles and bars for 80 forest plots in 2008 divided into 10 altitude groups; black circles and bars for 36 plots in 2015 divided into 6 groups.

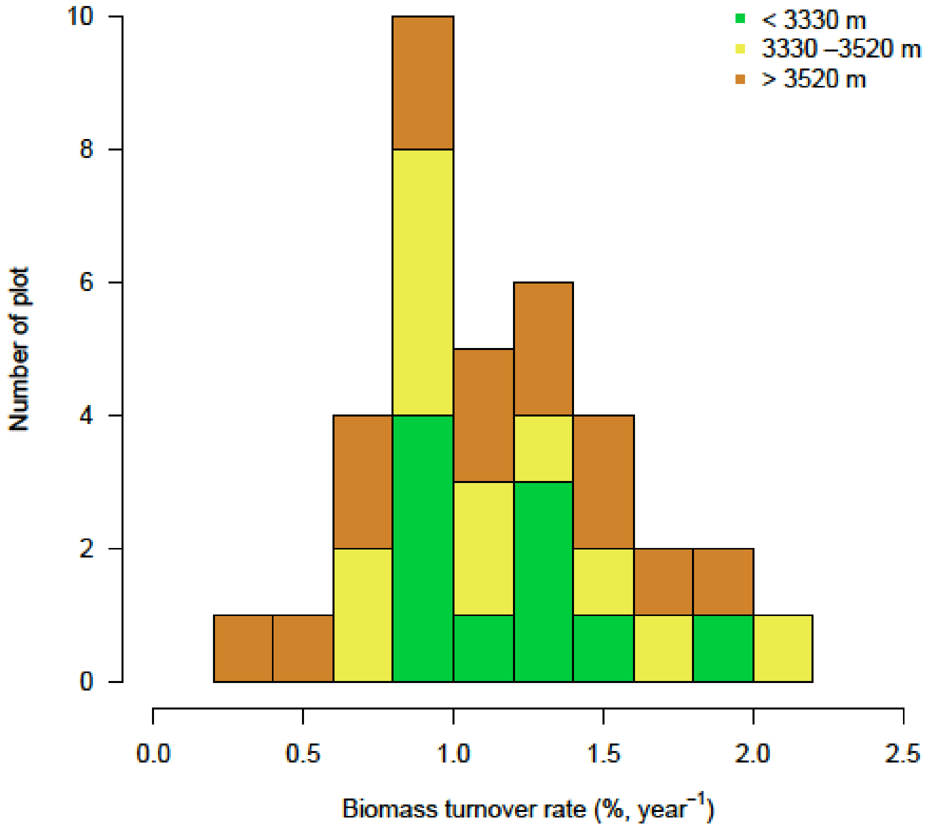

Figure 2-7. Distribution of biomass turnover rate (%, year$^{-1}$), i.e. coarse wood production rate over aboveground biomass of *Abies spectabilis*, for 36 forest plots in 2015.

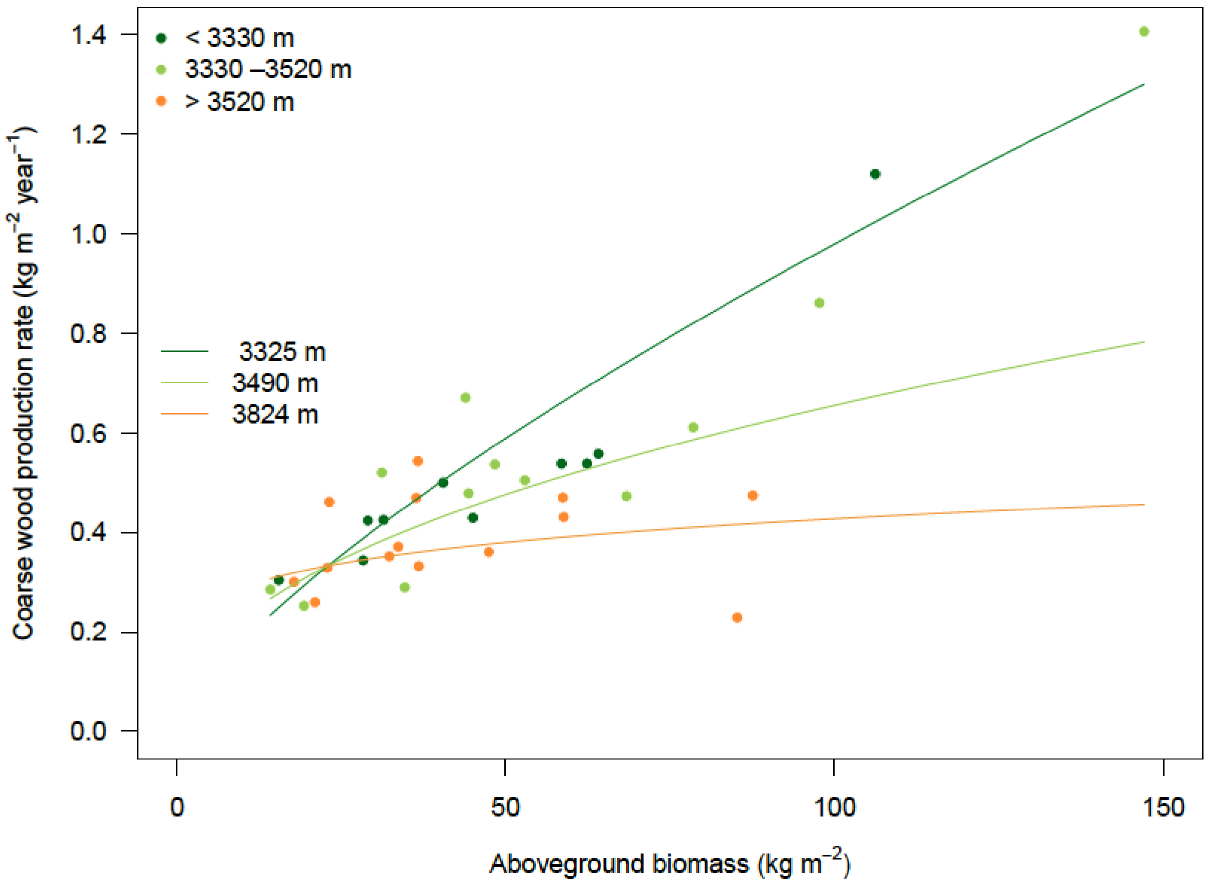

Figure 2-8. Coarse wood production rate against aboveground biomass in *Abies spectabilis* forest plots in 2015, and of which dependence on altitude.

Table 2-1. 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 | 86°20′-86°40′E | 2920 | 23.6 | 72.5 | 41.8 | | | Yoda (1967, 1968) |
| Eastern Nepal | 27°30′-27°45′N | 86°20′-86°40′E | 3120 | 23.1 | 73.3 | 40.1 | | | Yoda (1967, 1968) |
| Eastern Nepal | 27°30′-27°45′N | 86°20′-86°40′E | 3280 | 22.1 | 59.6 | 32.5 | | | Yoda (1967, 1968) |
| Eastern Nepal | 27°30′-27°45′N | 86°20′-86°40′E | 3420 | | 59.6 | 34.2 | | | Yoda (1967, 1968) |
| Eastern Nepal | 27°30′-27°45′N | 86°20′-86°40′E | 3530 | 21.9 | 49.9 | 27.1 | | | Yoda (1967, 1968) |
| Eastern Nepal | 27°30′-27°45′N | 86°20′-86°40′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 | 15.9 | 1.06 | 0.55 | Tadaki *et al*. (1970) |
| Central, Japan | 35°59′N | 138°22′E | 2300-2500 | | 63.6 | 20.3 | 1.11 | 0.55 | Kimura (1963) |
| Hokkaido, Japan | 43°13′N | 142°23′E | 230 | 11.7 | 32.6 | 9.41 | 1.47 | | Satoo (1973) |
| 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 | 45.5 | 1.89 | | Adhikari *et al.* (1995) |
| Rocky Mountains | 40° 20' N | 105°41' W | 3180-3400 | | 63 | 25.3 | 0.37 | | Binkley *et al*. (2003) |
| LNP, Nepal | 28°00′-28°20′N | 85°15′-86°00′E | 3100-3900 | 24.3 | 97.6 | 48.9 | | 0.48 | Present study |

# Chapter 3

## Specific contribution of co-dominant *Picea glehnii* and *Abies sachalinensis* to dynamic properties of subalpine forest on Mount Oakan, Hokkaido

## 3.1 Introduction

In subalpine regions in high-latitude Northern Hemisphere, there exist well-developed forests co-dominated by *Picea* spp. and *Abies* spp. (Takahashi 1994; Taylor *et al.* 1996; Takahashi and Kohyama 1999). Most part of the subalpine forest in Hokkaido is covered by *Picea glehnii*, *Picea jezoensis* and *Abies sachalinensis* with some deciduous broad-leaved species such as *Betula ermanii*. In a mixed fir-spruce forest, *Picea* spp. are present only in canopy and they are less in the sapling layer. On the other hand, *Abies sachalinensis* is typically represented by far denser small-sized saplings than canopy tress (Kubota and Hara 1996; Antosh and Parish 2002; Silva *et al.* 2012).

Forest regeneration patterns vary depending on the tree species composition and the environmental factors. Forest structure and composition are influenced by various factors such as disturbances and competitive interactions among tree species (North *et al.* 2004). Reconstruction of dynamic forest structure by tree demography, i.e. growth rate, mortality and recruitment rate, is essential for understanding of species differentiation, and collective dynamic ecosystem properties (Taylor *et al.* 1996).

The present study examined the records over ten years of change in tree populations in a primary subalpine coniferous forest of northern Japan to compare population dynamics between two dominant species in terms of demographic properties to understand the dynamics of tree community and forest biomass.

In species-rich tree communities, maximum size in tree size distribution has been related to size-dependent growth rate and mortality of species (Aiba and Kohyama 1997; Kohyama *et al.* 2003, 2015). In temperate forests, maximum size differentiation among dominant species is less clear than in tropical forests (King *et al.* 2006), and the coexistence of dominant canopy species needs to be related to interspecific differentiation not in maximum size. In this study, I examined tree size distributions between *Picea glehnii* and *Abies sachalinensis* in relation to demographic properties of these two canopy species. Tadaki *et al.* (1967, 1970) reported biomass and primary production rate of *Abies veitchii* populations in subalpine forests on Mt. Fuji in central Japan. Kimura (1963) studied the successional dynamics and primary production rate of subalpine *Abies veitchii–A. mariesii* forest in Yatsugatake Mountains, central Japan. Although there are several studies that examine structure and dynamics of *Picea-Abies* subalpine forests (Suzuki *et al.* 1987; Taylor *et al.* 1996; Kubota and Hara 1996; Takahashi and Kohyama 1999; Nishimura 2005; Mori *et al*. 2007), no study has related species properties to overall biomass and turnover rate in *Picea-Abies* forest.

This study addressed the following research questions. (1) How does tree stem architecture differ between the two species? (2) How are the aboveground biomass and production rate influenced by species-specific properties? (3) How do the tree growth rate and mortality differ between the two species?  To evaluate these questions, I analyzed the data of censuses over 11 years in a 1-ha permanent plot set in *Picea glehnii–Abies sachalinensis*.

### 3.2 Study area and methods

The study was conducted in the Akan National Park, Hokkaido, northern Japan. On the hoot of Mt. Oakan, 1-ha plot was set in July-October 2004, located at 43°27´15´´N, 144°09´40´´E at the NE-corner origin of the plot at altitude of 540 m. The area around the plot was covered by primary forest dominated by *Picea glehnii* and *Abies sachalinensis*. Mount Oakan is a young volcano, dated back to some 15 thousands years. The site with the plot is on the deposits of fallen debris of andesitic rock with relatively flat but angulated topography. The plot was covered by *Abies sachalinensis* and *Picea glehnii* with broad leaved species e.g. *Betula maximowicziana, Acer japonicum, Acer ukurunduense* and *Sorbus commixta.* Table 3-1 shows full species list with abundance.

According to the records of the Akanko Lakeside Weather Station at 450 m a.s.l. during 1981 and 2010, annual mean temperature was 3.9℃ (with monthly max. of 18.0℃ in August and min. of –10.5℃ in January). Annual mean precipitation was 1203 mm (with monthly max. 152 mm in August and min. 50 mm in February). To incorporate altitude difference of ca. 90 m between the plot and the station with the degree lapse rate of 0.6℃ per 100 m, Kira's warmth index WI = 42.9℃ month from May to October, and the coldness index CI = –62.1℃ month from November to April. These suggest that thermal condition for growing season is close to the lower elevation limit of subalpine forest (45 to 15℃ month in WI) with chilly winter (cf. CI at the forest limit of 3900 m in Langtang site, eastern Himalaya, was –28.3°C month as in Chapter 1).

*Field sampling and measurements*

The studied 1-ha permanent plot of 100 by 100 m was divided by 100 subplots of 10 by 10 m, each. All living trees ≥ 5 cm stem diameter at breast height (*D*, cm) were tagged, identified, measured in *D* and locations to nearest 10 cm. These tagged trees were re-measured in 2014 to record the fate (alive or dead), measured *D* if alive, and all new recruits ≥ 5 cm *D* were tagged, identified and measured. In 2004, top height (*H*, m) for selected trees of two coniferous species over the range of *D* was measured by a pole measure up to 15 m *H*, and a Vertex IV (Haglöf

Sweden AB) if above 15 m. $H$ of the same (alive) trees were again measured in 2015. Saplings, defined by height as $2.0 > H \geq 0.5$ m, of *A. sachalinensis* and *P. glehnii* were observed in 2014 in height $H$ and the current-year height increment. Because of the high density of *Abies sachalinensis* saplings, these only in the origin-position 5 by 5 sub-gird of each subplot were recorded (thus for 0.25 ha), while all saplings of *Picea glehnii* were recorded in total 1 ha.

Hemispherical photographs were taken on the every corner of 10 by 10 m subplots, in overcast sky condition. The relative light condition, from 0 to 1, was obtained from every scanned image as the relative proportion in the standardized overcast sky (SOC) in which light from zenith is three-times brighter than horizontal one. SOC for each subplot was defined to be the average of four-corner ones, and SOC at the midpoint of each 5 by 5 sub-grid was calculated by distance-based interpolation procedure.

### *Stem diameter-height allometry*

I employed the extended allometric equation (Ogawa *et al.* 1965) to fit asymptotic increase in tree top height $H$ (m) with stem diameter $D$ (cm):

$$1/H = 1/(AD^b) + 1/H_{\max}, \tag{3-1}$$

where $b$ is allometric coefficient, $A$ ($\mathrm{cm}^{-1}$) is allometric constant, and $H_{\max}$ (m) is asymptotic height for infinite $D$. To estimate three parameters of eqn 3-1, I took logarithm of eqn (1) such that

$$\ln H = -\ln\,[(1/AD^b) + 1/H_{\max}]. \tag{3-2}$$

I examined whether allometric coefficient, $b = 1$ or $b \neq 1$, and whether each of parameters ($A$, $b$, $H_{\max}$) are dependent on species identity, i.e., either *P. glehnii* or *A. sachalinensis*. I used NLME (Pinheiro *et al.* 2011) on R (R core team 2013) for non-linear mixed effect regression for parameter estimation. To select the best model, we compared all possible cases by means of AICc with R package MuMIn (Burnham and Anderson 2002).

### *Estimation of aboveground tree biomass*

For estimating the aboveground biomass in year 2004 and 2014, I used the $D$-$H$ allometry of eqn (3-2) to predict the height for all trees. I used 2015 allometry to predict $H$ of all alive trees for the year 2014, and 2004 allometry for $H$ in 2004.

I estimated aboveground biomass of a tree, $W$ (kg in dry mass), from $D^2H$ (cm$^2$ m) of the tree, applying a simple allometric equation using on total tree mass data of *Abies veitchii* in Mt. Fuji (Tadaki *et al.* 1970) (See Figure 2-2, Chapter 2) which is:

$$W = \exp(-3.08)\,(D^2H)^{0.893}. \qquad (3\text{-}3)$$

Tadaki *et al*. (1970) provided allometric equations that estimate mass of main stem, branches, and leaves separately, while I added them to estimate total aboveground tree mass to reduce uncertainty in biomass estimation.

### *Size-dependent tree growth rate and mortality*

I estimated size (=$D$) dependent change in growth rate $G(D)$ (cm year$^{-1}$) according to Kohyama *et al*. (2015). I obtained relative growth rate of diameter by $G(D)/D = (\ln D_{2014} - \ln D_{2004})/10$

(year$^{-1}$). I approximated within-population variation in $G(D)/D$ follows Gamma distribution around the mean relative growth rate $G(D)$. If ($\ln D_{2014} - \ln D_{2004}$) was non-positive, I set ($\ln D_{2014} - \ln D_{2004}$) = 0.001. I used the combination of exponential and power functions (Kohyama *et al*. 2015).

I estimated the mortality function, $M(D)$ (year$^{-1}$), as follows. The death probability of a tree is the expectation of a binomial distribution of being either dead or alive during the census period $t$ =10 years. The instantaneous mortality rate $M(D)$ for a tree at $D$ (cm) in 2004 census satisfies is $1 - \exp(-M(D)\ t)$. I used the mortality function with the same form of growth function (Rüger *et al*. 2011; Iida *et al*. 2014; Kohyama *et al*. 2015).

To estimate parameters of growth and mortality models, I used GLM for relative growth rate and mortality using offset term of $\ln t$ and distribution function families of Gamma with link function of log for relative growth rate, and binomial family with link function of cloglog for mortality. Species identity was set to be fixed effect such that

cloglog(death probability over $t$)

~ species*$D$ + species*ln $D$ + offset(ln $t$).

*Size and light dependent sapling growth rate*

Many saplings of the two species showed zero current-year growth. Therefore, I examined first the probability of zero growth between species by binomial distribution fitting. To examine whether sapling height growth rate depended on height and/or on light conditions, I modeled the distribution of sapling height growth rate $G_H$ (mm year$^{-1}$) to follow Gamma distribution with log link function. I used GLM by the form that $G_H$ ~ species*ln $H$*SOC, to see the dependence on size $H$ (mm in this fitting), light SOC, species and their interaction. I replaced zero height increment records with 0.01 mm, as gamma distribution doesn't take non-positive values.

*Biomass turnover rate*

I estimated annual rate of tree biomass increment, using tree-level biomass $W$ in 2004 and 2014 for all trees in 1-ha plot. As in Chapter 2, I employed the procedure of estimating annual increment rate from longer census interval by Sheil (1999), originally proposed for estimating per-capita recruitment rate of population size; see eqns (2-10, 2-11).

Biomass loss rate due to mortality of trees was calculated using the product of mortality rate of trees (year$^{-1}$) and aboveground biomass of 2004 for *A. sachalinensis* or *P. glehnii*.

Coarse wood loss rate due to mortality = $M_{\mathrm{wood}}\, B_{2004}$, and

$$M_{\mathrm{wood}} = 1 - (B_{\mathrm{survived}}/B_{2004})^{1/t}, \qquad (3\text{-}4)$$

where $M_{\mathrm{wood}}$ refers to specific loss rate of biomass by tree mortality (either *Abies sachalinensis* or *Picea glehnii*), $B_{\mathrm{survived}}$ is the aboveground biomass in 2004 for all trees alive in both 2004 and 2014, and $t$ is time period from 2004 to 2014, i.e. 10 years.

## 3.3 Results

*Allometry between stem diameter and tree height and size distribution*

The best allometric model between stem diameter $D$ and tree height $H$ with eqn (3-1) was that $b$ = 1 and that $A$ and $H_{\max}$ were species dependent. Estimated parameters were shown in Table 3-2. At the same $D$, $H$ of *Abies sachalinensis* was larger for understory trees with $D <$ ca. 50 cm, while $H$ of *Picea glehnii* was larger for canopy trees of $D >$ ca. 50 cm both in year 2004 and 2015 (Figure 3-1). Size distribution of the two populations in $D$ and $H$ showed that *A. sachalinensis* was much denser with high relative abundance of small sized trees compared to *P. glehnii* which dominated only in tall canopy with uni-modal size distribution (Figure 3-2).

### *Spatial variation in stand coverage*

There was small increase in basal area, from 37.7 to 39.7 cm$^2$ m$^{-2}$ during 10 years time period, from 2004 to 2014, for *Abies* and *Picea* trees (≥ 5 cm $D$) (Figure 3-3). In total 20 species appeared within the plot in both 2004 and 2014, basal area of *A. sachalinensis* increased from 18.8 to 22.5 cm$^2$ m$^{-2}$ and that of *P. glehnii* decreased from 18.8 to 16.9 cm$^2$ m$^{-2}$. The initial density of *A. sachalinensis* in 2004 was 1745 trees ha$^{-1}$ of which 113 trees ha$^{-1}$ had died by 2014, and the density of *P. glehnii* were decreased during 10 year duration (Table 3-1).

Aboveground biomass for *A. sachalinensis* was 4.92 kg m$^{-2}$ in 2004 and it was increased to be 6.75 kg m$^{-2}$ in 2014. In contrast, for *P. glehnii* population, it was slightly decreased from 7.72 kg m$^{-2}$ in 2004 to 7.19 kg m$^{-2}$ (Table 3-3). Across subplots, biomass showed strongly positive-skewed distribution (Figure 3-4).

The density of saplings ($0.5 < H < 2$ m) in 2014 was 4244 and 189 ha$^{-1}$ for *A. sachalinensis* and *P. glehnii* respectively. Super-dominance of *A. sachalinensis* brought about higher recruitment at $D$ = 5 cm and higher density of small trees for *A. sachalinensis* as in Figure 3-2.

*Tree size growth and mortality*

Estimated functions of mean absolute growth rate and mortality were both dependent on species identity. In growth model, estimates were (cf. Figure 3-5)

$G(D) = \exp(0.00202 - 0.126D)\, D^{2.55}$ for *Abies sachalinensis,*

$G(D) = \exp(0.000905 - 0.0495D)\, D^{2.15}$ for *Picea glehnii*.

In mortality model, they were (cf. Figure 3-6)

$M(D) = \exp(0.461 + 0.147D)\, D^{-2.36}$ for *Abies sachalinensis,*

$M(D) = \exp(0.818 + 0.04425D)\, D^{-1.63}$ for *Picea glehnii*.

Mean growth rate of understory trees ($D <$ ca. 30 cm) was larger for *A. sachalinensis,* whereas that of canopy trees ($D >$ ca. 30 cm) was larger for *P. glehnii* (Figure 3-5). Mortality rate of understory trees ($D <$ ca. 30 cm) was lower in *A. sachalinensis*, whereas that of canopy trees was lower for *P. glehnii* (Figure 3-6).

*Sapling growth rate*

The mean probability of positive height increment was 0.698 for *A. sachalinensis* and 0.693 for *P. glehnii.* For saplings with positive growth, the probability of the mean height increment rate was 0.420 and 0.468 (mm year$^{-1}$) for *A. sachalinensis* and *P. glehnii*, respectively. Figure 3-7 shows the observed distribution of height growth rate for saplings of the two species.

Figure 3-9 shows the SOC dependence of sapling growth rate. Sapling growth rate in height $H$ ($G_H$, mm year$^{-1}$) was increased with increase in absolute height and the standard overcast sky, SOC, for each grid 10 by 10 m for *P. glehnii* and sub-grid of 5 by 5 m for *A. sachalinensis*, as

$$\ln G_H = 0.355 + 0.224[\textit{P. glehnii}] + 0.111 \ln H + 0.099\ \mathrm{SOC}$$

where *A. sachalinensis* is set to be default. Model analysis showed that saplings increased absolute height growth rate with its height and light conditions similarly across two species, whereas *P. glehnii* showed better growth than *A. sachalinensis* in any conditions in average.

### *Coarse wood production and turnover rate*

Average coarse wood production rate (CWP) were 0.303 and 0.088 kg m$^{-2}$year$^{-1}$ for *A. sachalinensis* and *P. glehnii* respectively. The demographic turnover rate of aboveground biomass (CWP/AGB) were 4.48 and 1.23% year$^{-1}$ for *A. sachalinensis* and *P. glehnii*, respectively. Coarse wood production rate for the two species gathered varied across subplots of 10 by 10 m (Figure 3-10A) with the average value of 0.397 kg m$^{-2}$ year$^{-1}$. Cross-subplot variation in CWP was smaller than that for the aboveground biomass (AGB) as in Figure 3-4. The reason was that CWP showed asymptotic increase with AGB. By fitting this relationship to the Michaelis-Menten curve,

$$\mathrm{CWP} = 0.157\mathrm{AGB}/(1 + 0.283\mathrm{AGB})$$

thus the asymptotic CWP for infinite AGB was 0.55 kg m$^{-2}$ year$^{-1}$ (Figure 3-10B)

## 3.4 Discussion

Structure and dynamics of subalpine *Abies-Picea* forests are strongly influenced by species properties as well as interspecific interactions (Suzuki *et al*. 1987; Kubota *et al.* 1994; Takahashi and Kohyama 1999; Nishimura 2005; Mori *et al.* 2007). In the present study, I examined how the subalpine forest on Mt. Oakan showed interspecific variation in tree architecture, demography, biomass and biomass turnover rate between two co-dominant species, *Abies sachalinensis* and *Picea glehnii*. I found, as previous studies (Kubota *et al.* 1994; Kubota and Hara 1996; Takahashi and Kohyama 1999), that *A. sachalinensis* showed advantage in recruitment and understory vital rates and that *P. glehnii* showed advantage in canopy tree survival and growth. Overall change over 10 years suggested the gradual replacement of *P. glehnii* by *A. sachalinensis* in biomass turnover rate; meantime the long-term occupation of top canopy by *P. glehnii* suggests that the coexistence via vertical stratification would last for long while.

Tree height and stem diameter relationship suggests that top height of *A. sachalinensis* took less slender for canopy trees as compared to *P. glehnii* at the same stem diameter (Figure 3-1). This may be due to high physical stress in the canopy layer, e.g. strong wind and heavy snow load, influences more for *A. sachalinensis* (Suzuki *et al*. 1987; Nishimura 2005). A reverse tendency that *P. glehnii* had shorter height at a given stem diameter for short trees can be related to the fact that *P. glehnii* grow slower in stem diameter than *A. sachalinensis* in understory trees (Figure 3-5). Understory trees with slow growth rate would exhibit the stem form with high mechanical stability for persistence, rather than height gain.

Aboveground biomass and biomass increment rate strongly depend on the tree size distribution of the forest stand (Hiura 2005). Basal area and aboveground biomass in the present forest were relatively low as compared to other subalpine forests (Kimura 1963; Yoda 1968; Tadaki *et al*. 1970; Grier *et al.* 1981; Binkley *et al.* 2003). They are comparable to Satoo (1973), who reported low average basal area of 32.6 $cm^2$ $m^{-2}$ in *A. sachalinensis* stands. Binkley *et al*. (2003) reported low biomass record for a subalpine coniferous forest on Rocky Mountains. Previous studies usually used plots smaller than 1 ha, and there may be the tendency to set monitoring plots on mature stands with tall canopy. As I observed in cross-subplot variation in biomass (Figure 3-4), horizontal distribution of biomass was skewed towards low-biomass subplots on canopy gaps, and the large plot size can be the reason of low average biomass and basal area. Meantime, a high rate of canopy tree mortality (Figure 3-6) and biomass turnover rate by coarse wood production over biomass (0. 4/14 = 0.029 $year^{-1}$; cf. Figs 3-4 and 3-10) suggest high disturbance rate and canopy rotation rate, bringing about higher proportion of young-stage stands in overall landscape.

Mean growth rate and survival probability were higher for *A. sachalinensis* in understory, and they were higher for *P. glehnii* in canopy (Figs. 3-5 and 3-6). Takahashi and Kohyama (1999) suggested the tendency that the growth and recruitment rate of these two species are more suppressed by the same species rather than other species, and such process of reciprocal replacement enhance coexistence.

There were fewer saplings of *P. glehnii* as compared to *A. sachalinensis* in the study site. *A. sachalinensis* are late successional species and they mainly dominate the understory of *P. glehnii* dominated canopy layer (Kubota *et al.* 1994; Kubota and Hara 1996). In mixed stands of two conifer saplings, *Abies* sp. is superior competitor over *Picea* sp. under crowded competitive conditions (Kubota and Hara 1996). Saplings of *Picea glehnii* showed higher growth rate with better light conditions (Chen 1997; Chrimes and Nilson 2005), which is comparable to this study.

Coarse wood production rate for the entire forest is comparable to *Abies amabilis* forest of North America (Grier *et al.* 1981). Grier *et al.* compared both young and mature stands of *A. amabilis* and found lower rate of coarse wood production rate in mature stand. Coarse wood production rate in this study varied spatially across subplots. Although, mean coarse wood production rate was found low but asymptotic coarse wood production rate with aboveground biomass is comparable to other subalpine forests (Tadaki *et al.* 1970). I have recorded the higher biomass turnover rate (2.9% year$^{-1}$). This turnover rate is larger even though aboveground biomass and coarse wood production rate records were lower as compared to other subalpine forest in northern Japan (Kimura 1963; Tadaki *et al.* 1970).

Subalpine forest of Hokkaido indicates that fir-spruce dominated forest showed wide range of species interactions. The present studied forest indicated that the growth and persistence of *A. sachalinensis* are limited in canopy whereas *P. glehnii* is characterized by poor recruitment capacity. The studied forest showed low coverage in basal area and aboveground biomass as compared to other subalpine forests, while the biomass turnover rate is higher even though forest floor is affected by harsh edaphic (on andesitic debris) and climatic (chilly winter) conditions.

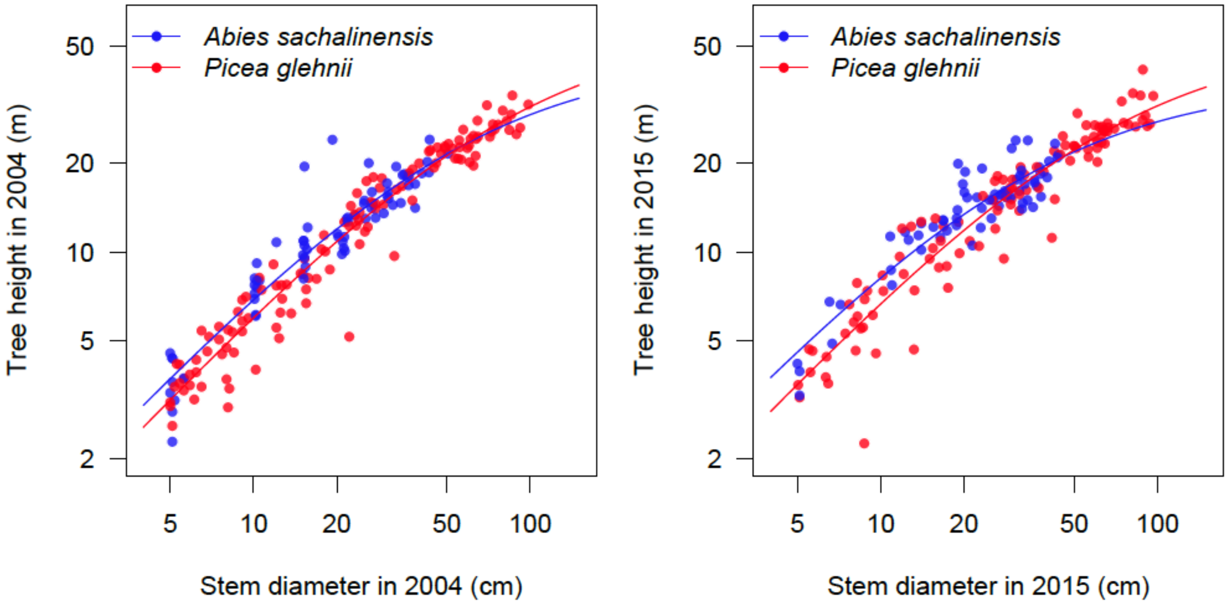

Figure 3-1. Height–diameter relationship among two conifer species, *Abies sachalinensis* and *Picea glehnii*, in 2004 and 2015.

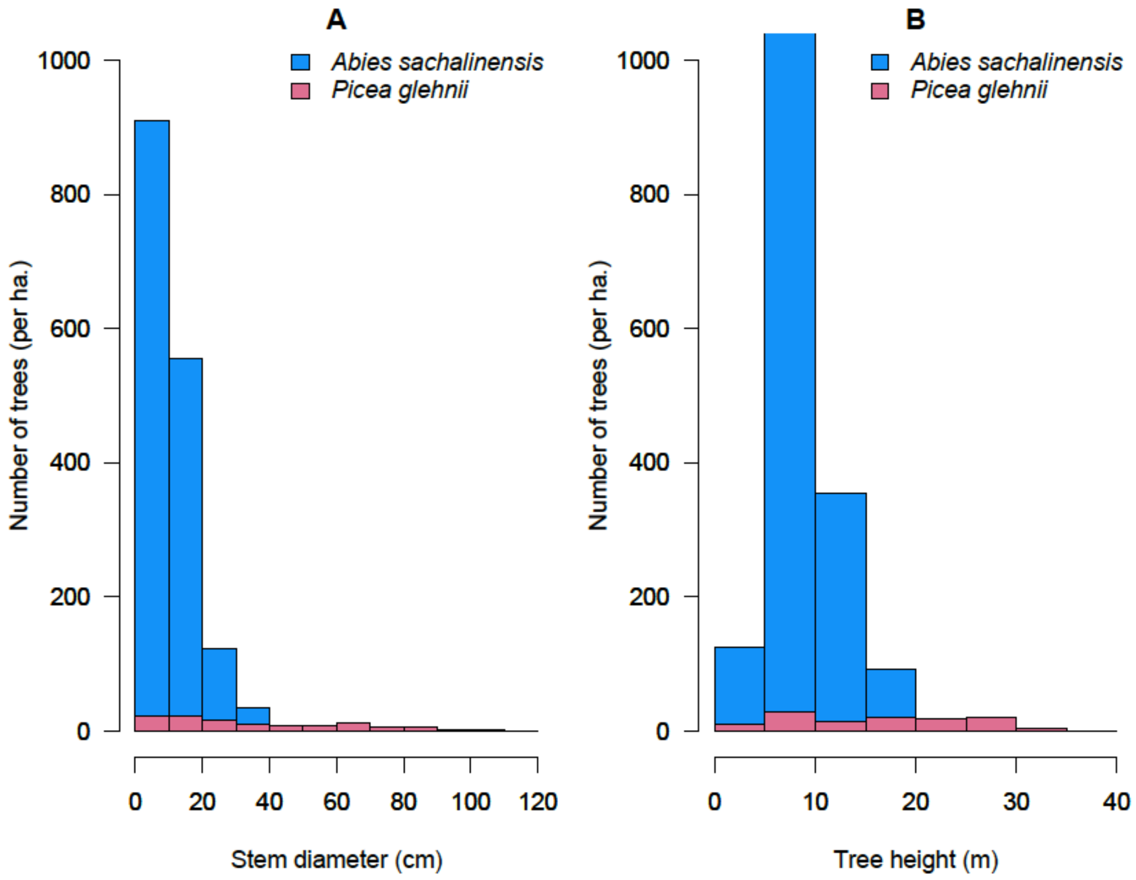

Figure 3-2. Size distribution of *Abies sachalinensis* (pale blue) and *Picea glehnii* (pink) in stem diameter at breast height (A) and tree top height (B).

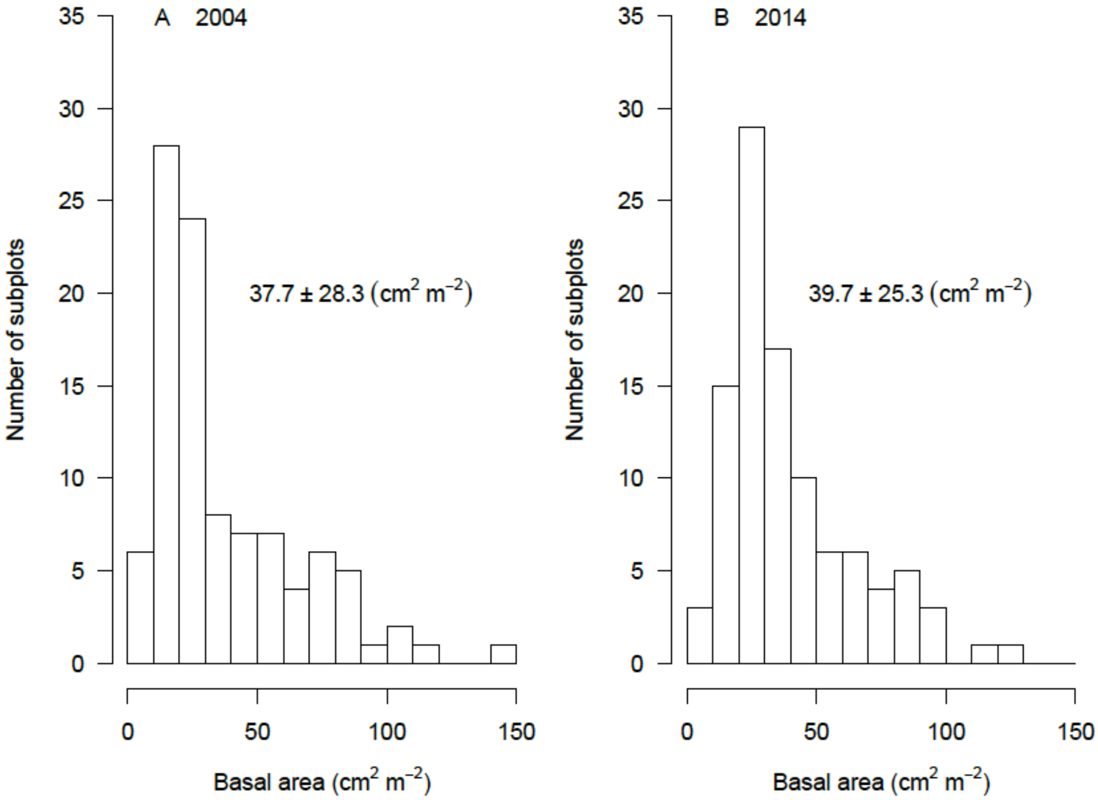

Figure 3-3. Basal area distribution for two conifer trees. A. Basal area per subplot in 2004; B, in 2014.

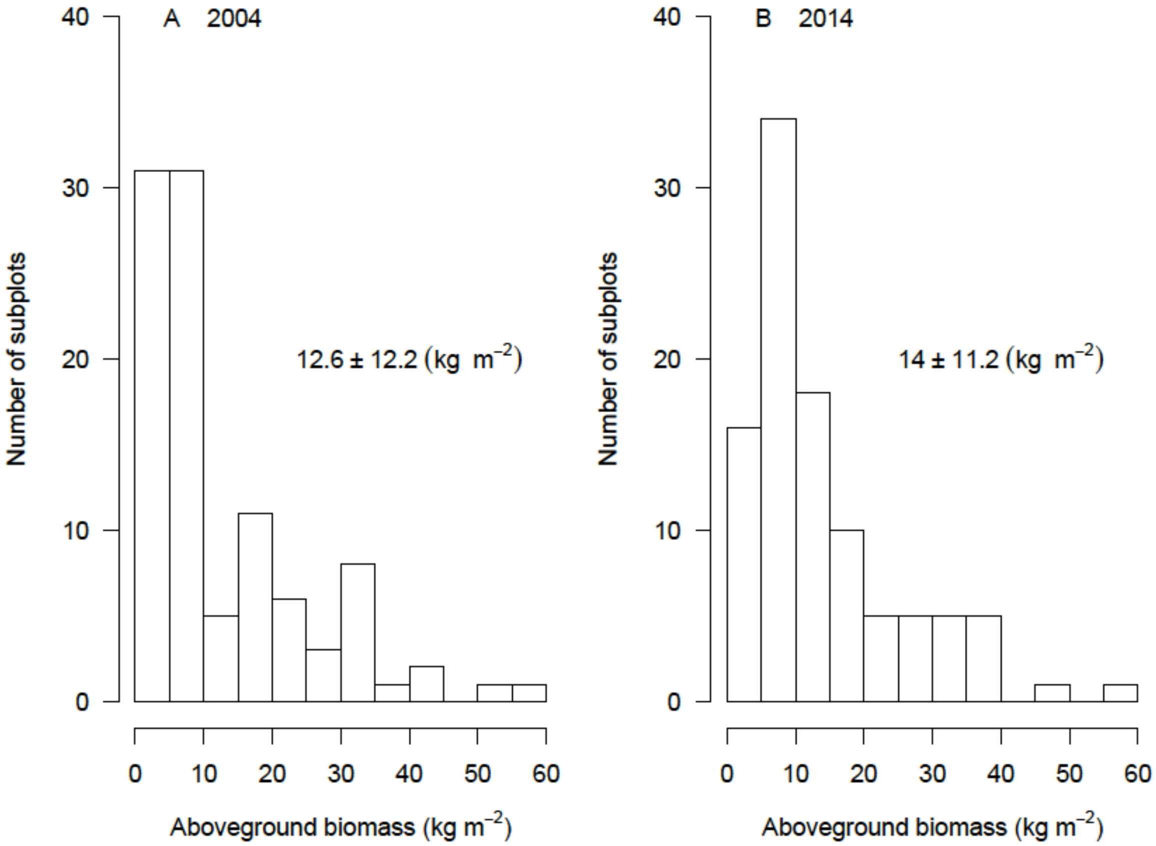

Figure 3-4. Aboveground biomass for two conifer trees. A, Aboveground biomass per subplot in 2004; B, in 2014.

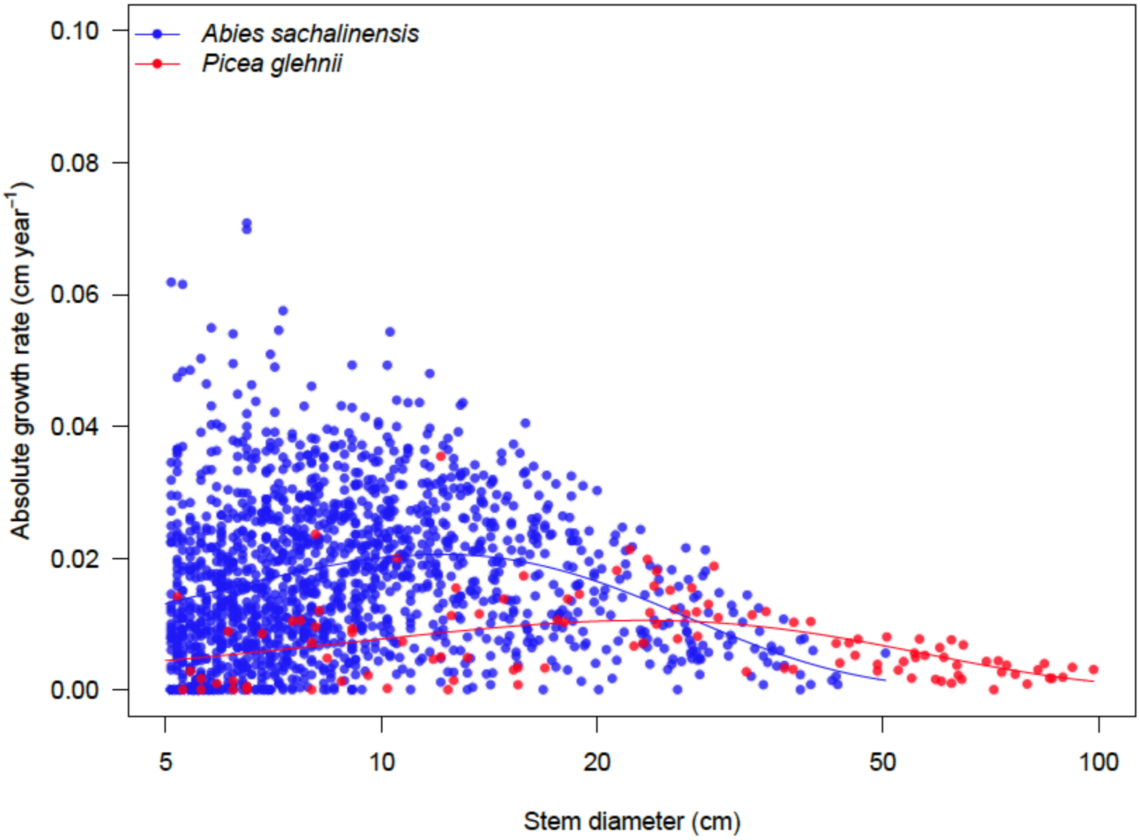

Figure 3-5. Absolute growth rate of stem diameter with respect to stem diameter for *Abies sachalinensis* and *Picea glehnii* based on the censuses of survivors during 2004 and 2014.

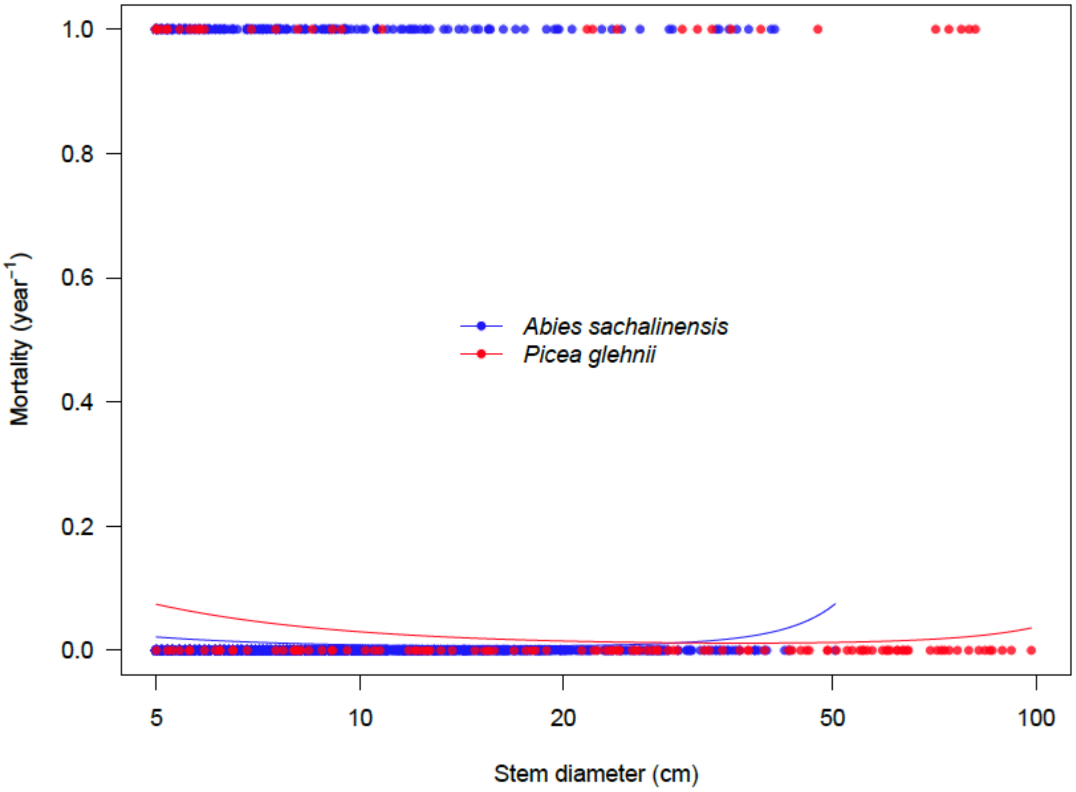

Figure 3-6. Change in instantaneous mortality with stem diameter at breast height for *Abies sachalinensis* and *Picea glehnii* with records of death and survival during 2004 and 2014.

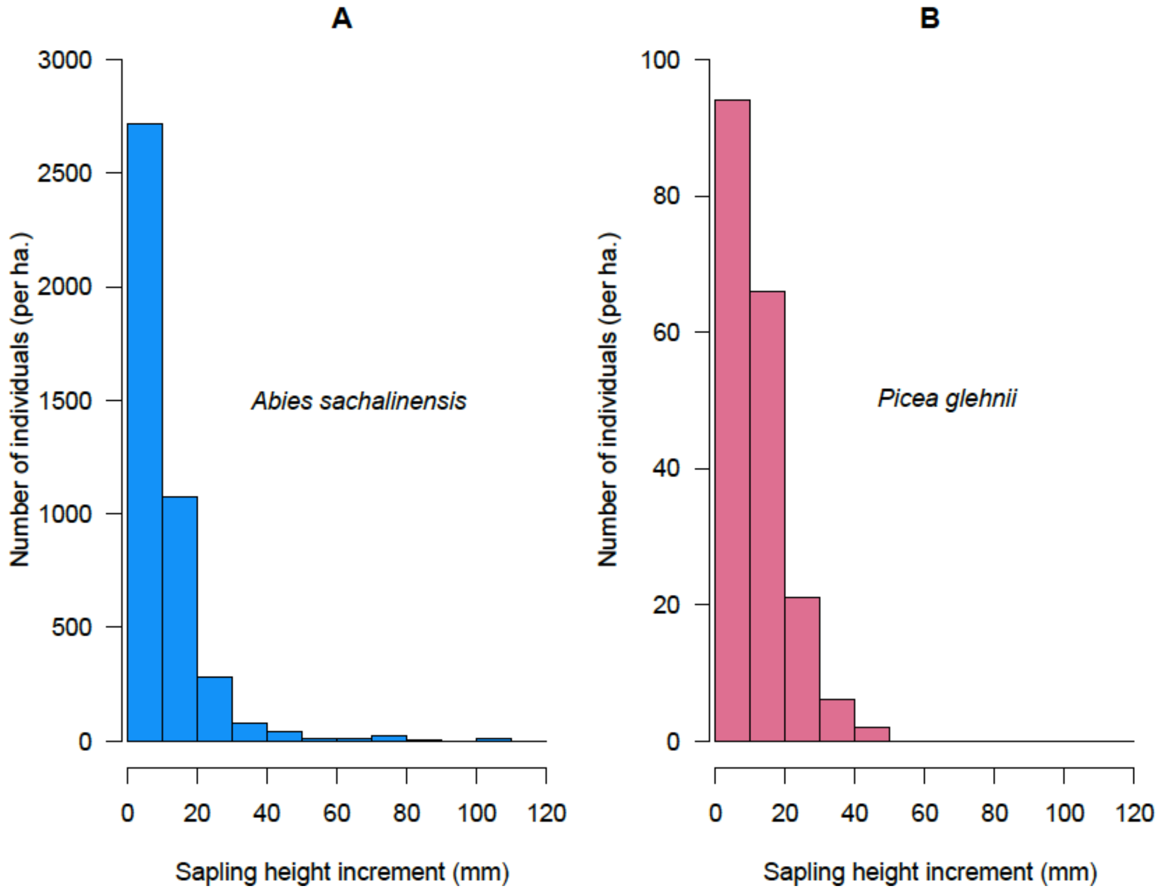

Figure 3-7. Distribution of the annual height growth. A, *Abies sachalinensis*; B. *Picea glehnii*.

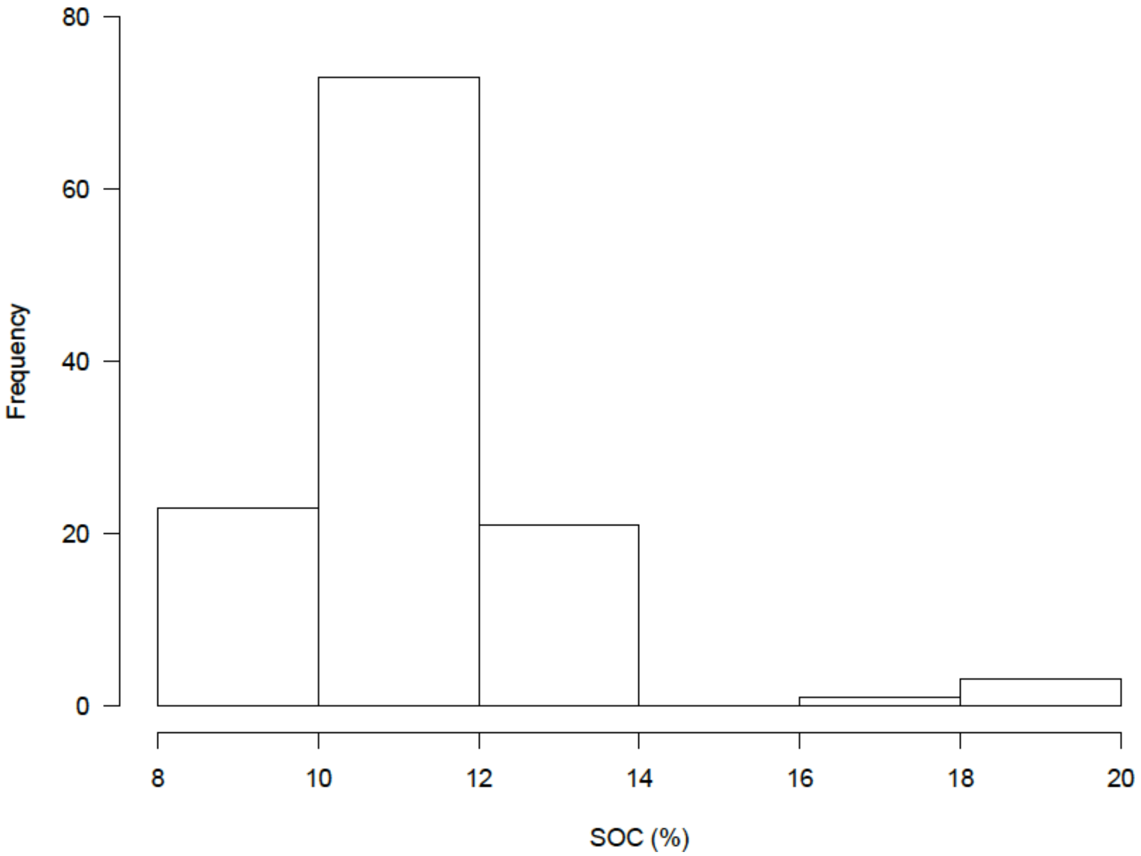

Figure 3-8. Frequency distribution of relative exposure in standard overcast sky (SOC, %), observed at sub-plot grids (*n* = 121).

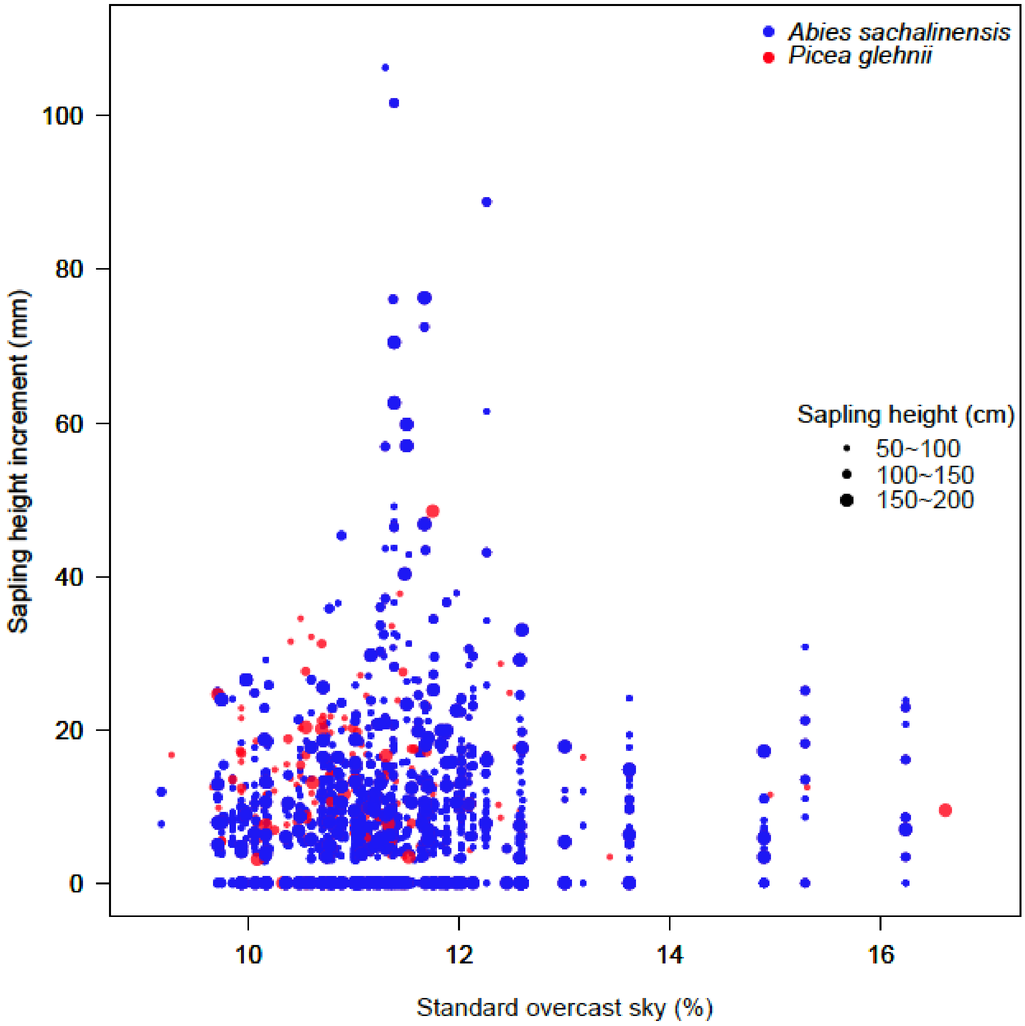

Figure 3-9. Relationship between height growth (mm year$^{-1}$) and relative exposure to light in SOC (%) for *A. sachalinensis* and *P. glehnii.*

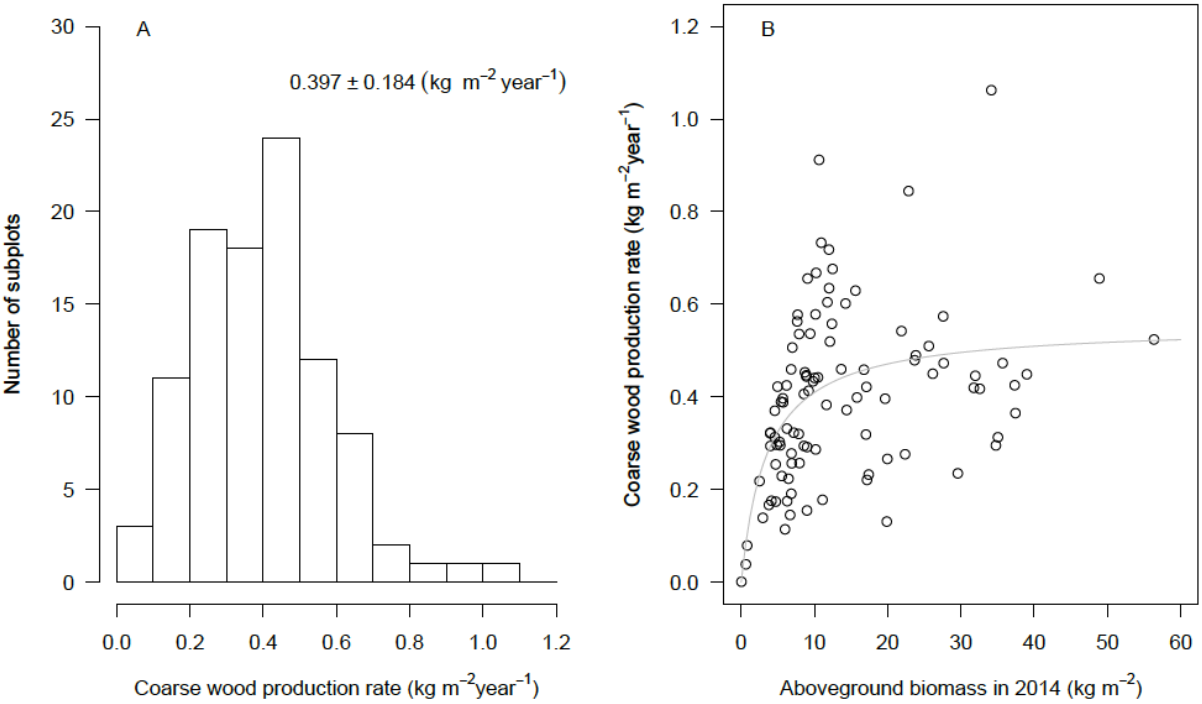

Figure 3-10. A, Distribution of coarse wood production rate across subplots. B, subplot-based coarse wood production rate against aboveground basal area, with fitting curve by Michaelis-Menten equation.

Table 3-1. Species composition and population attributes of trees ≥ 5 cm stem diameter at breast height in the examined 1-ha plot on Mt. Oakan in 2004 and 2014.

| | Tree density ($ha^{-1}$) | | Basal area ($cm^2$ $m^{-2}$) | |
|---|---|---|---|---|
| Species | 2004 | 2014 | 2004 | 2014 |
| *Abies sachalinensis* | 1745 | 1632 | 18.7 | 22.4 |
| *Picea glehnii* | 146 | 111 | 18.8 | 16.9 |
| *Sorbus commixta* | 140 | 117 | 0.771 | 1.02 |
| *Acer japonicum* | 136 | 115 | 0.851 | 0.744 |
| *Acer ukurunduense* | 132 | 103 | 0.613 | 0.546 |
| *Faxinus lanuginosa* | 110 | 73 | 0.824 | 0.635 |
| *Eleutherococcus sciadophylloides* | 77 | 69 | 0.886 | 1.04 |
| *Prunus maximowiczii* | 27 | 26 | 0.154 | 0.211 |
| *Taxus cuspidata* | 27 | 9 | 0.155 | 0.038 |
| *Betula maximowicziana* | 20 | 15 | 0.183 | 0.331 |
| *Magnolia obovata* | 14 | 14 | 0.238 | 0.307 |

Table 3-1. (Continued)

|  | Tree density ($ha^{-1}$) |  | Basal area ($cm^2\ m^{-2}$) |  |
|---|---|---|---|---|
| Species | 2004 | 2014 | 2004 | 2014 |
| *Padus ssiori* | 13 | 12 | 0.118 | 0.132 |
| *Kalopanax septemlobus* | 5 | 5 | 0.154 | 0.2 |
| *Prunus nipponica* | 4 | 4 | 0.024 | 0.033 |
| *Aria alnifolia* | 2 | 2 | 0.012 | 0.014 |
| *Cerasus sargentii* | 2 | 2 | 0.007 | 0.012 |
| *Quercus crispula* | 2 | 2 | 0.006 | 0.015 |
| *Acer palmatum* | 1 | 1 | 0.086 | 0.087 |
| *Acer mono* | 1 | 1 | 0.024 | 0.024 |
| *Tilia japonica* | 1 | 1 | 0.004 | 0.004 |

Table 3-2. The parameter estimates for non-linear model for height and diameter allometric relationship for the year 2004 and 2015.

| | $A$ in 2004 | $H_{\max}$ in 2004 | $A$ in 2015 | $H_{\max}$ in 2015 |
|---|---|---|---|---|
| *Abies sachalinensis* | 0.811 | 45.6 | 1.04 | 37.5 |
| *Picea glehnii* | 0.667 | 58.0 | 0.763 | 52.9 |

Table 3-3. Aboveground biomass and coarse wood production rate for two conifer species.

| Species | Aboveground biomass in 2004 (kg m$^{-2}$) | Aboveground biomass in 2014 (kg m$^{-2}$) | Coarse wood production rate (kg m$^{-2}$ year$^{-1}$) | Biomass loss rate (kg m$^{-2}$ year$^{-1}$) | Biomass turnover rate (%, year$^{-1}$) |
|---|---|---|---|---|---|
| *Abies sachalinensis* | 4.92 | 6.75 | 0.303 | 0.0638 | 4.48 |
| *Picea glehnii* | 7.72 | 7.19 | 0.0888 | 0.148 | 1.24 |
| Total | 12.64 | 13.84 | 0.397 | 0.211 | 2.86 |

## General Discussion

In this thesis, I focused on two contrastive subalpine forests, one in high-altitude fir forest (3100–3900 m) in Langtang Nepal and the other in a low-altitude fir-spruce forest (540 m) in eastern Hokkaido, Japan. They were contrastive not only in geographic setting nor climatic conditions, but also in ways local human communities depend on, such that peoples in high altitude Nepal use more provisional survives such as timber, fuel wood and livestock farming, compared to peoples in eastern Hokkaido who only relay on regulating and cultural services. Here I discuss their contrastive setting and the present results on forest structure and dynamics.

This thesis examined subalpine coniferous forests in contrastive regions; continental subtropical high-altitude subalpine zone, and insular cool-temperate low-altitude subalpine zone. Intra-annual variation in monthly temperature was about 10℃ in subtropical climate and was about 30℃ in cool-temperate climate in the Northern Hemisphere, reflecting latitude difference (Ohsawa 1990). Growing season thermal conditions were similar in the warmth index, within the range of 15–45℃ month by Kira (1991). Meantime, winter hardiness differs between these forest zones. Low winter temperature in Oakan forest is associated with disturbances by snow and rime-ice deposition, and stem breakage by freezing (Nishimura 2005). By contrast in Langtang forest at high altitude, plants suffer from low atmospheric pressure (and in partial $CO_2$ pressure) and high radiation to UV-B radiation.

Himalayan subalpine forests are often dominated by single species *Abies spectabilis* in the canopy for an entire range of moister slopes, while *Juniperus recurva* often dominates on drier slopes and by dwarf scrubs in alpine zone (Stainton 1972). The forest dominated by *Abies* population is most vulnerable to topsoil removal by anthropogenic disturbance such as trampling and influenced by topographic setting such as altitude and slope inclination

(Chapter 1). Meantime, subalpine forests in cool-temperate regions are often co-dominated by a couple of species, often spruce (*Picea* spp.) and fir (*Abies* spp.). We observed inter-specific differentiation between *Picea glehnii* and *Abies sachalinensis* (Chapter 3). *Picea* trees showed better growth and survival for canopy trees, whereas *Abies* trees did in understory, which is in accordance with previous studies (Kubota *et al.* 1994; Takahashi and Kohyama 1999). Such interspecific trade-off may contribute to their coexistence, through micro-succession after disturbances (Takahashi 1994; Takahashi and Kohyama 1999) and/or canopy-understory differentiation suggested by the foliage partitioning theory (Kohyama and Takada 2012).

Subalpine forest of Langtang is mono-dominated by *Abies spectabilis*. The reason of mono-dominance in subalpine Himalayas remains unsolved. In relatively mild winter conditions on wet, leeward slopes with coarse topography may enhance the selective exclusion by single canopy species, compared to temperate lower mountains with high frequency, and/or fine-scale climatic disturbances.

This study showed altitude dependence (Chapter 2), and species dependence of tree size structure (Chapter 3). This study recorded fairly large aboveground biomass, around 40-50 kg $m^{-2}$, in Langtang *Abies* forest (Chapter 2), which is in accordance with earlier studies carried out for *Abies spectabilis* forests in eastern Himalaya (Yoda 1967, 1968). In contrast, aboveground biomass in Oakan forest was about 14 kg $m^{-2}$, only one third of Langtang forest. Relatively mild winter in Himalayan subalpine forests may bring about lower rate of climatic disturbances compared to chilly cool-temperate subalpine forests in eastern Hokkaido, e.g. with higher snow and rime-ice damage on branches and stems, snapping down of saplings by snow load, and freezing breakage of main stems. Relatively higher biomass turnover in Oakan forest can be attributed to that there are high ratios of young stands in recovery from past disturbances.

Another possibility is the plot-size associated bias of biomass estimation. In Langtang forest, many small plots with 10 by 10 m along slope surface (thus less than 100 $m^2$ in horizontal area) were used for estimation. Small-sized plots tend to be set in stands with dense and tall canopy cover. By contrast, Oakan plot with 100 by 100 m in horizontal area is more than 100 times larger than a unit plot of Langtang forest, and the plot covered a range of stand conditions from tree-fall gaps, building-phase stands, and mature stands. Large plot size avoids artificial bias towards choosing developed mature stands, and which results in small biomass with large variation (Chapter 3). Despite of biomass difference, two forests in Nepal and Hokkaido showed similar coarse wood production rate (CWP), around 0.4–0.5 kg $m^{-2}year^{-1}$ (Chapters 2 and 3). If we add the biomass turnover by shorter-lived leaves and twigs, the estimate of aboveground net primary production rate (ANPP) would be doubled at 1.0 kg $m^{-2}year^{-1}$. Stands in subalpine forests achieve such asymptotic rate of CWP and NPP in an early phase of biomass accumulation (Kira and Shidei 1967; Tadaki *et al.* 1970), and the rate is found to be fairly high reflecting adaptation of subalpine conifers to cool growing season.

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