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ORIGINAL RESEARCH

# Stand Structure and Maintenance of *Picea jezoensis* in a Northern Temperate Forest, South Korea

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**Abstract** Stand structure and spatial distribution of *Picea jezoensis* (Siebold et Zucc.) Carrière on Mt. Gyebang, Korea was investigated to provide information on the structural characteristics and the maintenance of *P. jezoensis* population in northern temperate mixed coniferous forests. Height and diameter at breast height (DBH) distribution, age, growth, and spatial distribution patterns of *P. jezoensis* were examined in thirty nine 100-400 $m^2$ quadrats or circular plots. The overall stand structure attributes in the study sites are stem density of 709 trees $ha^{-1}$, a mean DBH of 12.8 cm, and a mean height of 5.6 m, with reverse J shapes of DBH and height distributions. The stem density of *P. jezoensis* population was 81 trees $ha^{-1}$, a mean DBH of 20.7 cm, and a mean height of 9.1 m, showing bimodal-like shapes in age and DBH distributions. Several growth release periods implied that *P. jezoensis* stands experienced small disturbances. The radius of patches of similar-sized *P. jezoensis* in the variogram was equivalent with the height of the tallest trees, indicating that patches were established following the fall of trees in the upper canopy layer. Small windthrows in this region contributed to the maintenance of the *P. jezoensis* stand by releasing sapling growth and providing nursing logs and space for seedlings.

**Keywords** Old-growth forests · Yezo spruce · Disturbance · Windthrow · Spatial distribution

## Introduction

Stand structure refers to the physical and temporal distribution of trees and other plants in stands (Oliver and Larson 1996). The word "temporal" conveys that the stand structure is changing dynamically and continuously. Stand structure changes toward various directions with time and disturbances. Forest structure is determined by various biotic and abiotic factors such as species life history characteristics, climate, soils, and disturbances. Among them, disturbance is the critical factor for determining the dynamics of a forest stand (Kincaid and Parker 2008).

Disturbance creates discontinuities within a community, leaving patches delineated by distinct boundaries depending on the disturbance severity. Because disturbance is a discrete event that could occur at various temporal and spatial scales, it operates diverse patches within a community providing heterogeneous environment (Pickett and White 1985). The responses of species to disturbance differ depending on their ability to occupy and adapt to disturbed patches. Gap created by disturbance provides space for young generation to release its growth or to regenerate, and affects the survival or reform of young generation in a community, often resulting in a single cohort patches. Thus plant communities show patch distribution and the size and structure of patches are subject to the disturbance regime of the region (Frelich 2002).

Species show different gap encroachment pattern along environmental gradient (Yoshida and Ohsawa 1996), and spatial distribution patterns of species are important information for understanding population dynamics, history, and competition as well as affect forest ecosystem function significantly (Pielou 1960; Haase 1995). Since the growth, survival, and reproduction condition of individual trees can be influenced by neighborhood trees, spatial pattern of trees can influence stand dynamics, and in turn, tree demography brings out and regulate the spatial pattern (Clark and Evans 1954; Barot et al. 1999). Knowledge on the spatial distribution pattern of trees is useful in understanding inter- and intra-specific relationships, and

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forest management that mimics natural processes (Salas et al. 2006). Therefore, ecologists have long been interested in the spatial patterns of a population (Morisita 1962; Anderson 1992).

*Picea jezoensis* (Siebold et Zucc.) Carrière (Yezo spruce) is a subalpine evergreen species with a maximum height of over 40 m and a maximum diameter at breast height (DBH) reaching 1 m (Lee and Cho 1993). It is one of the dominant and economically valuable species in boreal or subalpine forests in Northeast Asia (Nakagawa et al. 2003). *P. jezoensis* distributes within the latitude 35-56°N of the northern part of Sikhote-Alin, the eastern part of Okhotsk, Mt. Baekdu, Shantar Islands, Sakhalin Island, the South Kurils and Hokkaido. Disjunct localities are found in the middle part of Honshu Island, the central part of Kamchatka, the northeastern part of China in the Dulin mountain range, and Korea (Krestov and Nakamura 2002). While many studies of *P. jezoensis* have been conducted in Russia, Japan, and China, *P. jezoensis* in South Korea has been studied recently, and only limited information is available in spite of Korea's geographical importance as the southern limit of the latitudinal distribution of *P. jezoensis* (Song 1992; Park et al. 2006; Lee et al. 2007). Until now, the disjunct localities in South Korea have been reported only in a few areas: the heights of Mt. Jiri, Mt. Deogyu, Mt. Seorak, and Mt. Gyebang (Lee 1999; Kong 2004; Moriguchi et al. 2009). Isolated *P. jezoensis* populations on subalpine mountain tops in South Korea have small population sizes. Isolation may inhibit trait exchange among populations and the species may die out within certain limited areas (Koo et al. 2001; Lee and Cho 1993). Moreover, increasing air temperature due to climate change is physical stress to subalpine species that had adapted to chilly conditions. Also, increased competition against other plants expanded the hazards for survival in their habitats (Kong 2005) as the decline of *P. jezoensis* has been reported in Hokkaido (Fukuda et al. 1997).

*P. jezoensis* is a relatively shade tolerant species often dominating old-growth forests with firs (Wu 1990; Miyadokoro et al. 2004). Factors to enable *P. jezoensis* to share canopy dominance with more shade tolerant *Abies* include species ecological characteristics and environmental factors. Supply of large woody debris in old-growth forest provides substrate for *P. jezoensis* regeneration (Nakagawa et al. 2003; Mori et al. 2004; Doi et al. 2008). The persistent sapling bank of *P. jezoensis* is a key supporter of the maintenance of spruce forests in the absence of catastrophic disturbance (Wu 1990).

The complex structures of plant populations are connected to their complex functions, and it is essential to understand the attributes of structure for establishing species conservation strategy and effective forest management (Yang and Kim 2002). However, little information is available on the stand structure or the distributions of *P. jezoensis* stands on Mt. Gyebang, where the largest population of *P. jezoensis* in South Korea exists. This study aimed to examine stand structural characteristics of the northern temperate spruce forest to understand the dynamics and maintenance of this species on a northern temperate mountain.

## Methods

### Study Area

The study was conducted in *P. jezoensis* stands on the upper slopes of the Eulsudong valley watershed (37°44'N, 128° 28'E) at Mt. Gyebang, Korea (Fig. 1). Climate data from the near Long-Term Ecological Research site of the Korea Forest Research Institute showed that annual mean air temperature is 7.0°C. Mean temperatures in January and August are −8.8°C and 18.9°C, respectively. Based on meteorological data from the Daegwallyeong weather station from 1971 to 2000, mean wind velocity and mean annual precipitation were observed to be ca. 3.9 $ms^{-1}$ and 1,717.2 mm, respectively. Precipitation is concentrated from July to September, which is characteristic of a monsoonal climate (Korea Meteorological Administration 2007).

The mean altitude of *P. jezoensis* plots in Mt. Gyebang was 1,435.8 m asl with minimum and maximum altitudes of 1,263 and 1,565 masl, respectively. The mean slope of the site was around 49.3%. The population of *P. jezoensis* was mostly distributed in the aspects of N, NE, and SE (Table 1).

Almost all *P. jezoensis* stands were located on rocky areas or humus layers made from organic matter decomposed over a long time. Soil was very shallow with soil depth not more than 20 cm in most of plots. Mean soil pH of the study site was 4.6, mean soil moisture was 5.0%, mean soil organic matter content was 20.1%, mean cation exchange capacity (CEC) was 25.9 cmol $kg^{-1}$, mean total *N* was 0.69%, and available phosphorus was 37.2 mg $kg^{-1}$. The soil pH (4.6±0.08) of this site was considerably lower than the national average of forest soil in Korea (pH5.48). Low soil pH on this site is thought to be caused by the development of humus with high soil organic matter content (20.1±1.3%). Although soil pH is affected by many factors, such as the development of humus, parent materials, nitrification ratio of soils, and cation absorption of vegetation, high total N (0.69±0.06%), and high CEC (25.9±1.7 cmol $kg^{-1}$) also verify that this site has high organic matter content through humus.

### Data Collection

Thirty-seven circular plots and two quadrats of 100-400 $m^2$ plot size were established in *P. jezoensis* stands. The plots

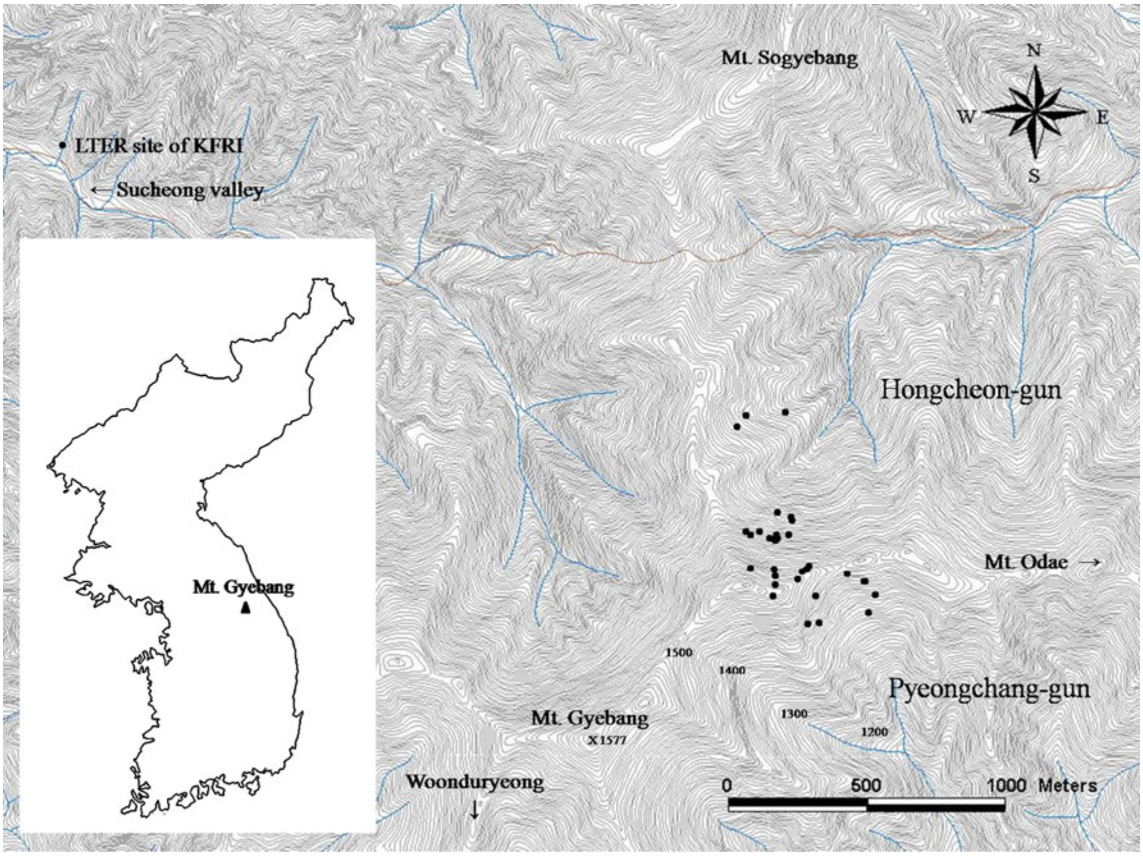



**Fig. 1** Location of the study site on Mt. Gyebang, Korea. *Points* indicate survey plots

were placed subjectively, in order to include *P. jezoensis*, and were dispersed widely over the entire range of *P. jezoensis* habitat in the Eulsudong valley watershed. All trees greater than 2.5 cm DBH in a plot were measured from May 2006 to October 2007. Species name, DBH, height, and geographic coordinates of each tree were recorded. Height was measured by hypsometer (Vertex laser, Haglöf, Sweden), while DBH was measured at 1.3 m above the ground.

To analyze spatial distribution patterns of *P. jezoensis* individuals, an additional 150×250 m quadrat was established covering all study plots. All *P. jezoensis* trees at least 2.5 cm in DBH were tallied and mapped and their geographic coordinates were recorded within the 150×250 m quadrat.

About 10% of the total surveyed individuals were sampled for age distribution. Because the stem densities of *P. jezoensis* individuals were low, eleven *P. jezoensis* trees were selected based on the DBH classes and cored at 0.2 m above ground using an increment borer for age determination and growth estimation. Regression equations between DBH and age were established, and the ages of the other trees were estimated.

**Table 1** Topographic and soil characteristics of *Picea jezoensis* stands on Mt. Gyebang, Korea

| | Variable | Mean±SE ($n$=39) |
|---|---|---|
| Topographic characteristics | Altitude (m) | 1,435.8±12.2 |
| | Slope (%) | 49.3±2.4 |
| | Aspect | N, NE, SE |
| | Rock exposure (%) | 46.5±5.5 |
| Soil characteristics | Soil moisture content (%) | 5.0±0.4 |
| | Soil organic matter content (%) | 20.1±1.3 |
| | Soil pH (1:5) | 4.6±0.08 |
| | Total $N$ (%) | 0.69±0.06 |
| | Available $P$ (mg kg$^{-1}$) | 37.2±7.8 |
| | CEC (cmol kg$^{-1}$) | 25.9±1.7 |

Soil cores (0–5 cm) were taken in 25 plots and depth of soil, soil moisture, soil pH (soil/water=1:5), organic matter contents, total N (Konen et al. 2002), available phosphorus (Kuo 1996), and CEC (Sumner and Miller 1996) were measured.

## Data Analysis

Species composition was investigated using the importance values for each species which were calculated using relative density, relative coverage, and relative frequency (Curtis and McIntosh 1951). Coverage was calculated using stem basal area at breast height. Frequency of a species was calculated as the number of plots where a species distributed divided by the total number of plots.

All wood cores were air dried, sanded with sand paper, and stored in woody mounts to analyze the growth rate. Annual rings were counted from pith to bark and their widths were measured to the nearest 0.1 mm. Crossdatings of individual trees were conducted by binocular magnifier and digital calipers (Mitutoyo, Japan). With the crossdated data, mean annual increment (MAI), and periodic annual increment (PAI) of diameters were evaluated from the extracted cores (Husch et al. 2003). MAI was calculated as tree diameter divided by tree age at the diameter measurement. PAI was radial increments of diameter (absolute growth) for each year. To detect growth-release events, PAI was divided by MAI.

A variogram using DBH and geographic coordinate data of each tree was introduced to analyze the spatial autocorrelation among *P. jezoensis* individuals (Choe 2002). The variogram characterizes the spatial continuity of a data set and represents the degree of similarity of DBH values of individual trees within certain distance (Dale 1999). Half of a variogram, a semivariogram, was often usesd (Choe 2002; Kang et al. 2003). The semivariogram is defined as follows:

$$\gamma(h) = \frac{1}{2n} \sum_{i=1}^{n} [z(x_i) - z(x_i + h)]^2$$

where, $h$ is the lag distance which represents the separation between two spatial locations, $n$ is the number of data in the lag distance $h$, $x_i$ is the spatial coordinates and $z(x_i)$ is the variable at the location $x_i$. Analyses were conducted using the computer program SADA ver. 3.1.84 (SADA 1996). All other descriptive statistics were performed by SPSS 12.0 K (SPSS inc. 2004).

## Results

The species of greatest importance value in the study area were *P. jezoensis*, *Taxus cuspidata* Siebold et Zucc., *Sorbus commixta* Hedl., *Acer komarovii* Pojark., *Prunus padus* L. and *Abies nephrolepis* (Trautv.) Maxim., respectively, in the order from greatest importance to least importance values (Table 2). *A. komarovii* had the highest stem density of 96 trees ha$^{-1}$ followed by *P. jezoensis* among tree species. *P. jezoensis* was also the second in basal area occupation next to *T. cuspidata*, resulting that *P. jezoensis* had the highest importance value among tree species in the study area. Although the stem density of *T. cuspidata* was only 32 trees ha$^{-1}$, *T. cuspidata* occupied the largest basal area ha$^{-1}$ among species. Deciduous species had higher stem density, however, less basal area occupation than coniferous species, and were not the dominant species in the top canopy layer. While coniferous species dominated top canopy layer (>6 m height) and under layer (<3 m height), deciduous species, especially *P. padus*, *A. komarovii*, and *S. commixta* shared dominance

**Table 2** Major tree species in *Picea jezoensis* stands on Mt. Gyebang, Korea

| | Density (stem ha$^{-1}$) | Basal area (m$^2$ha$^{-1}$) | Importance value (%) |
|---|---|---|---|
| *Picea jezoensis* | 93 | 4.87 | 15.7 |
| *Taxus cuspidata* | 32 | 6.38 | 13.1 |
| *Sorbus commixta* | 71 | 1.40 | 8.8 |
| *Acer komarovii* | 96 | 0.63 | 8.4 |
| *Prunus padus* | 68 | 0.79 | 7.1 |
| *Abies nephrolepis* | 39 | 1.69 | 6.5 |
| *Acer pseudosieboldianum* | 54 | 0.85 | 5.6 |
| *Betula ermanii* | 34 | 1.26 | 5.4 |
| *Quercus mongolica* | 26 | 0.96 | 3.6 |
| Other species | 197 | 3.46 | 26.0 |
| Total | 709 | 22.30 | 100.0 |

Importance value (%)=relative density+relative coverage+relative frequency for each species/3 in the middle layer (3-6 m height classes). *A. nephrolepis*, *A. komarovii*, and *P. jezoensis* were most abundant tree species in the layer less than 3 m height. In the herb layer, a broad range of herb species was found, including *Meehania urticifolia* (Miq.) Makino, *Parasenecio auriculata* var. *matsumurana* Nakai, *Veratrum oxysepalum* Turcz., *Dryopteris crassirhizoma* Nakai, and *Filipendula glaberrima* (Nakai) Nakai.

The overall stand density of study site was 709 trees ha$^{-1}$, the mean DBH was 12.8 cm, and the mean height was 5.6 m (Table 3). The mean herb coverage was 56.8% and the mean herb height was 0.4 m. The density of *P. jezoensis* population in Mt. Gyebang was ca. 81 trees ha$^{-1}$, the mean DBH was 20.7 cm, the mean height was 9.1 m, the mean crown width was 3.4 m, and the mean crown ratio was 53%.

While DBH distribution of overall species in *P. jezoensis* stands showed a reversed-J shape, *P. jezoensis* had a bimodal tendency in the DBH distribution (Fig. 2). Most of *T. cuspidata* distributed in the DBH class larger than 50 cm. The density of *P. jezoensis* was higher than that of *A. nephrolepis* in most DBH classes. However, more *A. nephrolepis* appeared in the DBH class less than 10 cm than *P. jezoensis,* indicating that the seedling density of *A. nephrolepis* was more than that of *P. jezoensis.* The density of deciduous species were less than 1 trees ha$^{-1}$ in DBH classes over 35 cm and most of deciduous species distributed in lower DBH classes less than 20 cm. The density of snags in *P. jezoensis* stands was 95 trees ha$^{-1}$. Snags appeared throughout the all DBH classes. The mean DBH of snags was 19.5 cm, which is larger than the mean DBH of living trees. Large snags over 40 cm of DBH distributed more than living trees of *P. jezoensis* and *A. nephrolepis.*

*A. nephrolepis* and *P. jezoensis* were distributed in the upper layer, while *T. cuspidata*, *A. komarovii*, *S. commixta*, and *Betula ermanii* were dominant species in the middle and lower canopy layers (Fig. 3). The number of individuals of all species except *P. jezoensis* decreased as height increased. However, *P. jezoensis* had a bimodal tendency. The density of *P. jezoensis* was high in <6 m and 12-15 m height classes, while similar number of *P. jezoensis* distributed in other height classes.

DBH and age had a significant relationship ($P$=0.044). Age structure was analyzed using the age-DBH equation based on the regression analysis ($R^2$=0.615). The age distribution of *P. jezoensis* showed a bimodal shape similar to the DBH distribution (Fig. 4). The numbers of *P. jezoensis* in the less than 20 year age class, 30-40 year age class and 50-70 year age class were higher compared to *P. jezoensis* in other age classes.

Diameter increment through years and the average MAI and PAI of *P. jezoensis* on Mt. Gyebang indicated that the initial growth of seedlings and saplings was very slow (Fig. 5a). However, most *P. jezoensis* individuals showed fast growth around 60-70 years ago. The growth rate tended to be stable in more recent years. The MAI and PAI of diameters met around age 120. The ratio of PAI to MAI showed that there were large PAIs 15, 30, 60-70, and 150 years ago (Fig. 5b).

The semiviogram detected a patch of similar sized *P. jezoensis* trees. Similar-sized *P. jezoensis* trees aggregated within certain distance (Fig. 6a). The estimator approached the sill value of 1.6 at a distance of 45 m (Fig. 6b) indicating that an aggregate of similar sized *P. jezoensis* had a radius of ca. 23 m.

## Discussion

The reversed-J shapes of the height and DBH distributions of overall species in the study area indicate that this site has maintained a continuous recruitment and mortality, implying the possibility of uneven-aged forest and old-growth forest (Meyer and Stevenson 1943; Oliver and Larson 1996). The stem density of *P. jezoensis* stands on Mt. Gyebang showed a similar pattern to a Japanese old-growth forest (Narukawa and Yamamoto 2001; Miyadokoro et al. 2003) as the stem density was quite low and spacing between trees was large. One of major characteristics of an old-growth forest is the existence of large snags which is also found in the study area (Tyrrell and Crow 1994). Thus, the study found that the *P. jezoensis* stand in Mt. Gyebang is close to old-growth stage. This type of forest can have a self-perpetuating or climax population for a long time unless large-scale disturbance or environmental change occurs (Whipple and Dix 1979). The stand condition revealed that the current structure would be maintained unless there was catastrophic change.

*P. jezoensis* and *A. nephrolepis* were two dominant species in the canopy layer. Both *P. jezoensis* and *A. nephrolepis* had a similar shape of DBH distribution;

**Table 3** Overall stand structural attributes and *Picea jezoensis* population attributes on Mt. Gyebang, Korea (mean±SE, $n$=39)

| Overall stand structure | | | | | *Picea jezoensis* population | | |
|---|---|---|---|---|---|---|---|
| Density (stem ha$^{-1}$) | DBH (cm) | Height (m) | Herb coverage (%) | Height of herb (m) | Density (stem ha$^{-1}$) | DBH of *P. jezoensis* (cm) | Height of *P. jezoensis* (m) |
| 709±344 | 12.8±10.7 | 5.6±3.9 | 56.8±4.9 | 0.4±0.03 | 81±58 | 20.7±15.3 | 9.1±5.9 |

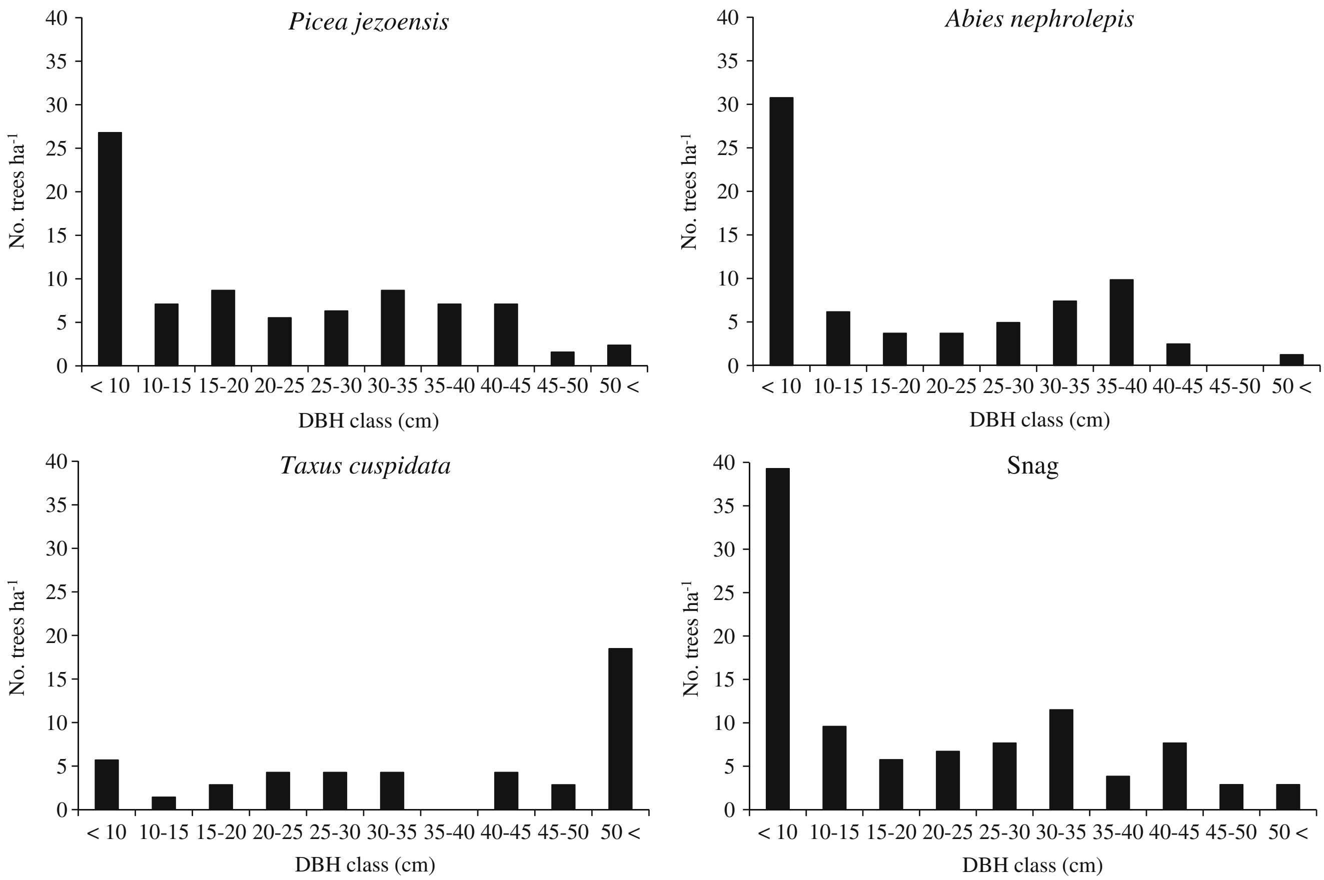



**Fig. 2** DBH distribution of major species in *Picea jezoensis* stands on Mt. Gyebang, Korea

however, their height distribution patterns were different. While *P. jezoensis* showed a bimodal shaped height distribution indicating that the regeneration of *P. jezoensis* might be discrete events, the height distribution of *A. nephrolepis* was a reversed J-shape. *A. nephrolepis* was more abundant in the 6-9 m and 9-12 m height classes than *P. jezoensis*. This status reversed in the greater height classes. Differences in densities between *P. jezoensis* and *A. nephrolepis* in different height classes could be partly explained by the idea of "maximum sustainable height" (Messier et al. 1999). The waiting height of fir is 7 m, while that of *P. jezoensis* is ca. 3 m (Kubota et al. 1994). The higher waiting height for fir is caused by the intrinsic ability to balance carbon management in life-history traits (Kubota et al. 1994; Messier et al. 1999). *A. nephrolepis* has a higher waiting height to increase its chances of reaching the canopy layer. However, entering the canopy layer means that the size becomes larger, requiring more light, while light intensity in the middle of the canopy decreases exponentially resulting in the increased possibility of mortality. Mori et al. (2008) also found out that the mortality of *Abies* trees was increased as they were closer to the canopy in subalpine coniferous forests of central Japan. On the other hand, the lower waiting height of *P. jezoensis* allows it to compensate for the relatively small number of seedlings with lower mortality in the understory layer (Kubota et al. 1994). The demographic characteristics support the two species' coexistence in this site with maintaining dominance. Short-lived *Abies* has more fecundity than *Picea*, but *Picea* has higher longevity and a lower mortality rate than *Abies* (White et al. 1985; Kubota et al. 1994; Takahashi and Kohyama 1999).

*P. jezoensis* has a long life span relative to other species on Mt. Gyebang. In spite of the low initial growth rate, saplings of *P. jezoensis* can survive under shaded conditions (Wu 1990). Once the canopy opens, saplings grow faster than other species and occupy the canopy (Mori and Takeda 2003). However, this process is only possible if *P. jezoensis* has shade-tolerance with a long life-span, and disturbances occur only intermittently. Especially, the intermittent disturbances are the crucial factor as a "non-equillibrium process" for the coexistence of *Abies* and *Picea* species in this subalpine forest (Mori and Takeda 2004). Without intermittent disturbances, *P. jezoensis* might not have the chance to grow to the upper canopy layer and might be suppressed to die out while more shade tolerant *A. nephrolepis* dominates the stand.

The peaks of PAI (regarded as growth-release events; Fig. 5) of *P. jezoensis* indicate that a few disturbances of

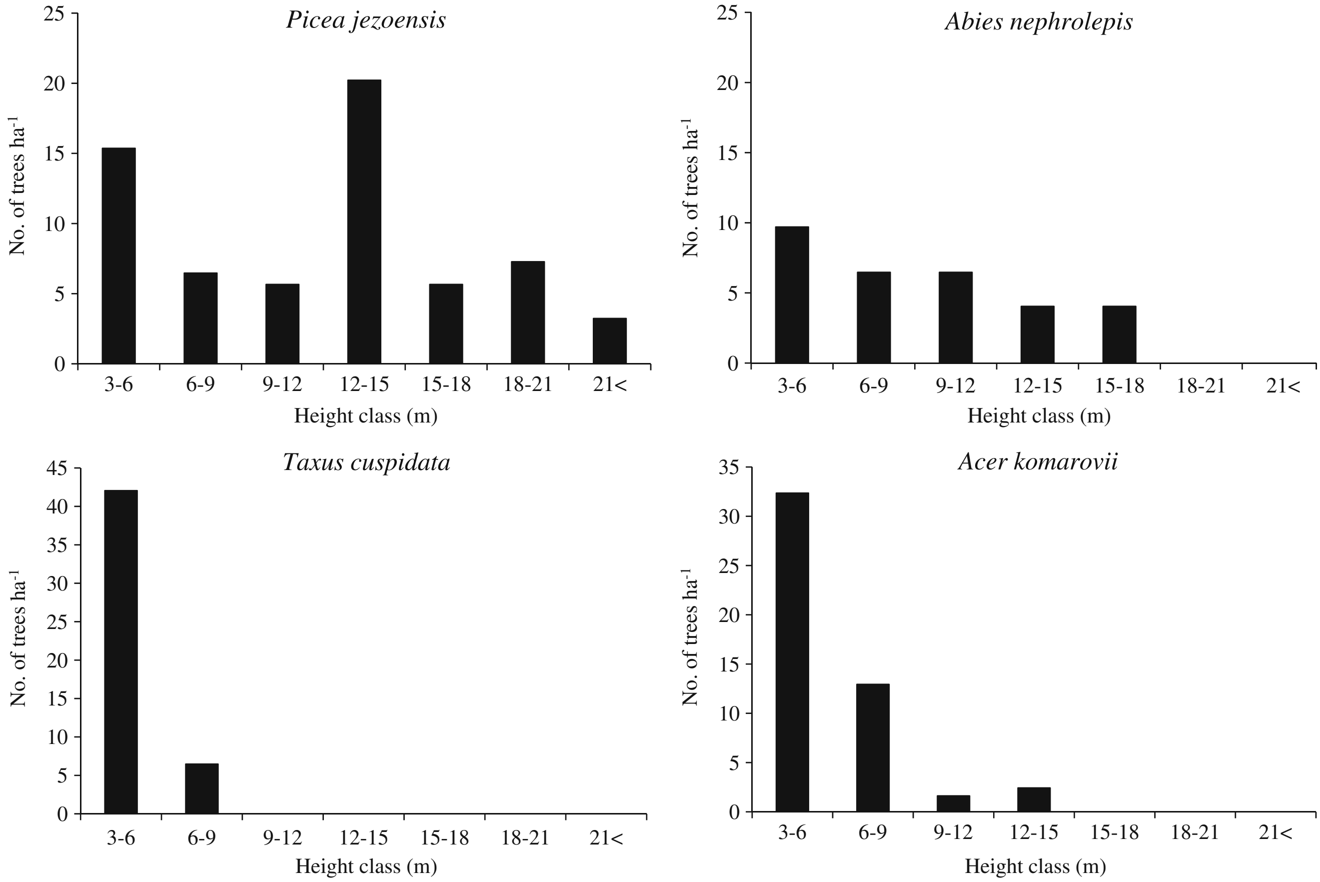



**Fig. 3** Height distribution of major species in *Picea jezoensis* stands on Mt. Gyebang, Korea

small scale and low intensity happened in this area. Small disturbance events might cause several tree deaths, providing space for growth release (Zielonka and Malcher 2009). However, growth release of saplings and adults of *P. jezoensis* implies that the disturbance severity was not so catastrophic as to destroy the whole stand, nor was the agent fire to which spruce and fir are susceptible. If this site had been disturbed frequently by forest fire, the organic matter content of the soil would not be so high in this area (Jeong et al. 2002). No evidence of logging or forest fire was observed in this area.

Several patches of similar-sized *P. jezoensis* also support the evidence of small disturbances which might have released the growth of suppressed *P. jezoensis* saplings under canopy resulting in reaching similar size within a same gap (Lorimer 1985; Duncan and Stewart 1991). In an

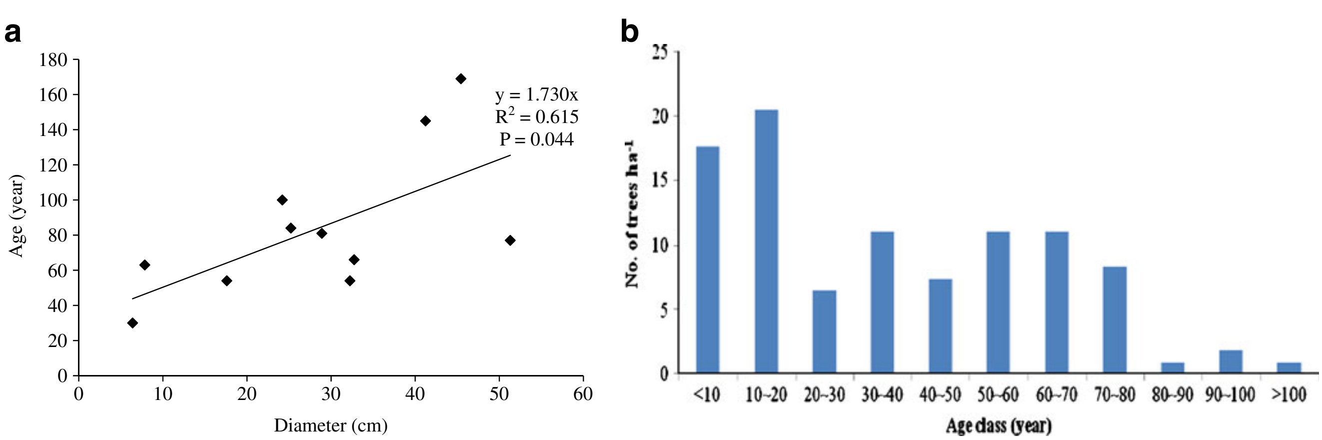



**Fig. 4** **a** Regression analysis between age and diameter at breast height and **b** estimated age distribution of *Picea jezoensis*

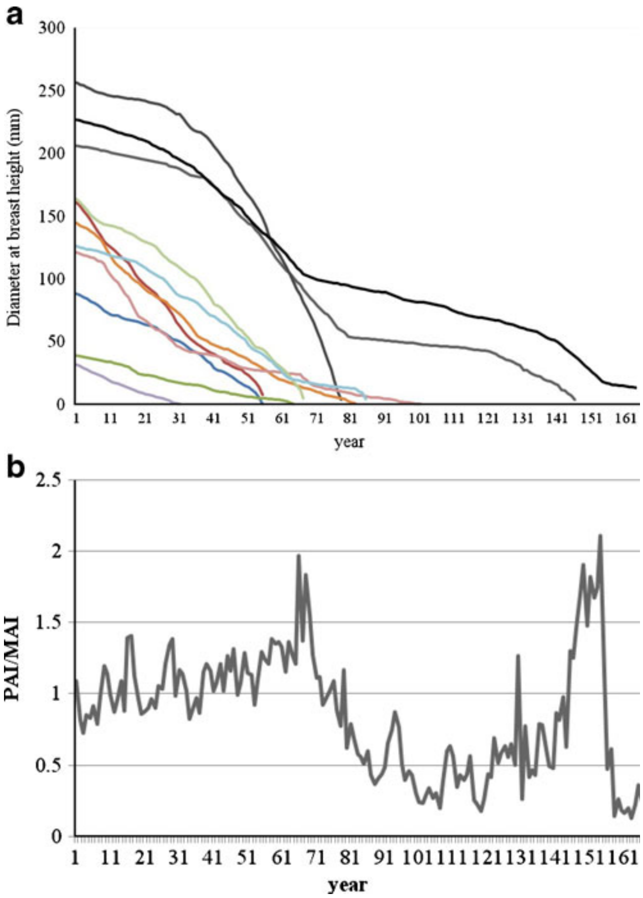
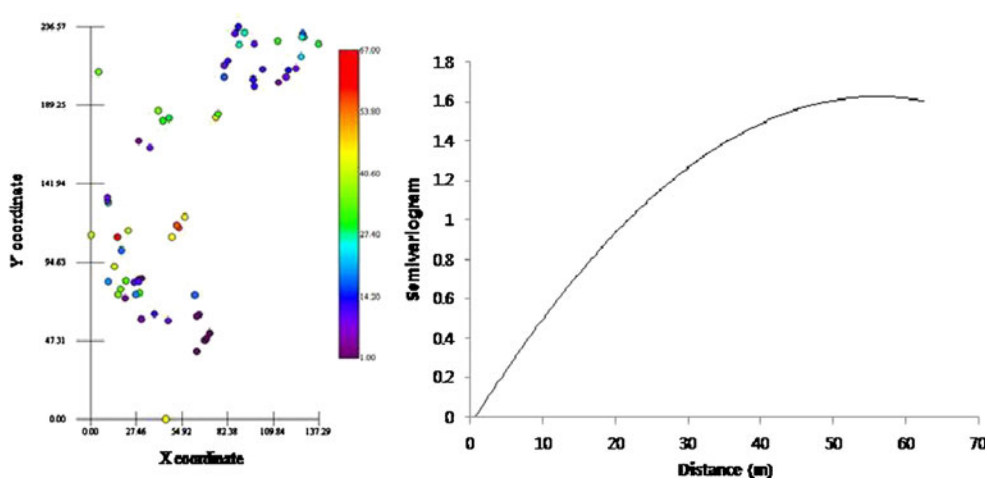



**Fig. 5** **a** Diameter at 0.2 m above ground of sample trees ($n$=11) and **b** ratio of PAI to MAI of *Picea jezoensis* individuals through the year. *Year* indicates number of years from the survey year as year 1 is 2006, and year 101 is 1906

old-growth forest, tree replacement takes place in canopy gaps caused by the death of one or more upper layer trees (Taylor et al. 2006). The size and distribution of patches show disturbance history as patch size reflects disturbance intensity and the mosaics of different patches indicates different disturbance events (Oliver and Stephens 1977; Taylor and Halpern 1991). With the height of the upper canopy layer trees in this site ca. 20-23 m, the main factor forming a gap and providing growth release or recruitment pulse was the falling down of large individuals. Windblown large *P. jezoensis* individuals were seen occasionally in the plots. These conditions can be attributed to wind as the main disturbance factor in the study area. Windthrow is a widespread disturbance factor and gap maker in spruce forests (Foster and Reiners 1986; Henbo et al. 2006; Gray and He 2009). This site has been damaged by typhoons almost every year, and the average maximum instantaneous wind speed at the Daegwallyeong weather station near the study site was 33.3 $\mathrm{m\,s^{-1}}$ from 1972 to 2006 (Korea Meteorological Administration 2007). Considering hurricanes with speed of more than 20 $\mathrm{m\,s^{-1}}$ could result in the catastrophic windthrow (Ulanova 2000), the wind speed in this region would be strong enough to cause severe windthrow. However, rough mountainous topography limits wind power, suppressing typhoon effects to small windthrow events and preventing stand-replacing disturbances. Additionally, the shallow soil depth in this site and shallow root depth make *P. jezoensis* susceptible to strong winds.

The soil organic matter content of the study area is over 20% while soil depth is shallow less than 20 cm, indicating plentiful supply of organics to the soil probably from woody debris derived from snags in the DBH range of less than 10 cm to over 50 cm in the study area. In mature forests, dead tree fall or tree breakage and uprooting by windthrow can be a major source of woody debris on the forest floor (Mitchell 1995). Recent studies have emphasized the important role of coarse woody debris on the forest floor which provides substrate for seed germination and seedling growth and survival. Fallen and appropriately decayed logs can give *P. jezoensis* seedlings a suitable place to germinate and survive, thus acting as nurse logs

**Fig. 6** **a** Mapped locations of *Picea jezoensis* trees in the 150×250 m plot and **b** semivariogram of DBH distribution of *Picea jezoensis* on Mt. Gyebang, Korea



(McCarthy 2001) or safe site (Mori et al. 2004). This phenomenon has been observed commonly around the world from temperate rainforests to subalpine or boreal old-growth forests (e.g., Harmon and Franklin 1989; Takahashi 1994). The fact that most *P. jezoensis* seedlings were found on the logs indicates that coarse woody debris such as fallen logs or stumps is needed for *P. jezoensis* seedlings to survive by avoiding competition with other herb species (Szewczyk and Szwagrzyk 1996; Takahashi 1994), and also explains pulses in estimated age distribution of *P. jezoensis*. A sustainable supply of woody debris supports the regeneration of *P. jezoensis*, and endemic windthrow is a major contributor to woody debris. We can conclude that small-sized disturbance patches created by intermittent low intensity wind disturbance is the important factor for the maintenance of *P. jezoensis* in this area.

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