



Original Article

Disturbance and regeneration dynamics of a mixed Korean pine dominated forest on Changbai Mountain, North-Eastern China



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ABSTRACT

We used dendrochronological methods to study disturbance history of a mixed Korean pine (*Pinus koraiensis* Siebold et Zuccarini) dominated forest on the northern slope of Changbai Mountain, North Eastern China, over 1770–2000. Frequent small-scale canopy gaps and infrequent medium-scale canopy disturbances dominated natural disturbance regime in the forest, which did not experience stand-replacing disturbances over the studied period. Percentages of growth releases in subcanopy trees were below 6% in most decades, suggesting that disturbances initiating these releases were of low intensity. Strong winds were likely cause of moderate disturbance events. Two episodes with increased disturbance rates (19% and 13%) were dated to the 1920s and 1980s, timing of the 1980s event was consistent with a hurricane occurred in 1986 on the western slope of the Changbai Mountain. Age structure and growth release analyses revealed species-specific regeneration strategies of canopy dominants. Shade-intolerant Olga bay larch (*Larix olgensis* Henry) recruited mainly before the 1860s. Recruitment of moderately shade-tolerant *P. koraiensis* occurred as several regeneration waves (1820s, 1850s, 1870–1880s, 1930s, and 1990–2000s) of moderate intensity. Shade-tolerant Jezo spruce (*Picea jezoensis* Carr. var. *komarovii* (V. Vassil.) Cheng et L.K.Fu) and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim.) regenerated continuously over the last 220 and 130 years, respectively. Enhanced recruitment of *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis* was observed during the 1930s and 1990s, coinciding with increased growth release frequency in the 1920s and 1980s, and suggesting disturbance events of moderate intensity. Our results indicate that the current disturbance regime of the mixed Korean pine dominated forest maintains coexistence of light-demanding and shade-tolerant species and that change in wind climate may be particularly important for future forest composition.

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Introduction

Natural disturbances have profound effects on forest dynamics, influencing growth, regeneration, diversity, and coexistence of tree species (Frelich and Lorimer, 1991; Abrams et al., 1999; Kubota, 2000; Bergeron et al., 2004). Studies in forest disturbance history are critical for understanding the present forest composition and predicting the future forest structure under different climate and management scenarios (Girardin et al., 2001; Kuuluvainen, 2002;

Dang et al., 2009). Dendroecological techniques are widely applied to reconstruct forest history, disturbance regimes, and past forest dynamics (Brisson et al., 1992; Tardif et al., 2001; Fraver and White, 2005). Tree ring analyses allow reconstruction of forest disturbance history through dating of growth release and analyzing the establishing dates in sampled individuals (Lorimer and Frelich, 1989; Frelich and Lorimer, 1991; Black and Abrams, 2003).

Disturbance regimes in the mixed forest are important in promoting coexistence of tree species (Runkle, 1985; Liu, 1997; Bergeron, 2000). In closed-canopy temperate forests, the gradient in forest disturbance severity ranges from small canopy gaps created by single or multiple treefalls to large-scale stand-replacing events (Runkle, 1985; Runkle and Yetter, 1987; Foster et al., 1998; Romme et al., 1998; Turner et al., 1998; Ilisson et al., 2005; Margolis et al., 2007). Variation in the size and frequency of disturbances causes spatial and temporal heterogeneity in environment affecting establishment, growth, and survival of trees

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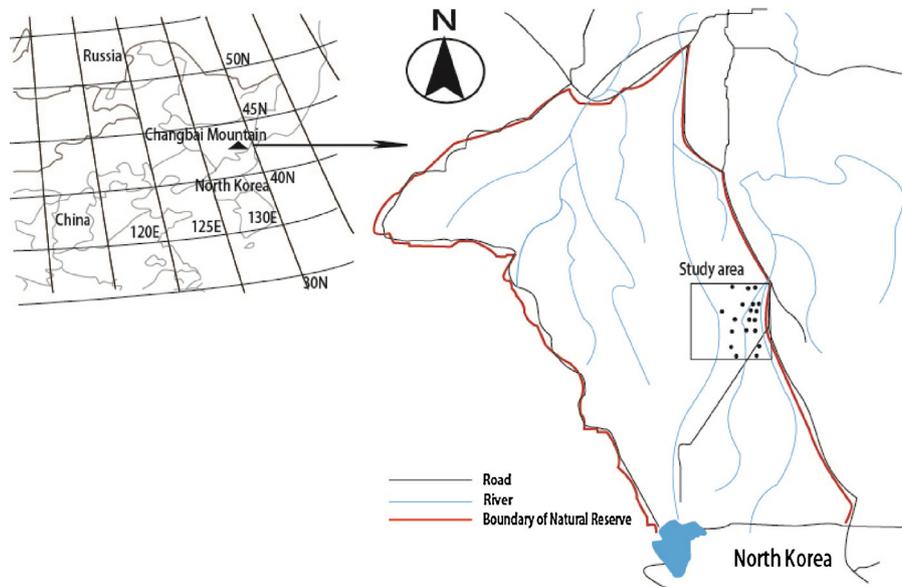


Fig. 1. The location of study sites on the northern slope of Changbai Mountain, North Eastern China.

(Liu, 1997; Mori and Takeda, 2004). Species may respond differently to the range of disturbance sizes and severities, depending on their own ecological characteristics such as shade tolerance and regeneration requirements (Runkle and Yetter, 1987; Bergeron et al., 1998; Drobyshev, 1999). Typically, shade-tolerant trees benefit from advanced regeneration and often colonize small canopy gaps, whereas shade-intolerant trees reveal faster growth rates but require large disturbance patches for establishment (Runkle and Yetter, 1987; Kobe et al., 1995; Liu, 1997). Diversity in disturbance events may therefore allow coexistence of both groups of trees within a community.

Mixed Korean pine (*Pinus koraiensis* Siebold et Zuccarini) dominated forest is a major forest type in the Northeastern China with Changbai Mountain as its core distribution area. Volcanism and wind are two main natural disturbance factors affecting forest dynamics in Changbai Mountain (Manchida et al., 1987; Liu, 1997; Dai et al., 2011). Volcanism results in large-scale and stand-replacing disturbances in the area. The most severe volcanic eruption in the Changbai Mountain occurred around 1100 AD and destroyed vegetation over the area of 100 km², the current vegetation cover originating largely after that event (Zhao, 1981). The most recent eruptions occurred in 1597, 1668, and 1702 and had spatially limited effects on local forests (Zhao, 1981; Manchida et al., 1987). Instead, wind mainly causes a wide range of disturbance events ranging from large blowdowns to single and multiple tree falls (Dai et al., 2011), all of which are considered important for forest dynamics in the Changbai Mountain. Large scale wind disturbances (>1000 m²) are important for persistence of shade intolerant species in the forest canopy, such as Olga bay larch (*Larix olgensis* Henry) (Yang et al., 1994; Okitsu et al., 1995; Liu, 1997). Wind-induced small canopy gaps maintain mid-tolerant *P. koraiensis* in broadleaf-Korean pine forest (Dai et al., 2011). Jezo spruce (*Picea jezoensis* Carr. var. *komarovii* (V. Vassil.) Cheng et L.K. Fu) and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim.) appear to be less dependent on canopy disturbances due to their shade tolerance (Yang et al., 1994; Okitsu et al., 1995; Liu, 1997). Historical records on the frequency and intensity of disturbance events themselves are largely missing, which precludes a deeper understanding of community dynamics in this part of the Eastern Asian temperate zone.

In an attempt to quantify the multi-century pattern of natural disturbances in Asian mixed temperate forests, we studied forest disturbance history and regeneration dynamics in a primary mixed Korean pine forest, the most typical forest type in the Changbai Mountain. Our specific objectives were (1) to investigate temporal patterns of tree species regeneration, (2) to reconstruct local disturbance history of this mixed forest, and (3) to understand the relationship between disturbance history and species coexistence. Based on our field observations and published studies (Yang et al., 1994; Okitsu et al., 1995; Liu, 1997; Dai et al., 2011), we hypothesized that (1) the forest disturbance regime is dominated by frequent small-scale disturbances, whereas medium or large-scale disturbances (>1 ha) are infrequent, and (2) both regeneration and growth patterns of three dominant species (*P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*) are synchronized by the canopy disturbances. Understanding the level of control exercised by the disturbance regime upon trees' regeneration is crucial for modeling future species population dynamics. We therefore discuss our results in the context of potential effects of climatic variability on natural disturbance regime and dynamics of the mixed Korean pine forests.

Materials and methods

Study area and climate

The study was conducted on the northern slope of Changbai Mountain in North Eastern China (1900 km², 41°31'–42°28'N, 127°9'–128°55'E, Fig. 1), within the territory of Changbaishan Natural Reserve. The area has a temperate continental climate, with long, cold, and windy winters and short, warm, and rainy summers. Annual mean temperatures vary from 7.3 °C at the low elevations (700 m a.s.l.) to 2.8 °C at the top of the mountain (2691 m a.s.l.). The mean annual precipitation along this gradient varies from 750 to 1340 mm (Zhao, 1981). The frequency of storms (episodes with wind speeds above 17 m s⁻¹) varies from 30 days year⁻¹ at 770 m a.s.l. to 267 days year⁻¹ at 2600 m a.s.l. (Liu, 1997). The topography of the area below 1700 m is gentle with slope inclinations being below 5°. Above 1700 m, the slope is relatively steep with an

Table 1

Stand structure of the studied mixed forest on the northern slope of Changbai Mountain, North-Eastern China. importance values (IV) defined as the average of relative density (% of the number of trees) and relative dominance (% of basal area). Data are mean (SD). Seedlings of *Acer* species were not recorded, though they were abundant across all study sites.

Species	Basal area (m ² /ha)	Density (stems/ha)			Relative density (%)	Relative dominance (%)	IV
		Seedlings	Saplings	Adult trees			
Canopy species							
<i>Pinus koraiensis</i>	11.61 (3.6)	795 (418.5)	13 (10.2)	104 (27.8)	6.1 (1.8)	23.6 (6.2)	14.9 (3.2)
<i>Larix olgensis</i>	11.43 (8.0)	0	0	105 (82.8)	5.3 (5.1)	23.7 (13.9)	14.5 (9.7)
<i>Picea jezoensis</i>	6.36 (3.0)	411 (262.9)	118 (119.5)	165 (50.1)	13.3 (5.8)	12.6 (5.3)	13 (4.5)
Subcanopy and understory species							
<i>Abies nephrolepis</i>	7.20 (1.7)	845 (406.3)	321 (130.6)	576 (151.4)	45.7 (17.4)	14.6 (2.6)	30.2 (9.8)
<i>Acer mono</i>	0.70 (0.9)	–	6 (5.5)	21 (25.8)	1.7 (1.6)	1.5 (2.0)	1.6 (1.8)
<i>Acer tegmentosum</i>	0.45 (0.7)	–	76 (102.0)	34 (72.6)	4.4 (4.7)	0.9 (1.4)	2.6 (3.0)
<i>Acer ukurunduense</i>	0.41 (0.4)	–	98 (104.3)	48 (57.2)	6.9 (6.7)	0.9 (0.7)	3.9 (3.5)
<i>Acer barbinerve</i>	0.18 (0.2)	–	115 (117.5)	13 (8.3)	6.7 (7.6)	0.5 (0.5)	3.6 (3.8)

average angle above 20°. Volcanic soils overlaying a deep layer of volcanic ash are common across the study area (Shao, 1996).

Distinctive vegetation zones are present along the elevation gradient on the northern slope of Changbai Mountain (Wang et al., 1980). From 750 to 1100 m, broadleaf-Korean pine forest is dominated by *P. koraiensis*, Amur linden (*Tilia amurensis* Rupr.), Korean aspen (*Populus davidiana* Dode), Asian white birch (*Betula platyphylla* Suk.), Manchurian ash (*Fraxinus mandschurica* Rupr.), and Usugumo maple (*Acer mono* Maxim.). Between 1000 and 1300 m, there is a transitional zone represented by mixed Korean pine dominated forest. In this zone, shade-intolerant *L. olgensis*, mid-tolerant *P. koraiensis*, and shade-tolerant *P. jezoensis* and *A. nephrolepis* are the dominant species. From 1300 to 1700 m, a zone of evergreen coniferous forest develops with *L. olgensis*, *P. jezoensis*, and *A. nephrolepis* as the most common species. Between 1700 and 2000 m, alpine birch forest with dwarf birch (*Betula ermanii* Cham.) is the dominant vegetation type.

The forests of Changbai Mountain experienced relatively little disturbance by human activity before the 19th century due to their remoteness (Burger and Zhao, 1988; Barnes et al., 1992). During the 20th century, human disturbance became more frequent and severe, and the area of primary forest decreased by 70.4% from 1950 to 1986 (Xin, 1987). Presently, old-growth primeval forests can only be found in the Changbaishan Natural Reserve. The Reserve was established in 1958 to protect the area from cutting and other forms of forest utilization such as corn picking and browsing by livestock (Wang et al., 1980). Although forest vegetation in the Reserve reveals the legacy of past forest use, it remains to be largely a result of natural succession.

Field and laboratory methods

Our study focused on the transitional zone between 1000 and 1300 m, where *P. koraiensis* and *P. jezoensis* are close to their upper and lower altitudinal distribution limits, respectively. We hypothesized that this part of their distribution range may be sensitive to environmental changes, including changes in natural disturbance regimes (Ries et al., 2004). To represent forest condition along the altitudinal gradient, 19 sample plots (20 m × 80 m each, the longer side being perpendicular to the slope) were set at seven altitudes (1050, 1100, 1120, 1150, 1180, 1220, and 1250 m) in the summers of 2007 and 2008. At each altitude, we established 2–3 plots. In each plot, we recorded the species identity, diameter at 1.3 m (DBH), and tree height of all trees above 1 cm in DBH. We also recorded height and diameter at the base of seedlings of the four dominant tree species (*L. olgensis*, *P. koraiensis*, *A. nephrolepis*,

and *P. jezoensis*). We classified sampled individuals as seedlings (height < 1.3 m), small saplings (height ≥ 1.3 m with DBH < 1 cm), saplings (1 cm ≤ DBH < 5 cm), or adult trees (DBH ≥ 5 cm).

To estimate age of seedling for *A. nephrolepis* and *P. jezoensis*, we counted internodes between branch whorls. The primary reason for choosing this method was limitations imposed by forest use regulations in the Reserve, which prevented us from cutting trees and using ring counting for age estimation. The technique proved unreliable for *P. koraiensis* since internodes of this species are not easily distinguishable. We therefore used regression equation between age and diameter of *P. koraiensis*, developed for Changbai Mountain (Hu et al., 2009) to estimate age of seedlings based on their diameter. The two variables were highly correlated and regression showed a high R^2 value ($A = 9.975D^{0.675}$, $R^2 = 0.92$, $p < 0.0001$, $n = 251$). Age of seedlings for *L. olgensis* was not available since no seedlings were observed during our survey. In total, age was estimated for 1838 *P. koraiensis*, 1515 *P. jezoensis*, and 2060 *A. nephrolepis* seedlings.

In the summer of 2008, we established 19 subplots (20 m × 20 m) within the areas of initially 19 sampled plots to evaluate the tree age structure at DBH level (1.3 m). Within the subplots, we cored all trees (one core per tree) of four dominant species (*L. olgensis*, *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*) with DBH above 3 cm. Only samples with solid (non-rotten) central parts were used for analyses. Most of the *L. olgensis* trees were rotten in their center, making it difficult to estimate precise age. Totally, we measured 680 trees (59 *L. olgensis*, 126 *P. koraiensis*, 189 *P. jezoensis*, and 306 *A. nephrolepis*). We neither core nor cut saplings with DBH between 1 and 3 cm since destructive sampling is not allowed within the Reserve. We considered the error associated with age estimation to be relatively minor due to the fact that the proportion of saplings with DBH between 1 and 5 cm for all four species was relatively small (for *P. koraiensis*, *L. olgensis*, *P. jezoensis*, and *A. nephrolepis* – 1.4%, 0%, 16.1%, and 17.1%, respectively, Table 1).

All the samples were dried, mounted, and sanded using up to 600 mm grit sandpaper until ring boundaries were clearly visible. Cores were visually cross-dated by using the pointer year technique (Stokes and Smiley, 1968). The ring widths were measured to the nearest 0.01 mm by the LinTab measuring stage and statistically verified by the software COFECHA (Holmes, 1983). If a core had missing pith, the age was determined by using the pith locator (Norton et al., 1987; Duncan, 1989). We corrected age estimate of cored trees (126 trees of *P. koraiensis*, 189 trees of *P. jezoensis*, and 306 trees of *A. nephrolepis*) to represent tree ages at the base of the tree, using regression equations between the age and the height of seedlings.

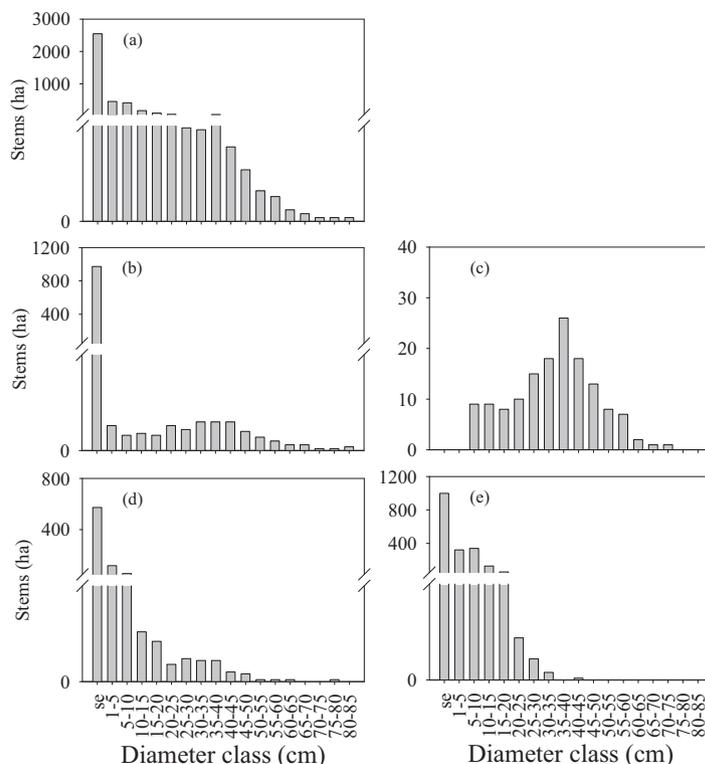


Fig. 2. Diameter distributions of four dominant species in a mixed Korean pine dominated forest on the northern slope of Changbai Mountain, North-Eastern China. (a) Combined data of the four species, (b) *P. koraiensis*, (c) *L. olgensis*, (d) *P. jezoensis*, (e) *A. nephrolepis*. The break at vertical axis is at 50 stems/ha.

Data analysis

To represent contribution of each tree species to forest canopy, we calculated importance values (IV) (Cottam and Curtis, 1956) as the average of relative density (% of the number of trees) and relative dominance (% of basal area) of a tree species in each plot, and then produced an average for the whole study area. To facilitate across-species comparisons, we presented age distributions as number of trees of a particular age class per hectare. A species age structure was presented at 10-year intervals to better reflect the actual dating accuracy affected by a possible error in counting branch whorls in seedlings, regressions used to estimate age in saplings, and in estimating of the pith years in adult trees.

For the analyses of growth releases, we used trees under main forest canopy and part of the chronologies of the modern canopy trees, representing the period when these trees were under canopy. Rationale for this protocol was an assumption that growth of understory trees is more light-limited and they show more pronounced response to increased light condition, as compared to canopy trees. To classify a tree as an *understory tree*, we used the height threshold of 25 m (Xu, 2001). The use of this method was complicated by the fact that the height of the cored trees could not be measured retrospectively. To address this problem, we used our knowledge of DBH – height relationships obtained for the respective species in the study area and established 25 m as a height threshold for a tree of any species, indicating its presence in the main forest canopy. We then associated 25 m height threshold to corresponding DBH thresholds to identify understory segment of tree's lifespan in modern canopy trees. Following this strategy, we combined chronologies representing understory trees and modern canopy trees during their stay under the canopy.

We utilized standard method of percent growth change (GC) to detect canopy disturbance events (Lorimer and Frelich, 1989;

Nowacki and Abrams, 1997; Abrams et al., 1999). The method involves determination of (a) the length of the time frame to calculate moving average of the tree ring increment and (b) the minimum GC threshold to be used as an indicator of a disturbance event. For this study, we used 10-year time spans to avoid problems with short-term climatically-induced variations in growth (Nowacki and Abrams, 1997) and, at the same time, to reflect high frequency of wind-induced canopy disturbances in the study area. We defined increase in growth, later referred to as growth release, as 100% increase as compared to the previous growth. Specifically, the percent growth change (GC) was calculated as

$$GC = \frac{M_2 - M_1}{M_1} \times 100$$

where GC was percentage growth change for a single year, M_1 and M_2 were the preceding and subsequent 10-year ring-width mean, respectively.

A drawback of the selected method of release identification was its inability to evaluate growth conditions, and subsequently-canopy openness during the period corresponding to the beginning of tree chronologies. First, the very first decade in each chronology could not be compared with the previous decade. Secondly, the initial growth of the tree might have been already large and indicative of the gap conditions, making following increases in growth unlikely to qualify for "growth release" according to selected criteria.

To identify gap and close-canopy conditions at the beginning of trees' lifespan, we used two alternative approaches. First, we compared cumulative basal area increments (BAI) of the first ten years of tree growth with BAI of cumulative 10-year increments during the identified release periods. Since BAI of young trees is generally smaller than the one of the adult trees, our analyses were very conservative in the way they detected gap episodes. We used Wilcoxon

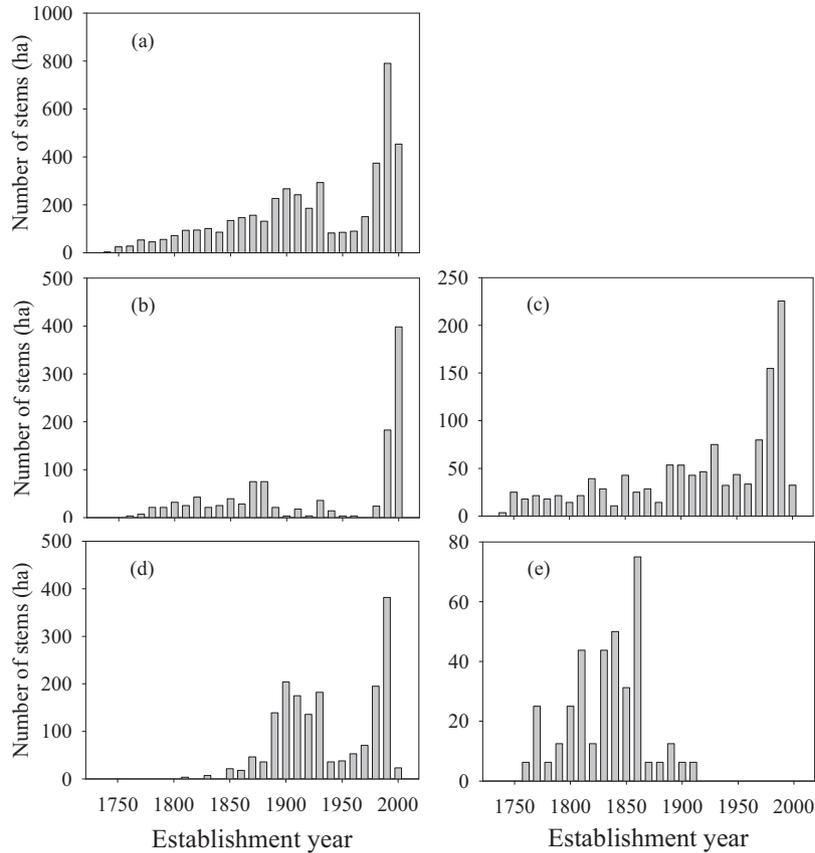


Fig. 3. Age structure of four dominants in a mixed Korean pine dominated forest on the northern slope of Changbai Mountain, North-Eastern China. (a) Combined data for all species, (b) *P. koraiensis*, (c) *P. jezoensis*, (d) *A. nephrolepis*, (e) *L. olgensis*. Age estimates for *L. olgensis* represent minimum ages at DBH level, since 84% (50 out of 59) samples exhibited rotten pith.

matched-pairs test (Gehan, 1965) to check for significant differences in means of respective increment distributions, arranged in 2 cm² classes.

Secondly, we compared initial growth rates with thresholds, indicative of the open conditions (canopy gaps). To the best of our knowledge, no published studies provide direct estimates of such growth thresholds for the studied region. Therefore we estimated the thresholds based on their average growth rates available elsewhere. In the study of Yu et al. (2006, 2011), the mean radial growth at radii level and respective SD have been estimated to be 1.57 ± 0.38, 1.63 ± 0.55, and 1.43 ± 0.38 mm for *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*, respectively. In the studies of Deng et al. (1999) and Gao et al. (2011), the mean growth rate during

the first 10 years were 1.5 (*P. koraiensis*), 0.8 (*P. jezoensis*), and 0.9 mm year⁻¹ (*A. nephrolepis*). Based on these studies and our own experience with analyzing the growth of the studied species in the region, we defined growth threshold, indicative of gap conditions, as respective mean growth rate increased by one SD, i.e. 1.95 mm year⁻¹ for *P. koraiensis*, 2.18 mm year⁻¹ for *P. jezoensis*, and 1.81 mm year⁻¹ for *A. nephrolepis*. We considered this approach to be more opportunistic, as compared to the first method. *L. olgensis* was not available for these analyses due to rotten center of many cored trees (84% of all sampled trees).

Results

Stand structure

The forest was dominated by four conifer species: *A. nephrolepis*, *P. koraiensis*, *L. olgensis*, and *P. jezoensis* (Table 1). In canopy layer, both *P. koraiensis* and *L. olgensis* had the largest basal area, but it was *P. jezoensis* which had the highest tree density. *A. nephrolepis* dominated in sub-canopy layer, mostly due to its high density. The other two sub-canopy species, Ukurundu maple (*Acer ukurunduense* Trautv. et Mey.) and bearded maple (*Acer barbinerve* Maxim.) had a high stem density but a small basal area. Among all species, *A. nephrolepis* showed the highest abundance in both seedling and sapling strata. *P. jezoensis* was abundant as seedlings and saplings, while *P. koraiensis* was common in seedling stratum but was rare as saplings. *L. olgensis* did not regenerate in the studied sites (Table 1).

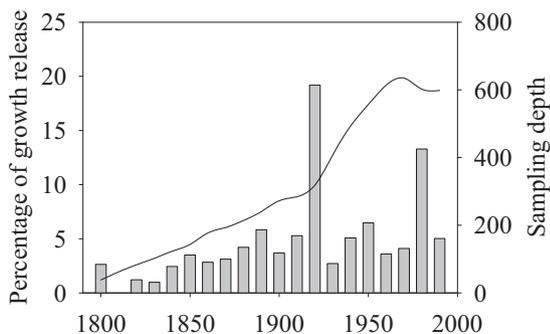


Fig. 4. Growth releases of four dominants in a mixed Korean pine dominated forest on the northern slope of Changbai Mountain, North-Eastern China.

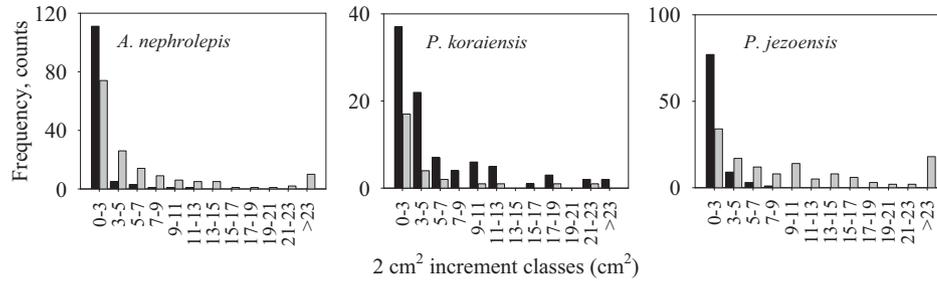


Fig. 5. Distribution of basal area 10-year cumulative increments for initial growth periods (black bars) and gap-associated (gray bars) periods in *A. nephrolepis*, *P. koraiensis*, and *P. jezoensis*.

Combined diameter distribution of all four species revealed an inverse *J* pattern, typical of an uneven-aged forest (Fig. 2a), although distributions of single species differed considerably. Excluding seedling classes, *P. koraiensis* showed a broadly normal distribution throughout the range of diameter classes, and dominated the large diameter class (>50 cm) across the stands (Fig. 2b). *L. olgensis* exhibited a bell-shape pattern dominated by the diameter class from 30 to 50 cm and had no trees in small DBH classes (<5 cm) (Fig. 2c). *P. jezoensis* was well represented from small to intermediate classes (1–40 cm) and reached large classes up to 75 cm DBH (Fig. 2d). *A. nephrolepis* dominated DBH classes below 20 cm (Fig. 2e).

DBH (x , cm) and height (y , m) were highly correlated in the four dominant species with high R^2 values: *L. olgensis* ($y = 0.5953x + 8.3889$, $R^2 = 0.61$, $p < 0.0001$), *P. koraiensis* ($y = 5.5872 + 0.4427x$, $R^2 = 0.71$, $p < 0.0001$), *P. jezoensis* ($y = 1.2908 + 0.6151x$, $R^2 = 0.88$, $p < 0.0001$), *A. nephrolepis* ($y = 1.5392 + 0.64x$, $R^2 = 0.82$, $p < 0.0001$). On average, *L. olgensis*, *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis* reached the height of the main canopy (25 m) at DBH of 27.9 cm, 43.9 cm, 38.5 cm, and 36.7 cm, respectively. The average canopy height was similar across plots and elevations (Appendix, Table A1), and correlation coefficients between DBH and height did not significantly differ across plots and species (Appendix, Fig. A1). This allowed us to set the same height threshold (25 m) attained forest canopy for all plots and species studied.

Age structure

To estimate establishment dates of *P. koraiensis*, we used the same regression equation ($A = 9.975D^{0.675}$) to correct years needed to reach 1.3 m (see section of method in seedling age estimation). On average, it took 11 years for a *P. koraiensis* seedling to reach 1.3 m. For *P. jezoensis* and *A. nephrolepis*, we developed regression equations between age and height from our seedling data. The correlation between age (x , year) and height (y , cm) was statistically significant for both species and showed high R^2 values: *P. jezoensis* ($y = -16.2802 + 4.0956x$, $R^2 = 0.74$, $p < 0.0001$, $n = 1454$) and *A. nephrolepis* ($y = -16.9840 + 4.0284x$, $R^2 = 0.66$, $p < 0.0001$, $n = 1692$). It took, on average, 36 and 35 years for spruce and fir, respectively, to reach 1.3 m. We could not make similar correction for *L. olgensis* since no seedling were observed during our surveys and inability to approximate age of the adult larch trees due to rotten pith.

Combined age distribution of the four species showed a multimodal pattern (Fig. 3a), with several regeneration waves of moderate intensity (1810–1830s, 1850–1870s, 1900s, 1930s, and 1990s). Age structure of *P. koraiensis* presented a multimodal pattern with five periods of increased recruitment: 1820s, 1850s, 1870–1880s, 1930s, and 1990–2000s (Fig. 3b). *P. jezoensis* also presented a multimodal pattern in age distribution and showed similar

increased recruitment periods as *P. koraiensis* (1820s, 1850s, 1930s, and 1990s, Fig. 3c). *A. nephrolepis* showed increased recruitment from the 1900s to the 1930s and the 1990s (Fig. 3d). For *L. olgensis*, projected pith ages indicated that trees recruited mainly between the 1800s and 1860s (Fig. 3e). Low densities of *P. jezoensis* and *A. nephrolepis* seedlings regenerated after 2000 were in line with low frequencies of growth releases (Fig. 4) suggesting below average disturbance rate during the 1990s. Estimates of the low densities, however, may be partly due to a sampling artifact error reflecting seedlings' small size and difficulties in their identification in the field.

Growth releases and initial growth of *P. koraiensis*

One third (34.6%) of sampled *P. koraiensis* trees experienced one or more releases. Growth release analyses indicated frequent small-scale disturbances and infrequent moderate disturbances over the last 200 years (Fig. 4). The percentage of trees showing releases was generally low (<6%) in each decade, except the two most pronounced release periods which were observed in the 1920s and 1980s, when the release frequency reached 19% and 13%, respectively.

In *P. koraiensis*, the initial 10-year BAI was significantly larger than the BAI during the release periods ($Z = -2.81$, $p = 0.005$, Fig. 5). Whereas the initial 10-year growth was significantly smaller than growth in the releases periods for *A. nephrolepis* ($Z = -2.12$, $p = 0.034$, Fig. 5) and *P. jezoensis* ($Z = -2.12$, $p = 0.034$, Fig. 5). 31% of *P. koraiensis* trees, 0% of *P. jezoensis*, and 1% of *A. nephrolepis* showed initial growth increment which was larger than respective growth threshold, indicative of canopy gap conditions.

Discussion

Disturbance regime

The history of mixed Korean pine dominated forest revealed no large-scale and stand replacing disturbances since the 1770s, as suggested by the lack of regeneration of pioneer *L. olgensis* as well as continuous regeneration and presence in the canopy of shade-tolerant *P. jezoensis* and *A. nephrolepis* (Table 1, Fig. 3c–e). However, the dominance of *L. olgensis* in the current forest canopy (Table 1) indicated a major disturbance event that took place outside the time frame covered by this study. The most recent volcanic eruption, which occurred in 1702 and was associated with forest fires (Manchida et al., 1987; Okitsu et al., 1995), was a likely candidate for such an event. Despite intensive field inventories, we did not find evidence of past fires (such as fire scars and charred stumps) in our sites, although stand replacing fires have been previously described as the main factor for the dynamics of mixed forest in Northeastern China (Chang et al., 2008). High humidity in the study

area and fire suppression policy (Wang et al., 1980) in the Reserve might effectively limit possibilities for effective ignitions and fire spread in the area.

Two medium-scale disturbance events likely occurred in the 1920s and 1980s. Increased number of growth releases during these decades (Fig. 4), followed by enhanced recruitment of *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis* in the 1930s and 1990s (Fig. 3b–d) suggested formation of rather large canopy gaps, probably exceeding 1000 m². Although we could not exactly identify the nature of the 1920s event nor the scale of canopy disturbances occurred at that time, we considered it a wind-induced disturbance since the timing of this event coincided with a large windthrow, which was dendrochronologically reconstructed on the western slope of Changbai Mountain and dated to 1920s (Yang and Xie, 1994). The timing of the 1980s event was consistent with documentary sources reporting a hurricane on the western slope of CBM in 1986 (Yang and Xie, 1994).

The canopy disturbances were common and small-scale as suggested by frequent growth releases with low percentage of trees exhibiting the release (<6%) in a single decade (Fig. 4). The wind was a likely factor causing these frequent small-scale disturbances. Two canopy dominants, *P. jezoensis* and *A. nephrolepis*, are particularly sensitive to strong winds due to their large amount of leaf biomass and shallow rooting depth (Liu, 1997), making the forests dominated by these two species especially prone to wind disturbance. Indeed, previous studies have showed regular occurrence of windthrows in our study area (Dai et al., 2011; Zhou et al., 2011) and reported that 40% of the gaps were formed by wind disturbances (Yu and Hao, 1998) typically smaller than 250 m² in size (Zhao et al., 2006). This is similar to the mean gap size in the geographically close temperate mixed forest in Japan, which has been estimated to be 70–140 m² (Miura et al., 2001; Fujita et al., 2003; Kubota, 2006). Size of canopy gaps appears therefore similar across many temperate forests in Northern Hemisphere – a common size of canopy gaps has been reported to be smaller than 200 m² both in the North American deciduous forest (Runkle, 1982, 1990; Runkle and Yetter, 1987), and in the European temperate forests (Kenderes et al., 2008; Motta et al., 2011).

Forest composition response to the disturbances

Although the current study did not quantify the whole range of disturbance events known for mixed Korean pine forests, it points to a large temporal variability in frequency and severity of disturbance events, resulting in a complex forest stand structure. Regeneration dynamics of the most shade-intolerant species *L. olgensis* exemplified the difficulties in understanding the role of the larger disturbance events. Lack of recent fire disturbance was in line with absence of *L. olgensis* regeneration and its presence in the forest exclusively as a canopy dominant (Table 1). However, some understory trees (5 cm < DBH < 15 cm, Fig. 2) were observed in the forest, suggesting that another important factor for regeneration of this species might have been severe windthrows which maintains presence of *L. olgensis* in the forest canopy (Okitsu et al., 1995; Liu, 1997). A previous study in the Changbai Mountain has shown that forest patches dominated by *L. olgensis* were larger than 1 km² in size (Liu et al., 2004), suggesting large-scale disturbance events creating these patches. In our sites, canopy gaps were typically smaller than 250 m² (field observation), which would explain the lack of *L. olgensis* regeneration (Table 1). Large-scale disturbance have also been shown to be important for the regeneration of Dahurian larch (*Larix gmelini* Rupr.) in old-growth larch forests of Da Xingan Ling Mountains, located to the North of Changbai Mountain (Ban et al., 1998).

Interval between reconstructed medium-scale disturbances in the studied forest was 60 years and shorter than the lifespan of all the dominant species, indicating that such events might provide important regeneration possibilities for canopy dominants. In particular, regeneration and growth of *P. koraiensis* benefited from the two medium-scale disturbance events (Figs. 3b and 4) and regular small-scale disturbances (Wang and Zhao, 2011; Dai et al., 2011). We suggest that high wind episodes creating canopy gaps with improved light conditions promote establishment and growth of *P. koraiensis*. Instead, decreased frequency of canopy gaps might reduce recruitment of this species. *P. koraiensis* is a mid-tolerant species, however its seedlings are shade-tolerant during the first 30 years of their lifespan and their saplings are shade-intolerant (Ge, 1994). Limited light availability under the closed canopy of mixed forests causes high mortality of *P. koraiensis* at sapling stage, decreasing overall density of this species under the forest canopy (Table 1).

The majority of sampled *P. koraiensis* trees apparently took advantage of canopy opening early in their lifespan, as suggested by comparison of the initial and gap-associated growth (Fig. 5). Since the trees in our study were sampled at DBH (1.3 m) and not at the ground level, it was not possible to deduce light conditions for these trees at the time of establishment. About one third of the sampled *P. koraiensis* trees experienced more than one release, indicating that the species need improved light conditions to grow into canopy layer. Indeed, previous studies have indicated that trees of *P. koraiensis* typically experience several canopy gap episodes before reaching the main canopy (Wang and Zhao, 2011), regeneration of this species benefiting from gaps as small as 250 m² (Yu and Hao, 1998; Zhao et al., 2006). In a study of an old-growth mixed forest in the Russian Far East, geographically close to our study area, 30–40% for *P. koraiensis* trees regenerated in the gaps (Ishikawa et al., 1999).

It was difficult to deduce exact forest dynamics due to limited precision of our age data and since more than 200 years passed since the occurrence of the last major disturbance event. However, survival of shade-tolerant *P. jezoensis* and *A. nephrolepis* under the forest canopy appeared to be less dependent on disturbances than that of light-demanding *P. koraiensis* and *L. olgensis*. Persistent recruitment of *P. jezoensis* and *A. nephrolepis* over the last 220 and 110 years (Fig. 3c and d), together with their low increments during the initial growth period (Fig. 5) suggested that two species might be independent of treefall gap episodes due to their high degree of shade-tolerance (Yang et al., 1994; Okitsu et al., 1995; Liu, 1997). Ability to withstand a prolonged period in suppressed condition with low radial growth, and fast response to improved light conditions allow them to maintain their presence in the canopy (Yang et al., 1994). This strategy is similar to the ones of other shade-tolerant species like Norway spruce (*Picea abies* (L.) Karst.) and silver fir (*Abies alba* Mill.) in European boreal forests, and balsam fir (*Abies balsamea* (L.) Mill.) in North American boreal forest. Regeneration of these species takes advantage of small-scale gaps (Kneeshaw and Bergeron, 1998; Drobyshev, 1999; Nagel et al., 2007; Firm et al., 2009; Zielonka and Malcher, 2009).

In a short-time perspective (<200 years), stand-replacing disturbance events were probably of limited importance as drivers of the forest dynamics in Changbai Mountain, primarily due to the fact that the interval between such disturbance events was longer than the typical maximum lifespan of dominant species. Volcanic eruptions occurred in the study region with the interval exceeding 600 year and were likely causes of stand-replacing fires (Zhao, 1981; Manchida et al., 1987). This interval was longer than the lifespan of dominant species *P. koraiensis* (~400 year), *P. jezoensis* (~300 year), *A. nephrolepis* (~200 year), and *L. olgensis* (~300 year) (Ishikawa et al., 1999; He et al., 2005). The similar pattern was also found in deciduous forests of the eastern United States, where

the average interval between severe disturbances was approximately 1000 years (Lorimer, 1977, 1989; Canham and Loucks, 1984; Whitney, 1986). In the absence of large-scale disturbances, forest structure and composition in such forests are largely driven by small-scale canopy disturbances due to wind-induced mortality of single trees or small group of trees (Runkle, 1985, 1991; Canham, 1989; Drobyshev, 2001; Motta et al., 2011).

Since no tree mortality data was available in the current study, we were unable to evaluate actual contribution of species and time-specific mortality patterns into overall canopy composition. However, joint analysis of growth release chronologies and tree age distributions suggested that current forest composition, expressed as DBH distributions of canopy trees, is driven by regeneration events and probably not by changes in mortality rates over time.

Effects of future climate on forest dynamics

Future climate changes affecting intensity and frequency of stand disturbances may have implications for forest structure and composition. We speculate that changes in wind climate (Dai et al., 2011) may be particularly important since they are directly connected to availability and size distribution of disturbed patches, which are important for the regeneration of canopy trees. Future climate projections suggest that China will experience more extreme events such as hurricanes and typhoons in the future (IPCC, 2007). Particularly, such storms will expand along the coast areas from south to northeast China within rising sea surface temperatures (IPCC, 2007). This may increase the frequency of medium and large-scale wind disturbances in the forest of northeast China. Since such disturbances favor the establishment of light demanding species the trend may benefit the growth release of *P. koraiensis* and *L. olgensis* in Changbai Mountain, increasing the share of shade-intolerant species in the forest canopies.

Increase in forest fire activity could be another consequence of climate change. Significant warming trends during the fire season (by 0.36 °C per 10 years in spring and by 0.22 °C per 10 years in summer) and decrease in precipitation (by 100 mm) have been observed since the 1960s in Changbai Mountain (Qian and Qin, 2006; Yu et al., 2006), this climate trend may indicate an increased chance of fire occurrence in coming decades. Beside direct effect on drought frequency and severity, future climate change may also affect forest flammability through a succession toward more

fire-prone vegetation. Simulation of the forest ecosystem response to climate warming in Changbai Mountain suggested that future climate would benefit *L. olgensis*, making vegetation more prone to forest fires (He et al., 2005).

In general, our results suggest an important role of climate variability on dynamics of a mixed Korean pine dominated forest over last 200 years. Indirect effects of climate variability such as changes in wind intensity and fire frequency will likely be important factors affecting forest dynamics in the future. We speculate that climatically driven changes in disturbance regimes and direct effects of climate on growth may be equally important in shaping the structure and dynamics of the mixed Korean pine dominated forests.

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Appendix A.

See

Table A1

Average canopy height (SD) of studied sites along the altitudinal gradient on Changbai Mountain.

Altitude (m)	Average canopy height (m)
1050	28.9 (2.4)
1100	29.6 (3.1)
1120	28.7 (1.5)
1150	26.5 (2.7)
1180	25.8 (1.8)
1220	29.1 (3.4)
1250	30.4 (2.5)

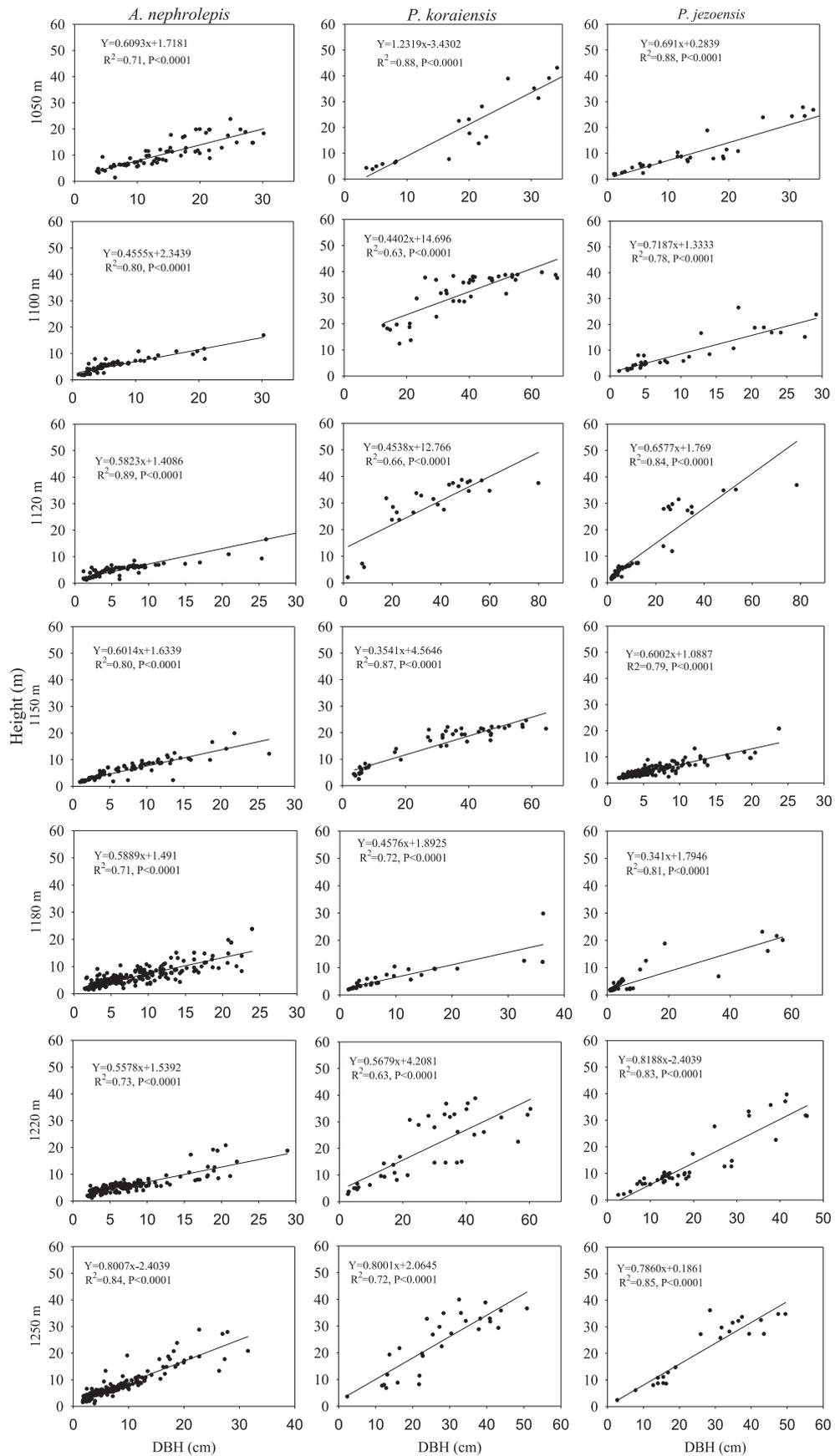


Fig. A1. DBH-height relationships of the three species at different sites. Correlation coefficients showed no significant differences between species in pair-wise comparisons: *A. nephrolepis* and *P. koraiensis* ($t=0.89$, $p=0.41$), *A. nephrolepis* and *P. jezoensis* ($t=-1.4$, $p=0.21$), and *P. koraiensis* and *P. jezoensis* ($t=-2.4$, $p=0.06$).

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