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1   **Disturbance and regeneration dynamics of a mixed Korean pine**

2   **dominated forest on Changbai Mountain, North-Eastern China**

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6

7   Abstract

8   We used dendrochronological methods to study disturbance history of mixed Korean pine (*Pinus*

9   *koraiensis* Siebold et Zuccarini) dominated forest on the northern slope of Changbai Mountain, North

10   Eastern China, over 1770-2000. Frequent small-scale canopy gaps and infrequent medium-scale canopy

11   disturbances dominated natural disturbance regime in the forest, which didn't experience stand-replacing

12   disturbances over the studied period. Percentages of growth releases in subcanopy trees were below 6%

13   in most decades, suggesting that disturbances initiating these releases were of low intensity. Strong winds

14   were likely cause of moderate disturbance events. Two episodes with increased disturbance rates (19%

15   and 13%) were dated to the 1920s and 1980s, timing of the 1980s event was consistent with a hurricane

16   occurred in 1986 on the western slope of the Changbai Mountain. Age structure and growth release

17   analyses revealed species-specific regeneration strategies of canopy dominants. Shade-intolerant Olga

18   bay larch (*Larix olgensis* Henry) recruited mainly before the 1860s. Recruitment of moderately

19   shade-tolerant *P. koraiensis* occurred as several regeneration waves (1820s, 1850s, 1870-1880s, 1930s,

20   and 1990-2000s) of moderate intensity. Shade-tolerant Jezo spruce (*Picea jezoensis* Carr. var. *komarovii*

21   (V.Vassil.) Cheng et L.K.Fu) and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim.) regenerated

22   continuously over the last 220 and 130 years, respectively. Enhanced recruitment of *P. koraiensis*, *P.*

23   *jezoensis*, and *A. nephrolepis* was observed during the 1930s and 1990s, coinciding with increased

24   growth release frequency in the 1920s and 1980s, and suggesting disturbance events of moderate

25   intensity. Our results indicate that the current disturbance regime of the mixed Korean pine dominated

26   forest maintains coexistence of light-demanding and shade-tolerant species and that change in wind

27   climate may be particularly important for future forest composition.

28   Keywords

30

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 (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 Changbai Mountain occurred around 1100 AD and destroyed vegetation over the area of 100 km^2, 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 Changbai Mountain. Large scale wind disturbances (> 1000 m^2) 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 on Changbai Mountain. Our specific objectives were (1) to investigate temporal patterns of tree species regeneration, (2) to reconstruct disturbance history of this mixed forest, and (3) to understand the relationship between disturbance history and species coexistence in the studied forest. Based on our field observations and literature review (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 past 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 forest.

Materials and methods

87   The study was conducted on the northern slope of Changbai Mountain in North Eastern China (1900 km²,

88   41°31′ - 42°28′ N, 127°9′ - 128°55′ E, Fig. 1), within the territory of Changbaishan Natural Reserve. The

89   area has a temperate continental climate, with long, cold, and windy winters and short, warm, and rainy

90   summers. Annual mean temperatures vary from 7.3 °C at the low elevations (700 m a.s.l.) to 2.8 °C at the

91   top of the mountain (2691 m a.s.l.). Variation in the mean annual precipitation along this gradient is from

92   750 mm to 1340 mm (Zhao, 1981). The frequency of storms (episodes with wind speeds above 17 m s^{-1})

93   varies from 30 days yr^{-1} at 770 m a.s.l. to 267 days yr^{-1} at 2600 m a.s.l.(Liu, 1997). The topography of the

94   area below 1700 m is gentle with slope inclinations being below five degrees. Above 1700 m, the slope is

95   relatively steep with an average angle above 20 degrees. Volcanic soils overlaying a deep layer of

96   volcanic ash are common across the study area (Shao, 1996).

97   Distinctive vegetation zones are present along the elevation gradient on the northern slope of Changbai

98   Mountain (Wang et al., 1980). From 750 to 1100 m, broadleaf-Korean pine forest is dominated by *P.*

99   *koraiensis*, Amur linden (*Tilia amurensis* Rupr.), Korean aspen (*Populus davidiana* Dode), Asian white

100   birch (*Betula platyphylla* Suk.), Manchurian ash (*Fraxinus mandschurica* Rupr.), and Usugumo maple

101   (*Acer mono* Maxim.). Between 1000 and 1300 m, there is a transitional zone represented by mixed

102   Korean pine dominated forest. In this zone, shade-intolerant *L. olgensis*, mid-tolerant *P. koraiensis*, and

103   shade-tolerant *P. jezoensis* and *A. nephrolepis* are the dominant species. From 1300 to 1700 m, a zone of

104   evergreen coniferous forest develops with *L. olgensis*, *P. jezoensis*, and *A. nephrolepis* as the most

105   common species. Between 1700 and 2000 m, alpine birch forest with dwarf birch (*Betula ermanii* Cham.)

106   is the dominant vegetation type.

107   The forests of Changbai Mountain experienced relatively little disturbance by human activity before the

108   19th century due to their remoteness (Burger and Zhao, 1988; Barnes et al., 1992). During the 20th century,

109   human disturbance became more frequent and severe, and the area of primary forest decreased by 70.4%

110   from 1950 to 1986 (Xin, 1987). Presently, primary forests can only be found in the Changbaishan Natural

111   Reserve. The Reserve was established in 1958 to protect the area from cutting and other forms of forest

112   utilization such as corn picking and browsing by livestock (Wang et al., 1980). Although forest

113   vegetation in the Reserve reveals the legacy of past forest use, it remains to be largely a result of natural

114   succession.

115   *Field and laboratory methods*

116   Our study focused on the transitional zone between 1000 and 1300 m, where *P. koraiensis* and *P.*

117   *jezoensis* are close to their upper and lower altitudinal distribution limits, respectively. We hypothesized

118   that this part of their distribution range may be sensitive to environmental changes, including changes in

119   natural disturbance regimes (Ries et al., 2004). To represent forest condition along the altitudinal gradient,

120   19 sample plots (20×80 m^2 each, the longer side being perpendicular to the slope) were set at seven

121   altitudes (1050, 1100, 1120, 1150, 1180, 1220, and 1250 m) in the summers of 2007 and 2008. At each

122   altitude, we established 2 to 3 plots. In each plot, we recorded the species identity, diameter at 1.3 m

123   (DBH), and tree height of all trees above 1cm in DBH. We also recorded height and diameter at the base

124   of seedlings of the four dominant tree species (*L. olgensis*, *P. koraiensis*, *A. nephrolepis*, and *P. jezoensis*).

125   We classified sampled individuals as seedlings (height < 1.3 m), small saplings (height $\geq$ 1.3 m with

126   DBH < 1cm), saplings (1cm $\leq$ DBH < 5cm), or adult trees (DBH $\geq$ 5cm).

127   To estimate age of seedling for *A. nephrolepis* and *P. jezoensis*, we counted internodes between branch

128   whorls. The primary reason for choosing this method was limitations imposed by forest use regulations

129   in the Reserve, which prevented us from cutting trees and using ring counting for age estimation. The

130   technique proved unreliable for *P. koraiensis* since internodes of this species are not easily

131   distinguishable. We therefore used regression equation between age and diameter of *P. koraiensis,*

132   developed for Changbai Mountain (Hu et al., 2009) to estimate age of seedlings based on their diameter.

133   The two variables were highly correlated and regression showed very high R^2 value (A=9.975D$^{0.675}$,

134   R^2=0.92, P<0.0001, n=251). Age of seedlings for *L. olgensis* was not available since no seedlings were

135   observed during our survey. In total, age was estimated for 1838 *P. koraiensis*, 1515 *P. jezoensis*, and

136   2060 *A. nephrolepis* seedlings.

137   In the summer of 2008, we established 19 subplots (20×20 m^2) within the areas of initially 19 sampled

138   plots to evaluate the tree age structure at DBH level (1.3 m). Within the subplots, we cored all trees (one

139   core per tree) of four dominant species (*L. olgensis*, *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*) with

140　DBH above 3 cm. Only samples with solid (non-rotten) pith were used for analyses. However, most *L.*

141　*olgensis* trees were rotten in their center, making it difficult to estimate precise age. Totally, 680 trees (59

142　*L. olgensis, 126 P. koraiensis, 189 P. jezoensis,* and *306 A. nephrolepis*) were used. We didn't core nor

143　cut trees with DBH between 1 and 3 cm since such inevitably destructive sampling was not allowed

144　within the Natural Reserve. We considered the introduced error as relatively minor due to the fact that

145　proportion of saplings with DBH between 1 and 5 cm for all four species was relatively small (for *P.*

146　*koraiensis, L. olgensis, P. jezoensis,* and *A. nephrolepis* - 1.4%, 0%, 16.1%, and 17.1%, respectively,

147　Table 1).

148　All the samples were dried, mounted, and sanded using up to 600 mm grit sandpaper until ring

149　boundaries were clearly visible. Cores were visually cross-dated by using the pointer year technique

150　(Stokes and Smiley, 1968). The ring widths were measured to the nearest 0.01 mm by the LinTab

151　measuring stage and statistically verified by the software COFECHA (Holmes, 1983). If a core had a

152　missing pith, the age was determined by using the pith locator (Norton et al., 1987; Duncan, 1989). We

153　corrected age of cored trees (126 trees of *P. koraiensis*, 189 trees of *P. jezoensis*, and 306 trees of *A.*

154　*nephrolepis*) for the years needed to reach 1.3 m by using regression equations.

155　*Data analysis*

156　We calculated Importance Values (IV, Cottam and Curtis, 1956) as the average of relative density (% of

157　the number of trees) and relative dominance (% of basal area) of a tree species in each plot, and then

158　produced an average for the whole study area. To facilitate comparison of different species, all the age

159　data was expressed as number of trees per hectare. Because of possible error in counting branch whorls in

160　seedlings and in estimating the pith years for adult trees, the age structures were presented at 10-year

161　intervals to better reflect the actual dating accuracy.

162　To analyze growth release, we used only trees under main forest canopy and part of the chronologies of

163　the modern canopy trees, representing the period when these trees were under canopy. Rationale for this

164　protocol was an assumption that growth of understory trees are more light-limited and they show more

165　pronounced response to increased light condition. To classify a tree as an *understory tree*, we used the

166　height threshold of 25 m (Xu, 2001). The use of this method was complicated by the fact that the height

167 of the cored trees could not be measured retrospectively. To address this problem, we used our knowledge

168 of DBH - height relationships obtained for the respective species in the study area. We associated 25 m

169 height threshold to corresponding DBH thresholds to identify understory trees and understory parts of

170 trees' lifespan for modern canopy trees. Following this strategy, we constructed a dataset of chronologies

171 representing understory trees and part of the lifespan of the modern canopy trees during the period when

172 they stood in the forest understory (i.e. under the dominant forest canopy).

173 We utilized standard method of percent growth change (GC) to detect canopy disturbance events

174 (Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Abrams et al., 1999). The method involves

175 determination of (a) the length of the time frame to calculate moving average of the tree ring increment

176 and (b) the minimum GC threshold to be used as an indication of the disturbance event. For this study, we

177 used 10-year time spans to avoid problems with short-term climatically-induced variations in growth

178 (Nowacki and Abrams, 1997) and, at the same time, to reflect high frequency of wind-induced canopy

179 disturbances in the study area. We defined increase in growth, later referred to as growth release, as 100%

180 increase as compared to the previous growth. Specifically, the percent growth change (GC) was

181 calculated as

182 $GC = (M_2 - M_1)/M_1 \times 100$

183 where GC was percentage growth change for a single year, M_1 and M_2 were the preceding and

184 subsequent 10-year ring-width mean, respectively.

185 A drawback of the selected method of release identification was its inability to evaluate growth

186 conditions, and subsequently-canopy openness during the period corresponding to the beginning of tree

187 chronologies. First, the very first decade in each chronology couldn't be compared with the previous

188 decade. Secondly, the initial growth of the tree might have been already large and indicative of the gap

189 conditions, making following increases in growth unlikely to qualify for "growth release" according to

190 selected criteria. To address this issue, we compared cumulative increments of the first ten years of tree

191 growth with cumulative 10-year increments during the identified release periods. We converted radial

192 increments into basal area increments (BAI) to allow comparison of growth estimates from trees at

193 different ages. *L. olgensis* was not available for this comparison due to rotten center of many cored trees

194   (84% of all sampled trees). We used Wilcoxon matched-pairs test (Gehan, 1965) to check for significant

195   differences in means of respective increment distributions, arranged in 2 cm^2 classes.

196   **Results**

197   *Stand structure*

198   The forest was dominated by four conifer species: *A. nephrolepis*, *P. koraiensis*, *L. olgensis*, and *P.*

199   *jezoensis* (Table 1). In canopy layer, both *P. koraiensis* and *L. olgensis* had the largest basal area, but it

200   was *P. jezoensis* which had the highest tree density. *A. nephrolepis* dominated in sub-canopy layer, mostly

201   due to its high density. The other two sub-canopy species, Ukurundu maple (*Acer ukurunduense* Trautv.

202   et Mey.) and bearded maple (*Acer barbinerve* Maxim.) had a high stem density but a small basal area.

203   Among all species, *A. nephrolepis* showed the highest abundance in both seedling and sapling strata. *P.*

204   *jezoensis* was abundant as seedlings and saplings, while *P. koraiensis* was common in seedling stratum

205   but was rare as saplings. *L. olgensis* didn't regenerate in the studied sites (Table 1).

206   Combined diameter distribution of all four species revealed an inverse *J* pattern, typical of an

207   uneven-aged forest (Fig. 2a), although distributions of single species differed considerably. Excluding

208   seedling classes, *P. koraiensis* showed a broadly normal distribution throughout the range of diameter

209   classes, and dominated the large diameter class (> 50 cm) across the stands (Fig. 2b). *L. olgensis*

210   exhibited a bell-shape pattern dominated by the diameter class from 30 to 50 cm and had no trees in

211   small DBH classes (< 5 cm) (Fig. 2c). *P. jezoensis* was well represented from small to intermediate

212   classes (1-40 cm) and reached large classes up to 75 cm DBH (Fig. 2d). *A. nephrolepis* dominated DBH

213   classes below 20 cm (Fig. 2e).

214   DBH (x, cm) and height (y, m) were highly correlated in the four dominant species with high R^2 values:

215   *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,

216   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

217   = 0.82, p < 0.0001). On average, *L. olgensis*, *P. koraiensis*, *P. jezoensis,* and *A. nephrolepis* reached the

218   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

219   average canopy height was similar across plots and elevations (Appendix, Table 1), and correlation

220   coefficients between DBH and height didn't significantly differ across plots and species (Appendix, Fig.

221   1). This allowed us to set the same height threshold (25 m) attained forest canopy for all plots and species

222   studied.

223   *Age structure*

224   To estimate establishment dates of *P. koraiensis*, we used the same regression equation ($A=9.975D^{0.675}$)

225   to correct years needed to reach 1.3 m (see section of method in seedling age estimation). On average, it

226   took 11 years for a *P. koraiensis* seedling to reach 1.3 m. For *P. jezoensis* and *A. nephrolepis*, we

227   developed regression equation between age and height from our seedling data. The correlation between

228   age (x, year) and height (y, cm) was statistically significant for both species and showed high R^2 values:

229   *P. jezoensis* (y = -16.2802+4.0956x, R^2 = 0.74, P < 0.0001, n = 1454) and *A. nephrolepis* (y =

230   -16.9840+4.0284x, R^2 = 0.66, P < 0.0001, n = 1692). It took, on average, 36 and 35 years for spruce and

231   fir, respectively, to reach 1.3 m. We could not make similar correction for *L. olgensis* since no seedling

232   were observed during our surveys and due to the fact that sampled larch trees often had rotten pith.

233   Combined age distribution of the four species showed a multimodal pattern (Fig. 3a), with several

234   regeneration waves of moderate intensity (1810-1830s, 1850-1870s, 1900s, 1930s, and 1990s). Age

235   structure of *P. koraiensis* presented a multimodal pattern with five periods of increased recruitment:

236   1820s, 1850s, 1870-1880s, 1930s, and 1990-2000s (Fig. 3b). *P. jezoensis* also presented a multimodal

237   pattern in age distribution and showed similar increased recruitment periods as *P. koraiensis* (1820s,

238   1850s, 1930s, and 1990s, Fig. 3c). *A. nephrolepis* showed increased recruitment from the 1900s to the

239   1930s and the 1990s (Fig. 3d). For *L. olgensis*, projected pith ages indicated that trees recruited mainly

240   between the 1800s and 1860s (Fig. 3e). The number for *P. jezoensis* and *A. nephrolepis* seedlings

241   regenerated after 2000 was low, which might be, in part, due to their small size and difficulties in their

242   identification in the field. Low densities of seedlings were in line low frequencies of growth releases (Fig.

243   XXX) suggesting below average disturbance rate during the 1990s.

244   *Growth releases and initial growth of P. koraiensis*

245   Two alternative protocols revealed similar patterns of growth releases (Fig. 4), suggesting the occurrence

246 of frequent small-scale disturbances and infrequent moderate disturbances over the last 200 years. The

247 percentage of trees showing releases was generally low ($< 6\%$) in each decade, except the two most

248 pronounced release periods which were observed in the 1920s and 1980s, when the release frequency

249 reached 19% and 13%, respectively.

250 In *P. koraiensis*, the initial 10-year increment was significantly larger than the increment during the

251 release periods (Z=-2.81, p=0.005, Fig. 5). The initial 10-year increment exceeded 3 cm^2 in 58.4% of *P.*

252 *koraiensis* trees, whereas the increment during the release periods exceeded that threshold only in 37% of

253 trees. Half of sampled *P. koraiensis* trees (54.1%) experienced one or more releases, the increment

254 during initial ten-year period exceeded that during their release periods. In contrast, the initial 10-year

255 growth was significantly smaller than growth in the releases periods for *A. nephrolepis* (Z=-2.12,

256 p=0.034, Fig. 5) and *P. jezoensis* (Z=-2.12, p=0.034, Fig. 5). The initial 10-year increment was less than

257 3 cm^2 for most trees of *A. nephrolepis* (91%) and *P. jezoensis* (86%).

Discussion

259 *Disturbance regime*

260 The history of mixed Korean pine dominated forest revealed no large-scale and stand replacing

261 disturbances since the 1770s, as suggested by the lack of regeneration of pioneer *L. olgensis* as well as

262 continuous regeneration and presence in the canopy of shade-tolerant *P. jezoensis* and *A. nephrolepis*

263 (Table 1, Figs. 3c, d, and e). However, the dominance of *L. olgensis* in the current forest canopy (Table 1)

264 indicated a major disturbance event that took place outside the time frame covered by this study. The

265 most recent volcanic eruption, which occurred in 1702 and was associated with forest fires (Manchida et

266 al., 1987; Okitsu et al., 1995), was a likely candidate for such an event. Despite intensive field inventories,

267 we didn't find evidence of past fires (such as fire scars and charred stumps) in our sites, although stand

268 replacing fires have been previously described as the main factor for the dynamics of mixed forest in

269 Northeastern China (Chang et al., 2008). High humidity in the study area and fire suppression policy

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

271 spread in the area.

272 Two medium-scale disturbance events likely occurred in the 1920s and 1980s. Increased number of

273 growth releases during these decades (Fig. 4), followed by enhanced recruitment of *P. koraiensis*, *P.*

274 *jezoensis*, and *A. nephrolepis* in the 1930s and 1990s (Figs. 3b, c, and d) suggested formation of rather

275 large canopy gaps, probably exceeding 1000 m^2. Although we could not exactly identify the nature of the

276 1920s event nor the scale of canopy disturbances occurred at that time, we considered it a wind-induced

277 disturbance since the timing of this event coincided with a large windthrow, which was

278 dendrochronologically reconstructed on the western slope of Changbai Mountain and dated to 1920s

279 (Yang and Xie, 1994). The timing of the 1980s event was consistent with documentary sources reporting

280 a hurricane on the western slope of CBM in 1986 (Yang and Xie, 1994).

281 The canopy disturbances were common and small-scale as suggested by frequent growth releases with

282 low percentage of trees exhibiting the release ($< 6\%$) in a single decade (Fig. 4). The wind was a likely

283 factor causing these frequent small-scale disturbances. Two canopy dominants, *P. jezoensis* and *A.*

284 *nephrolepis*, are particularly sensitive to strong winds due to their large amount of leaf biomass and

285 shallow rooting depth (Liu, 1997), making the forests dominated by these two species especially prone to

286 wind disturbance. Indeed, previous studies have showed regular occurrence of windthrows in our study

287 area (Dai et al., 2011; Zhou et al., 2011) and reported that 40% of the gaps were formed by wind

288 disturbances (Yu and Hao, 1998) typically smaller than 250 m^2 in size (Zhao et al., 2006). This is similar

289 to the mean gap size in the geographically close temperate mixed forest in Japan, which has been

290 estimated to be 70-140 m^2 (Miura et al., 2001; Fujita et al., 2003; Kubota, 2006). Size of canopy gaps

291 appears therefore similar across many temperate forests in Northern Hemisphere - a common size of

292 canopy gaps has been reported to be smaller than 200 m^2 both in the North American deciduous forest

293 (Runkle, 1982, 1990; Runkle and Yetter, 1987), and in the European mixed temperate forests (Motta et

294 al., 2011).

295 *Forest composition response to the disturbances*

296 Although the current study did not quantify the whole range of disturbance events known for mixed

297 Korean pine forests, it points to a large temporal variability in frequency and severity of disturbance

298 events, resulting in a complex forest stand structure. Regeneration dynamics of the most shade-intolerant

299 species *L. olgensis* exemplified the difficulties in understanding the role of the larger disturbance events.

300   Lack of recent fire disturbance was in line with absence of *L. olgensis* regeneration and its presence in the

301   forest exclusively as a canopy dominant (Table 1). However, some understory trees (5 cm < DBH <15 cm,

302   Fig. 2) were observed in the forest, suggesting that another important factor for regeneration of this

303   species might have been severe windthrows which maintains presence of *L. olgensis* in the forest canopy

304   (Okitsu et al., 1995; Liu, 1997). A previous study in the Changbai Mountain has shown that forest patches

305   dominated by *L. olgensis* were larger than 1 km^2 in size (Liu et al., 2004), suggesting large-scale

306   disturbance events creating these patches. In our sites, canopy gaps were typically smaller than 250 m^2

307   (field observation), which would explain the lack of *L. olgensis* regeneration (Table 1). Large-scale

308   disturbance have also been shown to be important for the regeneration of Dahurian larch (*Larix gmelini*

309   Rupr.) in old-growth larch forests of Da Xingan Ling Mountains, located to the North of Changbai

310   Mountain (Ban et al., 1998).

311   Regeneration and growth of *P. koraiensis* benefited from the two medium-scale disturbance events (Figs.

312   3b and 4) and regular small-scale disturbances (Wang and Zhao, 2011; Dai et al., 2011). We suggest that

313   high wind episodes creating canopy gaps with improved light conditions promote establishment and

314   growth of *P. koraiensis*. Instead, decreased frequency of canopy gaps might reduce recruitment of this

315   species. *P. koraiensis* is a mid-tolerant species, however its seedlings are shade-tolerant during the first

316   30 years of their lifespan and their saplings are shade-intolerant (Ge, 1994). Limited light availability

317   under the closed canopy of mixed forests causes high mortality of *P. koraiensis* at sapling stage,

318   decreasing overall density of this species under the forest canopy (Table 1).

319   The majority of sampled *P. koraiensis* trees apparently took advantage of canopy opening early in their

320   lifespan, as suggested by comparison of the initial and gap-associated growth (Fig. 5). Since the trees in

321   our study were sampled at DBH (1.3 m) and not at the ground level, it was not possible to deduce light

322   conditions for these trees at the time of establishment. About half of the released *P. koraiensis* trees

323   experienced improved light conditions early in their lifespans, their initial growth was higher than growth

324   during the release periods. Indeed, previous studies have indicated that trees of *P. koraiensis* typically

325   experience several canopy gap episodes before reaching the main canopy (Wang and Zhao, 2011),

326   regeneration of this species benefiting from gaps as small as 250 m^2 (Yu and Hao, 1998; Zhao et al.,

327   2006).

328   It was difficult to deduce exact forest dynamics due to limited precision of our age data and since more

329   than 200 years passed since the occurrence of the last major disturbance event. However, survival of

330   shade-tolerant *P. jezoensis* and *A.nephrolepis* under the forest canopy appeared to be less dependent on

331   disturbances than that of light-demanding *P. koraiensis* and *L. olgensis*. Persistent recruitment of *P.*

332   *jezoensis* and *A. nephrolepis* over the last 220 and 110 years (Figs. 3c and d), together with their low

333   increments during the initial growth period (Fig. 5) suggested that two species might be independent of

334   treefall gap episodes due to their high degree of shade-tolerance (Yang et al., 1994; Okitsu et al., 1995;

335   Liu, 1997). Ability to withstand a prolonged period in suppressed condition with low radial growth, and

336   fast response to improved light conditions allow them to maintain their presence in the canopy (Yang et

337   al., 1994). This strategy is similar to the ones of other shade-tolerant species like Norway spruce (*Picea*

338   *abies* (L.) Karst.) and silver fir (*Abies alba* Mill.) in European boreal forests, and balsam fir (*Abies*

339   *balsamea* (L.) Mill.) in North American boreal forest. Regeneration of these species takes advantage of

340   small-scale gaps (Kneeshaw and Bergeron, 1998; Drobyshev, 1999; Nagel et al., 2007; Firm et al., 2009;

341   Zielonka and Malcher, 2009).

342   In a short-time perspective (< 200 years), stand-replacing disturbance events were probably of limited

343   importance as drivers of the forest dynamics in Changbai Mountain, primarily due to the fact that the

344   interval between such disturbance events was longer than the typical maximum lifespan of dominant

345   species. Volcanic eruptions occurred in the study region with the interval exceeding 600 yr and were

346   likely causes of stand-replacing fires (Zhao, 1981; Manchida et al., 1987). This interval was longer than

347   the lifespan of dominant species *P. koraiensis* (~400 yr), *P. jezoensis* (~300 yr), *A. nephrolepis* (~200 yr),

348   and *L. olgensis* (~300 yr) (Ishikawa et al., 1999; He et al., 2005). The similar pattern was also found in

349   deciduous forests of the eastern United States, where the average interval between severe disturbances

350   was approximately 1000 years (Lorimer, 1977, 1989; Canham and Loucks, 1984; Whitney, 1986). In the

351   absence of large-scale disturbances, forest structure and composition in such forests are largely driven by

352   small-scale canopy disturbances due to wind-induced mortality of single trees or small group of trees

353   (Runkle, 1985, 1991; Canham, 1989; Drobyshev 2001; Motta et al., 2011). Interval between

354   medium-scale disturbance in the studied forest was 60 years and shorter than the lifespan of all the

355   dominant species. It follows that intermediate disturbance events might provide important regeneration

356   possibilities for canopy dominants.

357 Since no tree mortality data was available in the current study, we were unable to evaluate actual

358 contribution of species and time-specific mortality patterns into overall canopy composition. However,

359 joint analysis of growth release chronologies and tree age distributions suggested that current forest

360 composition, expressed as DBH distributions of canopy trees, is driven by regeneration events and

361 probably not by changes in mortality rates over time.

362 *Effects of future climate on forest dynamics*

363 Future climate changes affecting intensity and frequency of stand disturbances may have implications for

364 forest structure and composition. We speculate that changes in wind climate (Dai et al., 2011) may be

365 particularly important since they are directly connected to availability and size distribution of disturbed

366 patches, which are important for the regeneration of canopy trees. Future climate projections suggest that

367 China will experience more extreme events such as hurricanes and typhoons in the future (IPCC, 2007).

368 Particularly, such storms will expand along the coast areas from south to northeast China within rising

369 sea surface temperatures (IPCC, 2007). This may increase the frequency of medium and large-scale wind

370 disturbances in the forest of northeast China. Since such disturbances favor the establishment of light

371 demanding species the trend may benefit the growth release of *P. koraiensis* and *L. olgensis* in Changbai

372 Mountain, increasing the share of shade-intolerant species in the forest canopies.

373 Increase in forest fire activity could be another consequence of climate change. Significant warming

374 trends during the fire season (by 0.36°C per 10 years in spring and by 0.22 °C per 10 years in summer)

375 and decrease in precipitation (by 100 mm) have been observed since the 1960s in Changbai Mountain

376 (Qian and Qin, 2006; Yu et al., 2006), this climate trend may indicate an increased chance of fire

377 occurrence in coming decades. Beside direct effect on drought frequency and severity, future climate

378 change may also affect forest flammability through a succession towards more fire-prone vegetation.

379 Simulation of the forest ecosystem response to climate warming in Changbai Mountain suggested that

380 future climate would benefit *L. olgensis*, making vegetation more prone to forest fires (He et al., 2005).

381 In general, our results showed the frequency and intensity of canopy disturbances associated with wind in

382 a mixed Korean pine dominated forest over last 200 years, and suggested that indirect effects of climate

383 variability such as changes in wind intensity and fire frequency would be important affecting disturbance

384   regime in future. We speculate that this relationship and direct effects of climate on growth may be

385   equally important in shaping the structure and dynamics of the mixed Korean pine dominated forests.

386   **Acknowledgements**

395

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576   Research 39(11), 2215-2223.

577 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
578 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
579 abundant across all study sites.

580

| Species	Basal area (m²/ha)	Density (stems/ha)			Relative density (%)	Relative dominance (%)	IV
		seedlings	saplings	adult trees			
Canopy species							
Pinus koraiensis	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)
Larix olgensis	11.43 (8.0)	0	0	105 (82.8)	5.3 (5.1)	23.7 (13.9)	14.5 (9.7)
Picea jezoensis	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							
Abies nephrolepis	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)
Acer mono	0.70 (0.9)	/	6 (5.5)	21 (25.8)	1.7 (1.6)	1.5 (2.0)	1.6 (1.8)
Acer tegmentosum	0.45 (0.7)	/	76 (102.0)	34 (72.6)	4.4 (4.7)	0.9 (1.4)	2.6 (3.0)
Acer ukurunduense	0.41 (0.4)	/	98 (104.3)	48 (57.2)	6.9 (6.7)	0.9 (0.7)	3.9 (3.5)
Acer barbinerve	0.18 (0.2)	/	115 (117.5)	13 (8.3)	6.7 (7.6)	0.5 (0.5)	3.6 (3.8)

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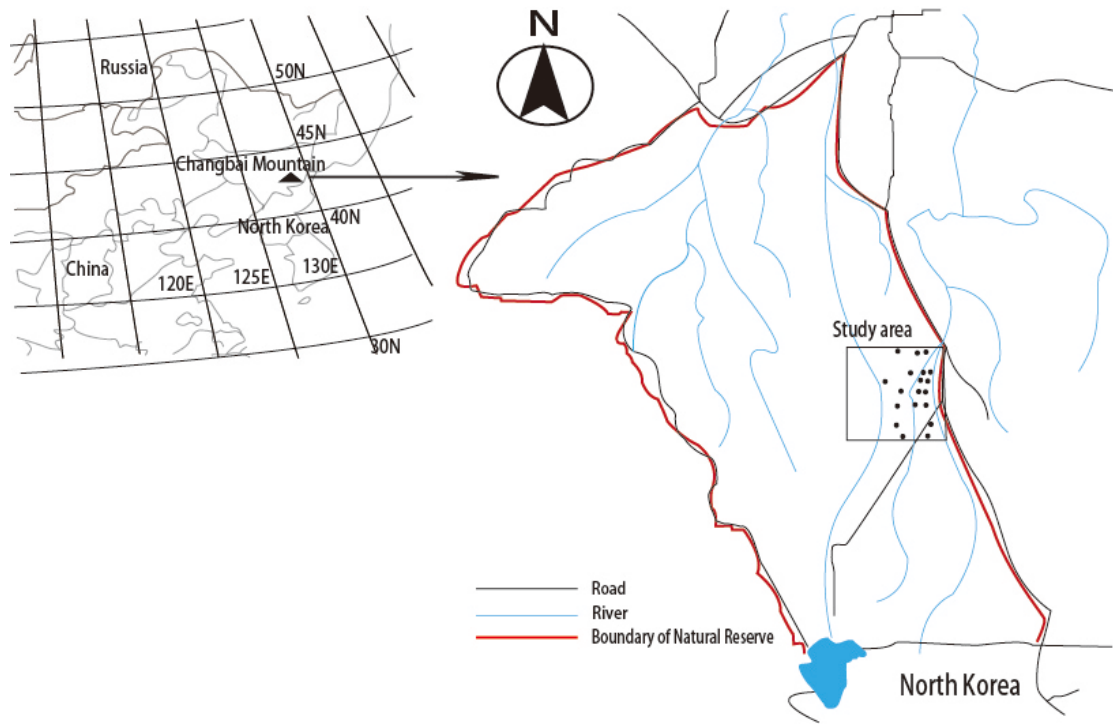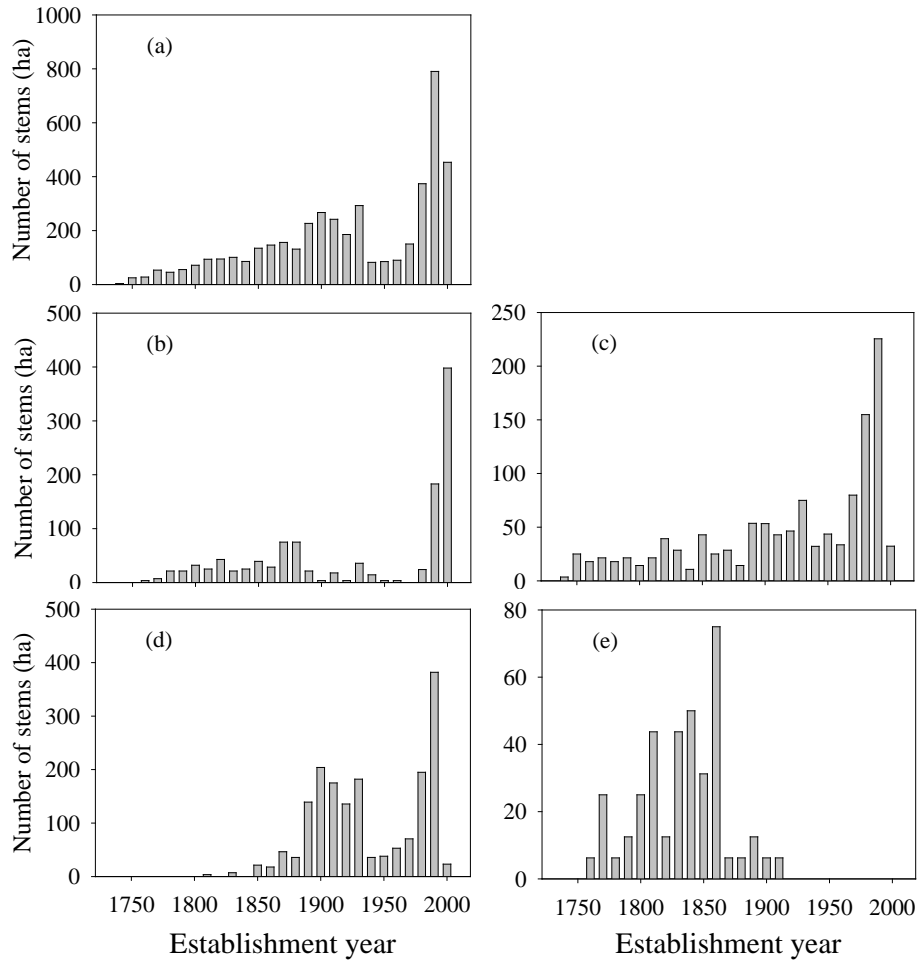

582

583

584   Fig. 2. Diameter distributions of four dominant species in a mixed Korean pine dominated forest on the

585   northern slope of Changbai Mountain, North-Eastern China. (a) Combined data of the four species, (b) *P.*

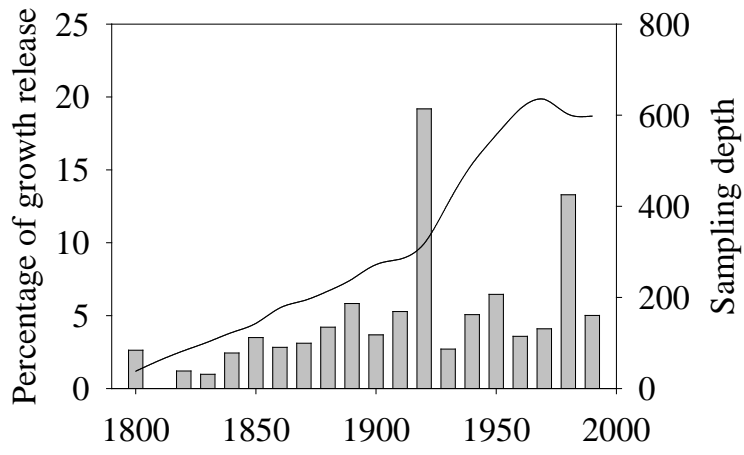586   *koraiensis*, (c) *L. olgensis*, (d) *P. jezoensis*, (e) *A. nephrolepis*. The break at vertical axis is at 50 stems/ha.
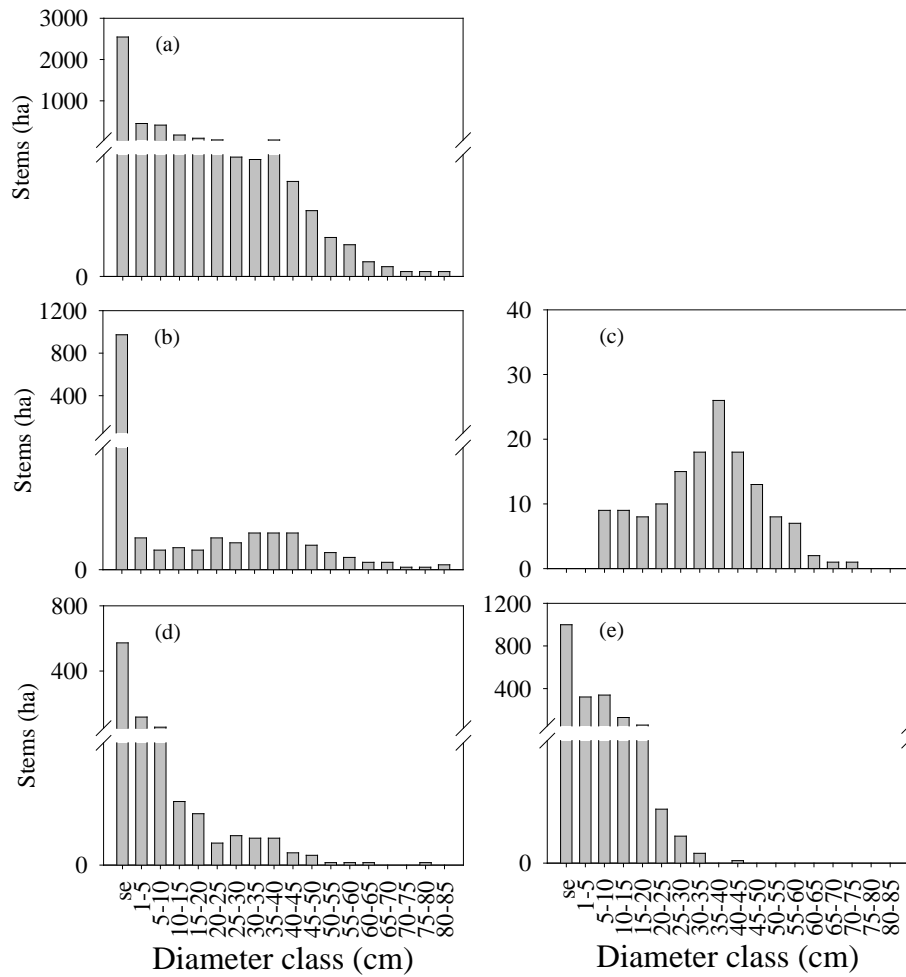
587

588

589 Fig. 3. Age structure of four dominants in a mixed Korean pine dominated forest on the northern slope of

590 Changbai Mountain, North-Eastern China. (a) Combined data for all species, (b) *P. koraiensis*, (c) *P.*

591 *jezoensis*, (d) *A. nephrolepis*, (e) *L. olgensis*. Age estimates for *L. olgensis* represent minimum ages at

592 DBH level, since 84% (50 out of 59) samples exhibited rotten pith.
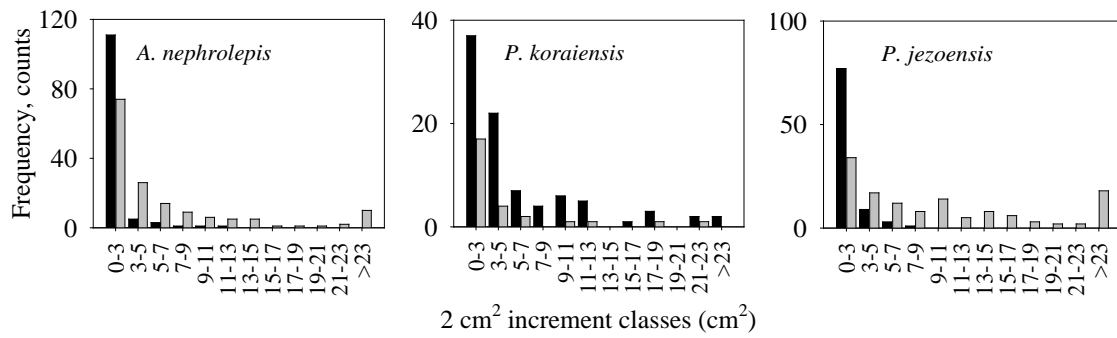

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