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Disturbance history and natural regeneration of an old-growth Korean pine-broadleaved forest in the Sikhote-Alin mountain range, Southeastern Russia



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ABSTRACT

We used a dendroecological approach to reconstruct the disturbance history of the old-growth Korean pine (*Pinus koraiensis* Siebold et Zucc.)-broadleaved forest in the southern part of the Sikhote-Alin mountain range (Southeastern Russia). We also performed a point pattern analysis to study the population structures of the five dominant tree species, and our findings demonstrate that there were no intense, stand-replacing disturbances from 1800 to 2000. Low- and medium-intensity disturbance events predominated, and the most probable cause of these disturbances was windthrow due to strong winds. The age structure of the coniferous species indicates recruitment continuity, so the stand is unevenly aged, but regeneration waves associated with the disturbances can be distinguished. The population structure of the dominant species is characterized by similar features, and the aggregate distribution pattern is typical of immature plants. The virginal and generative plants of most species are uniformly distributed, but the generative individuals of some species tend to be hyperdispersed over a small spatial scale. The advanced regeneration pool is mostly composed of immature plants of both shade-tolerant coniferous and light-demanding deciduous species, which confirms that immature deciduous species are characterized by significant shade tolerance, although to a lesser extent than coniferous plants. In virginal plants, light demand is greater for both coniferous and deciduous species. The populations of the dominant species are stable, so the current disturbance regime promotes the coexistence of shade-tolerant and light-demanding species but affects the abundance of the various plant species in the stand.

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1. Introduction

Natural disturbances play a crucial role in the dynamics of forest communities; they affect the regeneration and growth of tree, shrub and other species as well as their coexistence, eventually influencing species diversity (Frelich and Lorimer, 1991; Abrams et al., 1999; Ishikawa et al., 1999; Kubota, 2000; Bergeron et al., 2004). Research into the disturbance history of forest communities is necessary to understand how modern stands were formed and to predict their future structure and species composition (Girardin et al., 2001; Kuuluvainen, 2002; Dang et al., 2009; Zhang et al., 2014). Various dendroecological approaches based on the dating of growth releases are used to reconstruct stand histories and disturbance regimes. Improved conditions for growth typically occur

when canopy gaps are formed (Lorimer and Frelich, 1989; Frelich and Lorimer, 1991; Brisson et al., 1992; Tardif et al., 2001; Black and Abrams, 2003; Fraver and White, 2005).

In mixed forests, variations in disturbance intensity promote the coexistence of species with different life strategies and ecological characteristics (Runkle, 1985; Liu, 1997; Bergeron, 2000). In closed-canopy temperate forests, disturbances vary from small canopy gaps formed by the loss of one or several trees 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). Variations in the intensity, frequency, and spatial distribution of disturbances have a spatio-temporal effect on the regeneration, growth, and survival of trees (Liu, 1997; Mori and Takeda, 2004). Regeneration of certain tree species, in turn, can affect future disturbance regimes, because tree species have differences in their life-span and resistance to various factors of disturbances (e.g. strong winds). Species with different life strategies exhibit various responses to differences in

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gap size and disturbance intensity depending on their ecological characteristics, such as shade tolerance and regeneration strategy (Runkle and Yetter, 1987; Bergeron et al., 1998; Drobyshev, 1999). Shade-tolerant species typically have an advantage due to advanced regeneration as rather small canopy gaps are sufficient for their development. In contrast, light-demanding species are characterized by more rapid growth, but they require much larger canopy gaps for establishment (Runkle and Yetter, 1987; Kobe et al., 1995; Liu, 1997). However, this pattern can be more complex because the light demand of an individual plant changes during development as it passes through different ontogenetic stages. In particular, light-demanding species can be characterized by higher shade tolerance in early ontogenetic stages, and shade-tolerant species may require a significant amount of light to sustain their growth at certain life stages (Evstigneev, 1991; Lebedev and Chumachenko, 2002). As a result, the spatiotemporal diversity of disturbance events allows species from both groups to stably coexist within forest communities.

Korean pine (*Pinus koraiensis* Siebold et Zucc.)-broadleaved forests are the main forest vegetation type in the Sikhote-Alin mountain range of the southern portion of the Russian Far East. This area is the northeastern limit of the range of Korean pine-broadleaved forests, which are also found in northeastern China (the central part of the range), on the Korean peninsula, and in Japan. The Sikhote-Alin mountains is one of the few places where significant areas of old-growth Korean pine-broadleaved forests remain. In the absence of volcanic activity, which is a source of strong natural disturbances in the central part of the range (Liu, 1997; Ishikawa et al., 1999; Dai et al., 2011), wind is the primary disturbance factor on this territory. Wind causes a wide range of disturbance events, from individual tree falls to large blowdowns (Dai et al., 2011). According to the published data, large canopy gaps are crucial for the survival of light-demanding species, such as Yellow birch (*Betula costata* (Trautv.) Regel.) and Amur linden (*Tilia amurensis* Rupr.) in Korean pine-broadleaved forests (Ishikawa et al., 1999). Smaller gaps promote the regeneration of mid-tolerant Korean pine (Ishikawa et al., 1999; Dai et al., 2011), but Yezo spruce (*Picea jezoensis* (Siebold et Zucc.) Carr.) and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim) are less dependent on canopy disturbances due to their shade tolerance (Yang et al., 1994; Okitsu et al., 1995; Liu, 1997; Ishikawa et al., 1999).

There is almost no historical information on disturbances in the Sikhote-Alin mountain range, which is a significant impediment to the analysis of data obtained from dendroecological approaches and the investigation of the dynamics of forest communities in general.

In this work, we studied the disturbance history and regeneration dynamics of old-growth Korean pine-broadleaved forest, which is the most typical vegetation type of the southern Sikhote-Alin mountain range. Our primary objectives were (1) to reconstruct the local history of the natural disturbances that have shaped the stand and controlled its dynamics over the last two centuries and (2) to understand the relationship between the disturbance history and the current species composition of the stand.

2. Materials and methods

2.1. Study area

We studied the western macroslope of the southern part of the Sikhote-Alin mountain range (Southeastern Russia) at the Verkhneussuriysky Research Station of the Institute of Biology and Soil Science, Far East Branch of the Russian Academy of Sciences (4400 ha; N 44°01'35.3", E 134°12'59.8", Fig. 1).

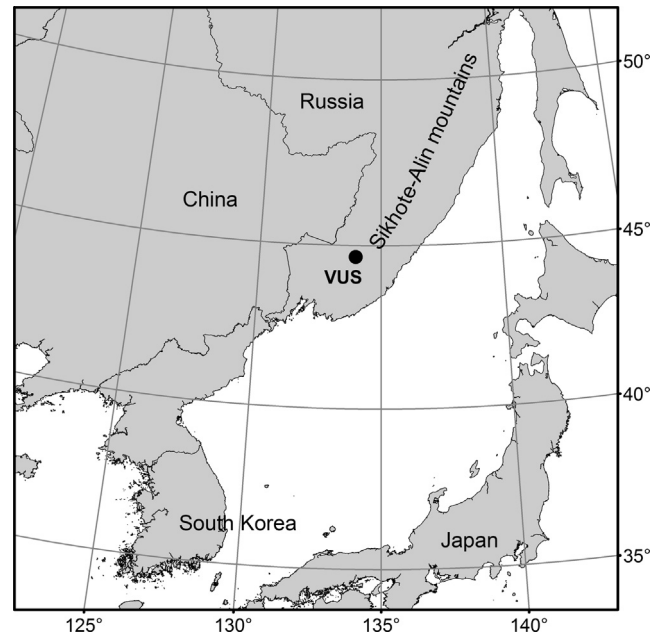


Fig. 1. Location of the study area on the Sikhote-Alin mountains, Southeastern Russia. VUS is Verkhneussuriysky Research Station.

The territory is characterized by a monsoon climate with relatively long, cold winters and warm, rainy summers. The average annual air temperature is 0.9 °C; January is the coldest month (−32 °C average temperature), and July is the warmest month (27 °C average temperature). The average annual precipitation is 832 mm (Kozhevnikova, 2009). Southerly and southeasterly winds predominate during the spring and summer, while northerly and northwesterly winds predominate in autumn and winter. Winds are typically weak, with an average speed lower than 3 m s^{−1}, and the number of stormy days with wind gusts over 20 m s^{−1} is approximately 20 per year, mostly in the spring (April) and autumn (November). The terrain includes mountain slopes with an average angle of ~20°, and the study area is characterized by brown mountain forest soils (Ivanov, 1964).

Mixed forests with Korean pine are the main vegetation type in the study area, and they form an altitudinal belt up to 800 m above sea level. They are gradually replaced by coniferous fir-spruce forests at high altitudes (Kolesnikov, 1956). Korean pine-broadleaved forests are formed by up to 30 tree species with *A. nephrolepis*, *B. costata*, *P. jezoensis*, *P. koraiensis*, and *T. amurensis* being dominant.

A. nephrolepis, *P. jezoensis*, and *P. koraiensis* are shade-tolerant species (Usenko, 1968). However, according to the literature, seedlings and saplings of *P. koraiensis* require a large amount of light to reach the stand canopy. Therefore, this species is considered mid-tolerant by some authors (Ge, 1994; Ishikawa et al., 1999). *T. amurensis* and *B. costata* are regarded as light-demanding species, although *T. amurensis* is sometimes classified as a mid-tolerant species (Usenko, 1968).

Approximately 60% of the Research Station area had been subjected to selective clear-cutting before the Station was established in 1972. The remaining 40% of its area has never been clear-cut and is covered by unique old-growth forest.

2.2. Discrete description of ontogenesis

In this work, the demographic and other study questions are based on the concept of the discrete description of the ontogenesis of plants. During their life, plants go through successive stages

known as the ontogenesis of a species (Gatsuk et al., 1980), and each individual within the population is characterized by both its absolute (calendar) age and its biological age depending on its morphological, anatomical and physiological characteristics, which are altered during ontogenesis (Smirnova et al., 2002). While the alterations in plants may vary with different ontogenetic stages, they are genetically determined and weakly dependent on the absolute age (Gatsuk et al., 1980; Smirnova et al., 2002; Silveira et al., 2012). Ontogenetic stages are characterized by differences in ecological parameters, but they also differ according to the role that individuals play in the population and the community (Smirnova and Bobrovskii, 2001). When conducting population studies, it is more reasonable to consider the ontogenetic stages relative to the biological age of plants rather than to their absolute age because individuals belonging to different species and life forms, as well as different individuals within the same species, require different amounts of time to reach certain stages. However, individuals of same ontogenetic stages play similar roles in the life of a population despite the differences in their absolute age (Smirnova et al., 2002).

The qualitative signs of their ontogenetic stages can be used to describe any spermatophyte species (East-European forests (Russia), 2004) and are characterized as follows (Smirnova et al., 2002; Smirnova and Bobrovskii, 2001; Komarov et al., 2003):

germlings (p) – mixed nutrition from the root and seed; there is a morphological connection with the seed and germinal structures;

juvenile (j) – indicators and properties typical of an adult plant have not yet been formed; plants usually have the primary root and sprout but not seed lobes;

immature (im) – indicators and properties that are transitional between juvenile and adult plants; branching typical of a certain species occurs; the sprouting type changes, but individual elements of the primary sprout are retained;

virginal (v) – features typical of the life form of the species are formed at this stage; the plants have the adult leaves, sprouts, and root system typical of the species but do not possess generative organs;

young generative (g₁) – characterized by the emergence of generative organs; new-growth processes prevail over die-off processes; all of the adult structures have already been formed;

middle-aged generative (g₂) – new-growth and die-off processes are in equilibrium; plants are characterized by the maximum size, the maximum number of generative organs, and the maximum annual biomass production;

old generative (g₃) – die-off processes start to prevail; the generative function decreases; root and shoot formation is reduced;

subsenile (ss) – die-off processes prevail significantly; no generative organs are formed; immature leaves occur;

senile (s) – dead plant parts accumulate; the life form is simplified, and juvenile features emerge.

The duration of ontogenetic stages and the size achieved by an individual mostly depend on conditions to which it is exposed; hence, the individuals can be differentiated according to vitality based on the set of quantitative indicators (East-European forests (Russia), 2004):

normal vitality usually occurs under optimal conditions; plant has maximal size and biomass; size and biomass increments strongly correlate with the calendar age until the senile ontogenetic stage;

subnormal vitality – a plant has smaller size compared to the normal one; residuals of dying tops are visible on the trunk;

low vitality (suppressed) – a plant has minimal size and biomass and grows very slowly; treetop frequently dies off; and the crown has many dead branches.

Fig. 2 shows an example of virginal *P. jezoensis* plants of different vitality. Plants of certain species in different ontogenetic stages located within a certain area form the so-called population pattern (East-European forests (Russia), 2004).

2.3. Data collection

Our study is based on the data collected in the 1.5-ha (150 × 100 m) permanent plot (Omelko and Ukhvatkina, 2012), which was located in the middle portion of the west-facing slope with an angle of 22° at an altitude of ~750 m above sea level. The forest in the plot was a late-successional stand belonging to the middle type of Korean pine-broadleaved forests at the upper bound of the distribution of Korean pine, where it forms mixed stands of Korean pine-spruce and spruce-broadleaved forests (Kolesnikov, 1956).

In addition to the five dominant tree species (*A. nephrolepis*, *B. costata*, *P. jezoensis*, *P. koraiensis*, and *T. amurensis*), the stand in the plot was formed by the following species: *Acer mono* Maxim., *Acer tegmentosum* Maxim., *Acer ukurunduense* Trautv. et Mey., *Cerasus maximowiczii* (Rupr.) Kom., *Sorbus amurensis* Koehne, *Taxus cuspidata* Siebold et Zucc. ex Endl., and *Ulmus laciniata* (Trautv.) Mayr. The shrubs included *Acer barbinerve* Maxim., *Eleutherococcus senticosus* (Rupr. & Maxim.) Maxim., *Philadelphus tenuifolius* Rupr. et Maxim., *Ribes maximoviczianum* Kom.; lianas: *Actinidia kolomikta* Maxim. et Rupr., and *Schizandra chinensis* (Turcz.) Baill.

In the summer of 2010, we surveyed the plot to study the population patterns of the tree species. The plot was divided into 150 square areas that were 10 × 10 m in size, and the surveys were conducted within these squares. All of the living trees were stem-mapped, tagged, and identified to species; we included plants at the following ontogenetic stages: immature, virginal, young generative, middle-aged generative, and old generative. The age and vitality states of *A. nephrolepis*, *P. jezoensis*, and *P. koraiensis* were determined based on studies of their ontogenesis (Komarova and Trofimova, 2010; Komarova et al., 2010; Ukhvatkina et al., 2010), and we referenced the general signs described by Smirnova and Bobrovskii (2001) for the remaining tree species. Vitality was only specified for virginal plants because

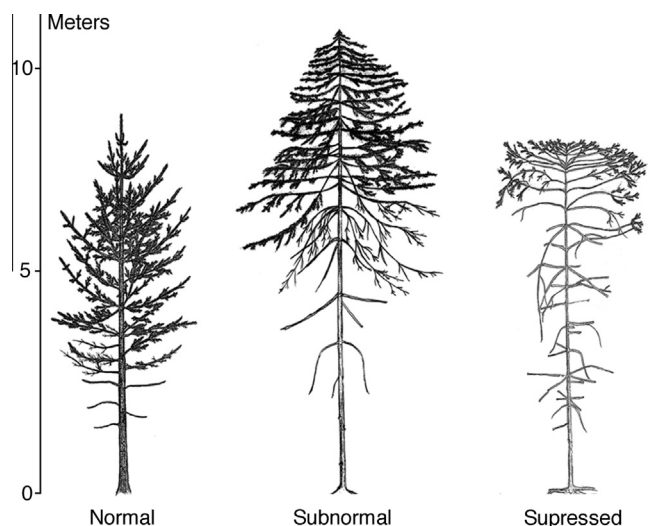


Fig. 2. Appearance of virginal plants of *P. jezoensis* with different vitality.

immature plants are found in the shrub layer, so almost all of them are suppressed; generative plants are tall, and it is difficult to evaluate crown features from the ground.

To investigate the reasons for the variation in the vitality of virginal plants, we described their location with respect to canopy gaps as follows: (1) within the gap, (2) at the periphery of the gap, and (3) under the canopy. The plants whose crowns were mostly located within the gap were classified as the first group, and the second group included coniferous trees whose treetops were located at the gap border while a portion of the crown was under the canopy of the stand. This group also included deciduous trees if their base was under the canopy while their crown grew through the canopy gap either partially or completely (because deciduous trees are more flexible compared to conifers). Trees whose crowns were completely located under the stand canopy were classified as the third group.

The total number of stem-mapped living trees was 6479 in 2010, representing 12 species. In addition to living trees, we stem-mapped standing dead trees, for which we determined species and the ontogenetic stage of those trees before they died, as well as stumps, which were only identified to species. The total numbers of stem-mapped dead standing trees and stumps were 195 and 279, respectively.

We extracted core samples from trees of five dominant species from 2010–2012 to reconstruct the disturbance history of the stand. Sampling was performed at a height of 1.3 m perpendicular to the direction of the slope to minimize the influence of reaction wood. Core samples were obtained from all of the trees (one core per tree) beginning with those at the virginal ontogenetic stage (when tree diameter was at least 5–6 cm at a height of 1.3 m). In the cases where the extracted core was very short due to pith rot, we tried to extract an additional core from a different direction, and if the second core was also very short (approximately 50% of the cases), the tree was not included in sample collection. In total, 419 core samples were obtained. Preliminary preparation included drying, cutting, and contrast enhancement. The widths of the growth rings were measured using the Velmex® TA Measurement System (Bloomfield, USA) to an accuracy 0.01 mm. Cross-dating and the identification of missing growth rings were performed using Cofecha (Holmes, 1983) and TsapDos software (Rinntech®, Heidelberg, Germany).

We also extracted core samples near the base of the stem to determine the absolute age of the virginal and generative plants. Sampling was performed for the same trees where the core samples were collected at a height of 1.3 m. If a sampled tree turned out to be rotten, it was not used to determine the age of the tree. In this case, the number of missing growth rings was not estimated (Duncan, 1989; Rozas, 2003) because if rot was present, its percentage was typically at least 50% of the radius of the tree, especially in middle-aged and old generative plants. Furthermore, young trees are often suppressed for a long time (Kozin, 2013), so the number of missing growth rings can be significantly underestimated. Hence, we only used core samples with preserved pith to determine the age of the plant. We also collected cross-cut samples from well-preserved, windthrown generative trees to determine their age.

In 2013, we randomly placed four additional 30 × 30-m plots close to the study plot in similar conditions, and on these additional plots, we cut immature plants at the base to determine their age. No samples were taken within the study plot because disturbing the vegetation was not allowed. The number of immature plant samples was 268 for *P. koraiensis*, 329 for *P. jezoensis*, 576 for *A. nephrolepis*, 15 for *B. costata* and 17 for *T. amurensis*. Furthermore, we cut at the base of 10 virginal plants of *P. koraiensis* and 5 plants of *B. costata* on the additional plots because they are relatively rare; we had only few cores from

the study plot. The number of annual growth rings in the cross-cut samples was counted.

2.4. Reconstruction of disturbance history

We used the boundary line criteria to detect release events (Black and Abrams, 2003, 2004). This procedure is based on the assumption that abrupt increases in the radial growth of trees in a stand are due to improved conditions for surviving trees as their neighbors die (Lorimer and Frelich, 1989; Rubino and McCarthy, 2004), i.e., a tree responds to better conditions by increasing its growth. To detect growth release events, we calculated the relative changes in the percent radial growth (%GC) in the chronology of each core sample using the following formula (Nowacki and Abrams, 1997):

$$\%GC = ((M2 - M1)/M1) \times 100, \quad (1)$$

where $M1$ is the average growth over the past 10 years, including the current year (prior growth), and $M2$ is the average growth over the next 10 years. Averaging over decades smooths the changes in growth caused by annual climate fluctuations (Nowacki and Abrams, 1997).

Then we fit a specific boundary line curve to the data according to the method (Black and Abrams, 2003, 2004). If the %GC value is greater than 20% or 50% of the boundary line function value at a specific $M1$ value, it is indicative of a minor release or major release, respectively. Because each %GC value is associated with a certain core for a tagged tree, we can identify which individual experienced growth release in a given year.

2.5. Spatial point pattern analysis

Ripley's K function and the pair correlation function $g(r)$ are commonly used in environmental studies to analyze point patterns (Ripley, 1981), but these functions were developed to examine the patterns characterized by homogeneous disturbance intensity over an entire study area (Ripley, 1981). Spatial variations in intensity bias the estimated function, indicating significantly greater spatial aggregation compared to the actual pattern. Heterogeneous intensity over the study area causes the phenomenon known as "virtual aggregation" (Wiegand and Moloney, 2004), in which the empirical curve $g(r)$ lies above the simulation envelopes over the entire analysis range and slowly approaches the value predicted by the null hypothesis. This effect obscures important information about the true pattern, especially over a small scale (Strandt et al., 2007).

The patterns of the plants (immature and virginal ones in particular) analyzed in this study are usually heterogeneous, which can be detected through field surveys and visual inspection, so we used the $K2(r)$ function to avoid virtual aggregation (Schiffers et al., 2008; Wiegand and Moloney, 2014). Identical to the way that the pair correlation function shows the expected difference in the number of points between the concentric circles, the $K2(r)$ function calculates the expected differences in the number of points between the consecutive distances. Thus, as with the mathematical relationship between the $K(r)$ and $g(r)$ functions, the $K2(r)$ function can be heuristically interpreted as the first derivative of the $g(r)$ function:

$$K2(r) = dg(r)/dr.$$

In contrast to the $g(r)$ function, the $K2(r)$ function does not indicate a range of distances but the upper limit of a range of distances beyond which events are not randomly distributed. It should be noted that the positive value is indicative of a transition from lower to higher intensity and thus (other than a positive value in a $g(r)$ function, which would indicate attraction among point events) the upper limit of a range of scales at which the pattern

is regular. The negative value is indicative of the transition from higher to lower intensity and the upper limit of the range of scales at which the pattern is aggregated.

In our study, the univariate $K2(r)$ statistic was used to analyze the spatial patterns of five dominant species, and three size classes were established: immature trees, virginal trees and generative trees. We combined all of the generative trees into the one class because of the insufficient number of young generative and old generative trees in the almost all species. The complete spatial randomness (CSR) null model was used to reveal significant univariate second-order interactions. Significant departures from the null hypothesis of the CSR process were evaluated using the fifth lowest and highest value of 99 Monte Carlo simulations of the null model to generate approximately 99% simulation envelopes (Wiegand and Moloney, 2014). We used a 1-m² grid to analyze plant interactions at spatial scales from 0 to 35 m, and we used a goodness-of-fit (GoF) test to assess significant departures from the null model. Point pattern analyses were conducted using Programita software (Wiegand and Moloney, 2014).

3. Results

3.1. Stand structure

The forest stand in the study plot is composed of 12 tree species, eleven of which have living plants at least 1.3 m tall (Table 1). *T. amurensis* comprises the largest proportion of total basal area in the canopy layer; *P. jezoensis* and *P. koraiensis* have slightly lower proportions; *B. costata* characterizes the lowest proportion. A comparison of the total basal areas and stand densities shows that *P. koraiensis* and *B. costata* are represented by large, sparsely distributed trees, while *T. amurensis* and *P. jezoensis* are represented by relatively abundant but smaller trees.

A. nephrolepis is dominant in the subcanopy layer, and it is also present in the highest density. The total basal area of the remaining seven tree species in the subcanopy layer is less than 4% of the basal area of the stand, and most of these 4% belong to *A. ukurunduense*. The remaining six species in the plot are represented by single trees and currently do not play a crucial role in stand structure. Thus, the basal area of the five dominant species, with four species belonging to the canopy layer (*T. amurensis*, *P. jezoensis*, *P. koraiensis*, and *B. costata*) and one species (*A. nephrolepis*) belonging to the subcanopy layer, is 96.1% of the total. The number of living plants accounts for 88.6% of the total number of plants.

The predominant standing dead tree species are *P. jezoensis* and *A. nephrolepis*. Their basal area is 80.0% of the total, and the ratio between stand density and the basal area is the same as for living trees. Single *P. koraiensis*, *B. costata*, *T. amurensis*, and *A. ukurunduense* dead trees were found, but no standing dead trees of other species were observed.

We used the data on the ontogenetic stages of the plants to create ontogenetic spectra for the dominant species (Fig. 3), and all of the resulting spectra share some common features.

First, the spectra are inverse J-shaped, i.e., the number of immature and virginal tree species is several-fold higher than the number of generative species. Second, the spectra are bimodal; the first peak corresponds to immature plants, and the number of plants then decreases to the young generative stage. The second peak corresponds to middle-aged generative plants, and single old generative plants of all species were found. The ratio between the number of generative and pregenerative (immature and virginal) plants differs significantly between coniferous and deciduous species. Thus, the number of immature and virginal plants of *P. koraiensis*, *P. jezoensis* and *A. nephrolepis* is 8–20 times higher than that of the generative ones, but the number of pregenerative plants of *T. amurensis* and *B. costata* is much lower, 3–5 times higher than the number of generative plants. For almost all of the species, the number of virginal plants is much lower than the number of immature ones; *T. amurensis* is the only exception, for which the number of virginal plants differs from the number of immature plants by only 5%.

3.2. Disturbance history

We analyzed 249 of 419 core samples. The core samples with ring numbers less than 50 were excluded from the analysis, as the number of remaining rings was small after the first and last 10 years are excluded according to the boundary line criteria. The total stand disturbance history period that we analyzed was 200 years (from 1801 to 2000), and the lower boundary of this period was determined based on the time for which at least 10 core samples could be used for the analysis. The upper boundary was 2000 because the past 10 years cannot be taken into account due to the averaging used in formula (1). The boundary line function describing the maximum change in radial growth (%GC) depending on prior growth was selected for each species (Appendix, Fig. A1).

An analysis of the distribution of growth releases over the decades indicates frequent, small-scale disturbances and rarer, moderate disturbances over the past 200 years (Fig. 4).

Table 1

Basal area, (BA) and density (D, seedlings/saplings and adults) of the tree species on the sample plot; seedling are plants with height < 1.3 m (immature plants), saplings and adults have height ≥ 1.3 m (mainly virginal and generative plants).

Species	BA, m ² /ha		BA, %		D, stems/ha		D, %	
	Live	Dead	Live	Dead	Live	Dead	Live	Dead
Canopy species								
<i>Tilia amurensis</i>	9.85	0.20	22.75	4.32	247/155	4/6	7.2/13.9	20.0/4.7
<i>Picea jezoensis</i>	8.43	2.43	19.48	52.12	886/183	4/52	25.9/16.4	20.0/40.1
<i>Pinus koraiensis</i>	8.41	0.38	19.43	8.20	795/65	2/8	23.2/5.8	10.0/6.4
<i>Betula costata</i>	6.07	0.21	14.01	4.43	109/37	2/2	3.2/3.3	10.0/1.7
Subcanopy species								
<i>Abies nephrolepis</i>	8.84	1.39	20.41	29.73	821/549	6/60	23.9/49.2	30.0/45.9
<i>Acer ukurunduense</i>	1.14	0.06	2.63	1.19	347/115	2/2	10.1/10.3	10.0/1.2
<i>Ulmus laciniata</i>	0.21	0.00	0.49	0.00	19/3	0/0	0.6/0.3	0.0/0.0
<i>Taxus cuspidata</i>	0.18	0.00	0.42	0.00	4/2	0/0	0.1/0.1	0.0/0.0
<i>Acer mono</i>	0.10	0.00	0.24	0.00	18/2	0/0	0.5/0.1	0.0/0.0
<i>Acer tegmentosum</i>	0.05	0.00	0.12	0.00	174/5	0/0	5.1/0.4	0.0/0.0
<i>Sorbus amurensis</i>	0.01	0.00	0.02	0.00	2/2	0/0	0.1/0.1	0.0/0.0
<i>Cerasus maximowiczii</i>	–	–	–	–	2/2	0/0	0.1/0.1	0.0/0.0
Total	43.30	4.66	100.00	100.00	4542/1117	148/130	100.0/100.0	100.0/100.0

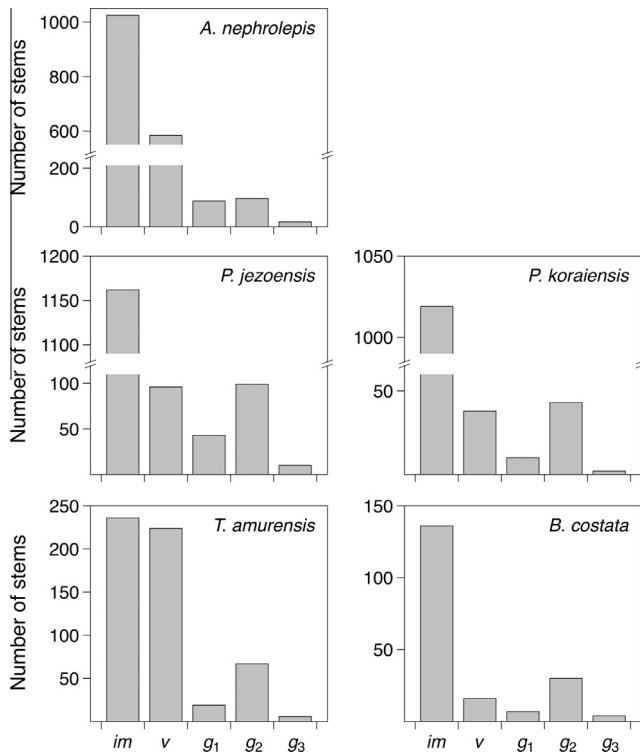


Fig. 3. Ontogenetic spectra of five dominant tree species.

The distribution of releases is relatively uniform, especially for major releases; in most decades, the number of releases (the total of the major and minor ones) varies within 15–30%. Meanwhile, relatively high values are also observed, but the maximum ones are 39.1% (1811–1820), 40.4% (1951–1960), and 32.7% (1991–2000), but these values are only insignificantly higher than the total level. The minimum number of releases (less than 15%) was observed from 1851–1860 and 1901–1910.

All of the trees under analysis experienced at least one growth release, and multiple releases were detected for 91.7% of *P. koraiensis* trees, 89.3% *P. jezoensis* trees, and 54.7% *A. nephrolepis* trees. Some of these trees experienced more than one major release, 25.0%, 33.3%, and 2.3% for these species, respectively.

3.3. Absolute age of plants and the age structure

We used the resulting data to determine the absolute age ranges for each ontogenetic stage (Table 2) of the five dominant species. We also constructed the age spectra (Fig. 5) for three coniferous species

(*A. nephrolepis*, *P. jezoensis*, and *P. koraiensis*), but the spectra for the deciduous species (*B. costata* and *T. amurensis*) could not be built because of the insufficient number of samples.

P. koraiensis trees reached the highest maximum age in the stand (527 years, Table 2), and the maximum ages of the *B. costata* and *P. jezoensis* trees were much lower (340 and 317 years, respectively). Trees of *T. amurensis* and *A. nephrolepis* had the lowest maximum age (250 and 214 years, respectively), so the age of the oldest *P. koraiensis* trees is approximately 1.5 times greater than that of old *B. costata* and *P. jezoensis* trees and more than twice the age of old *T. amurensis* and *A. nephrolepis* trees. The absolute age of the plants at each ontogenetic stage varies over a wide range. For coniferous species, the variation in age, even in immature plants, is over 100 years (Table 2), but the most immature coniferous trees are younger than 30 years (Fig. 5a–c). For virginal and generative trees, the variation in absolute age can be more than 250 years (285 years for old generative *P. koraiensis* trees and 270 years for virginal *P. jezoensis* trees), and the age distribution of both (except for old degenerative ones because only single trees are present) is bell-shaped (Fig. 5d–l). For deciduous trees, the range in the variation of absolute age is significantly lower (Table 2). Notably, the range in the variation of absolute age does not necessarily increase with the ontogenetic stage of the plants. For example, differences in the absolute age of *P. koraiensis* are maximal for old degenerative trees, while the age differences are maximal in virginal *P. jezoensis* trees. The absolute age ranges for coniferous trees at different ontogenetic stages significantly overlap, so the age of almost all of the young generative *P. koraiensis* trees lies within the range for virginal plants (Fig. 5d and g). The ages of a significant number of virginal, young generative, and middle-aged generative *P. jezoensis* trees coincide (Fig. 5e, h and k), and the absolute age ranges of virginal, young and middle-aged generative *A. nephrolepis* trees are identical to a significant extent (Fig. 5f, i and l).

The age structure of the coniferous species indicates that the recruitment of new plants has been a continuous process over the past centuries (Fig. 5p–r). However, the age structure is multimodal for each species, i.e., several medium-intensity regeneration waves are apparent. In particular, four regeneration waves starting after the 1810s, 1880s, 1920s, and 1950s are identified for *P. koraiensis* (Fig. 5p); two waves starting after the 1880s and 1950s for *A. nephrolepis* (Fig. 5r); and four waves starting after the 1810s, 1840s, 1880s, and 1950s for *P. jezoensis* (Fig. 5q).

3.4. Differentiation of the vitality of virginal plants

The number of virginal plants belonging to different species in the study plot differs significantly, but the results share an important common feature. Namely, virginal plants with normal

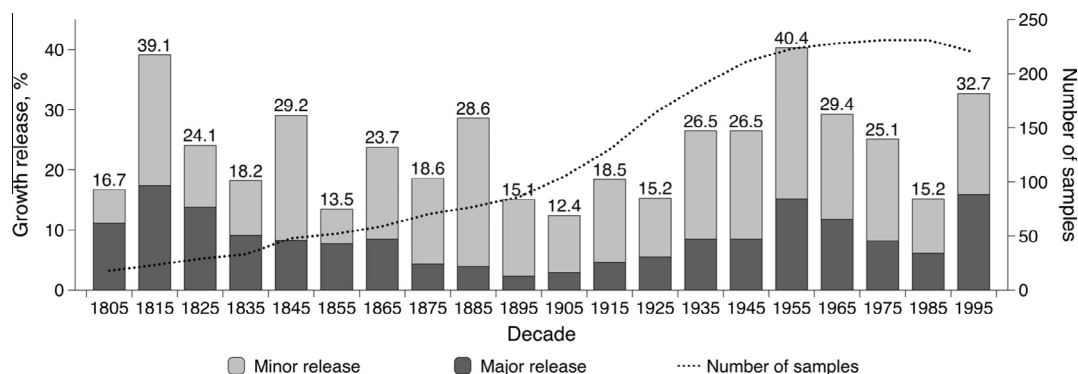


Fig. 4. Growth releases of five dominant trees in a mixed Korean pine-broadleaved forest in the South of the Russian Far East (Southern Sikhote-Alin, Russian Far East).

Table 2

Absolute age ranges for the different ontogenetic stages of five dominant tree species of mixed Korean pine-broadleaved forest. N – number of samples, pcs., A – absolute age range, years (min–max).

Ontogenetic stage	<i>P. koraiensis</i>		<i>P. jezoensis</i>		<i>A. nephrolepis</i>		<i>B. costata</i>		<i>T. amurensis</i>	
	N	A	N	A	N	A	N	A	N	A
Immature (<i>im</i>)	268	6–107	329	7–110	576	6–121	15	1–43	18	13–37
Virginal (<i>v</i>)	44	47–192	104	28–298	104	52–171	17	31–65	41	28–60
Young reproductive (g_1)	31	79–281	34	85–269	43	75–151	5	40–120	8	58–161
Mature reproductive (g_2)	26	158–303	30	69–317	24	67–166	7	85–224	9	105–235
Old reproductive (g_3)	8	242–527	9	183–269	36	116–214	3	258–340	3	120–250

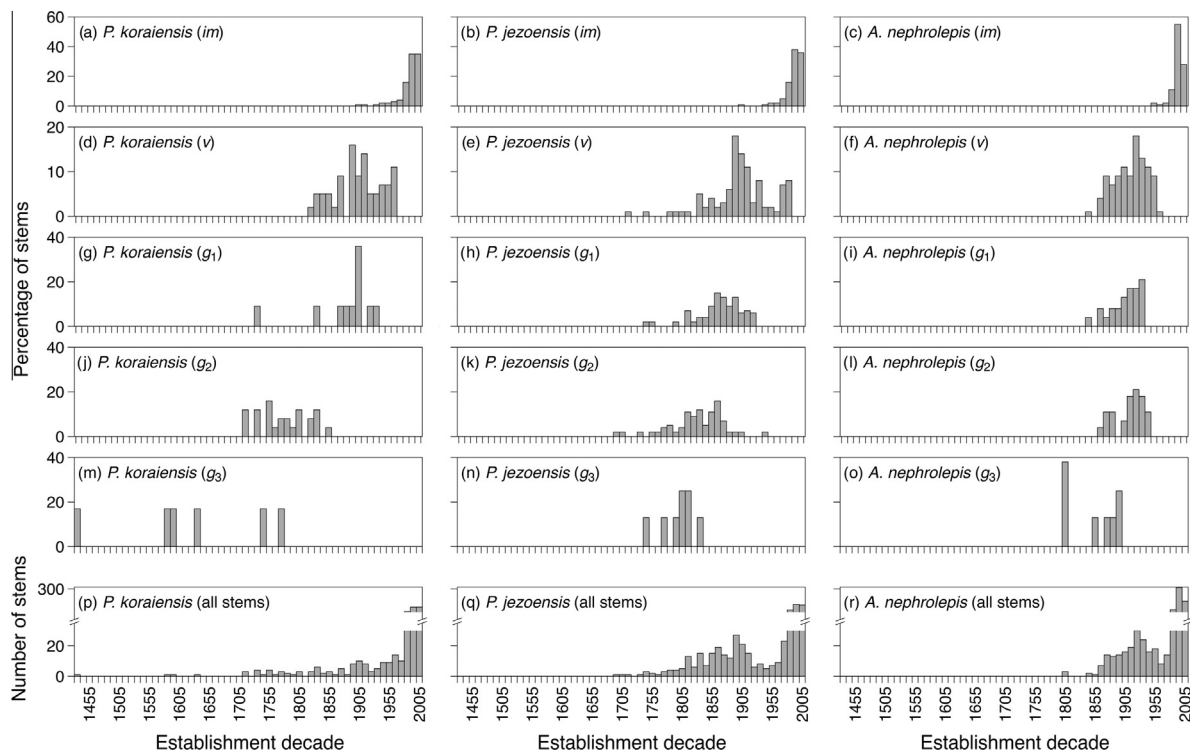


Fig. 5. Age structure of dominant conifer species in the mixed Korean pine-broadleaved forest.

vitality occur almost exclusively within the canopy gaps or at their periphery (Fig. 6) with their number being significantly higher in the canopy gaps. In contrast, all of the tree species under the canopy are characterized by subnormal and low vitality. Also there are typical differences between the diagrams for coniferous and deciduous species. A significant number of coniferous trees (*A. nephrolepis*, *P. jezoensis*, and *P. koraiensis*) grow under the stand canopy; their number is 3 to 4 times higher than the number of trees within the gaps. The number of deciduous trees under the canopy is much lower than within canopy gaps (*T. amurensis*), or deciduous trees are virtually absent (*B. costata*).

3.5. Populations pattern structure

An analysis of the combined patterns of the dominant species (Appendix A, Fig. A2) shows that immature trees are distributed very non-uniformly and form dense aggregates (Fig. 7a); virginal plants are distributed uniformly (Fig. 7g). Generative plants are distributed virtually uniformly, but hyperdispersion is present at scales of 0.5 and 1.5 m (Fig. 7m).

Analyzing the patterns of immature plants of certain species also showed an aggregated distribution, and aggregation takes place at several spatial scales in four out of five of the species. For *A. nephrolepis* and *T. amurensis*, immature plants are aggregated at two spatial scales: 0.5–4.5 m and 8.5–12.5 m and 0.5–4.5 m and 10.5–19.5 m,

respectively (Fig. 7b and f). For *P. jezoensis* and *B. costata*, immature plants are also aggregated at several spatial scales (Fig. 7c and e), but it is difficult to separate them. The average radius of the aggregates of immature *P. koraiensis* plants is approximately 12.5 m (Fig. 7d); the plants are aggregated at the same spatial scale.

Virginal plants of most species have either uniform or nearly uniform distributions, and an aggregated distribution is only observed for *T. amurensis* at scales of 0.5–1.5 m and 6.5–8.5 m (Fig. 7l). In contrast, hyperdispersed distributions are apparent for *A. nephrolepis* and *P. koraiensis* at scales of 0.5 and 1.5 m, respectively (Fig. 7h and j).

Generative plants are mainly distributed uniformly; statistically significant hyperdispersion is detected only for *A. nephrolepis* at scales of 0.5 and 1.5 m (Fig. 7n). However, *P. koraiensis* and *B. costata* show a tendency toward hyperdispersed distribution at the same scales (Fig. 7p and q), but this distribution is not statistically significant.

4. Discussion

4.1. Reconstruction of local disturbance regime

Neither large-scale nor stand-replacing disturbances took place in the Korean pine-broadleaved mixed forest over the last

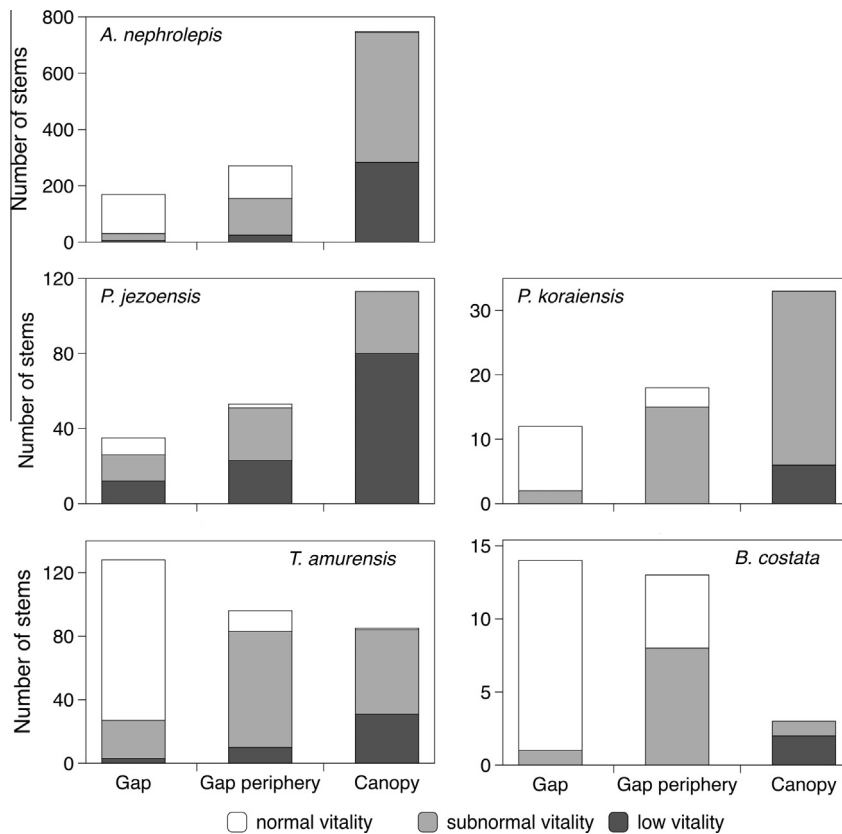


Fig. 6. Vitality of virginial plants depending on their location with respect to canopy gaps.

200 years. First, this is supported by the continuous regeneration and domination of shade-tolerant coniferous species *P. jezoensis* and *A. nephrolepis* and mid-tolerant *P. koraiensis* in the canopy and subcanopy layers. Second, the relatively slow increase and decrease in the number of trees that displayed growth release indicates that some of the released trees are gradually replacing the other ones, which could only happen when small- and medium-scale disturbances took place. The *P. koraiensis* trees were aged over 500 years, and the absence of fire scars on the core samples, cross-cut samples, and living trees as well as the absence of charcoal in the soil, burned tree stumps, stems, and branches indicates that the stand experienced neither fires nor clearcutting over the past several centuries.

Meanwhile, the number of trees that showed growth release increased during some decades, which implies increasingly intense of disturbances and, therefore, a greater number and size of canopy gaps. Three medium-scale disturbance events likely took place in the 1810s, 1950s, and 1990s, less intense disturbance events occurred in the 1840s, 1880s, and the 1930–40s. These disturbance events were followed by waves of enhanced recruitment of *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis* (Fig. 5p–r). The disturbance events manifested as an increased number of releases in the 1990s as well as the 1950–60s and were most likely to be associated with typhoons in 1989 and 1956, respectively (Kitamoto, 2013). The typhoons are accompanied by strong wind and heavy rain (Xi, 2015), which can be responsible for the fall of a large number of trees (Altman et al., 2013). We cannot determine the reasons and scale of the remaining disturbance events that took place during that time, but they were most likely to be caused by strong winds. Other studies carried out in Korean pine-broadleaved forests in the geographically adjacent areas have demonstrated that windthrows were the most common reasons

for small- and medium-scale disturbance events (Yang et al., 1994; Ishikawa et al., 1999; Zhang et al., 2014).

There were common, small-scale canopy disturbances implied by frequent growth releases with the relatively small percentage of trees that showed release (15–30%) over a single decade (Fig. 4). Wind was one of the most probable factors causing these frequent small-scale disturbance events. Tall coniferous trees *P. koraiensis* and *P. jezoensis* rising above the canopy exhibit the highest wind sensitivity because they are simultaneously characterized by a large sail area and significant leaf biomass. *P. jezoensis* trees are less wind-resistant because they also have a shallow root system (Liu, 1997; Ukhvatkina et al., 2010). However, strong winds can make all coniferous trees break at the base as pith rot is very common, and such a strong windthrow (resulting in both the uprooting and breakage of rotten trees at their base) was observed in the autumn of 2014. The importance of winds in creating periodic disturbance events in *P. koraiensis* forests was reported earlier (Ishikawa et al., 1999). It has been shown that windthrows are very frequent for the Changbai Mountain forests (the central part of the range of Korean pine-broadleaved forests) (Dai et al., 2011; Zhou et al., 2011). Heavy snowfall with wet snow sticking to tree branches followed by a sudden drop in temperature and strong wind is another factor that may cause periodic disturbance events. Trees with fragile wood (in particular *B. costata*) are especially prone to these snowfalls, and we observed that the crowns in a large number of trees of this species were completely destroyed by the heavy snowfall in the spring of 2015. Because individual trees or, less frequently, small tree groups are missing as a result of small-scale disturbances, the gap size will be comparable to the area of the tree crowns. Using data on average crown area for the tree species forming the canopy at the study plot (Omelko and Ukhvatkina, 2012), we can estimate the size of these gaps to

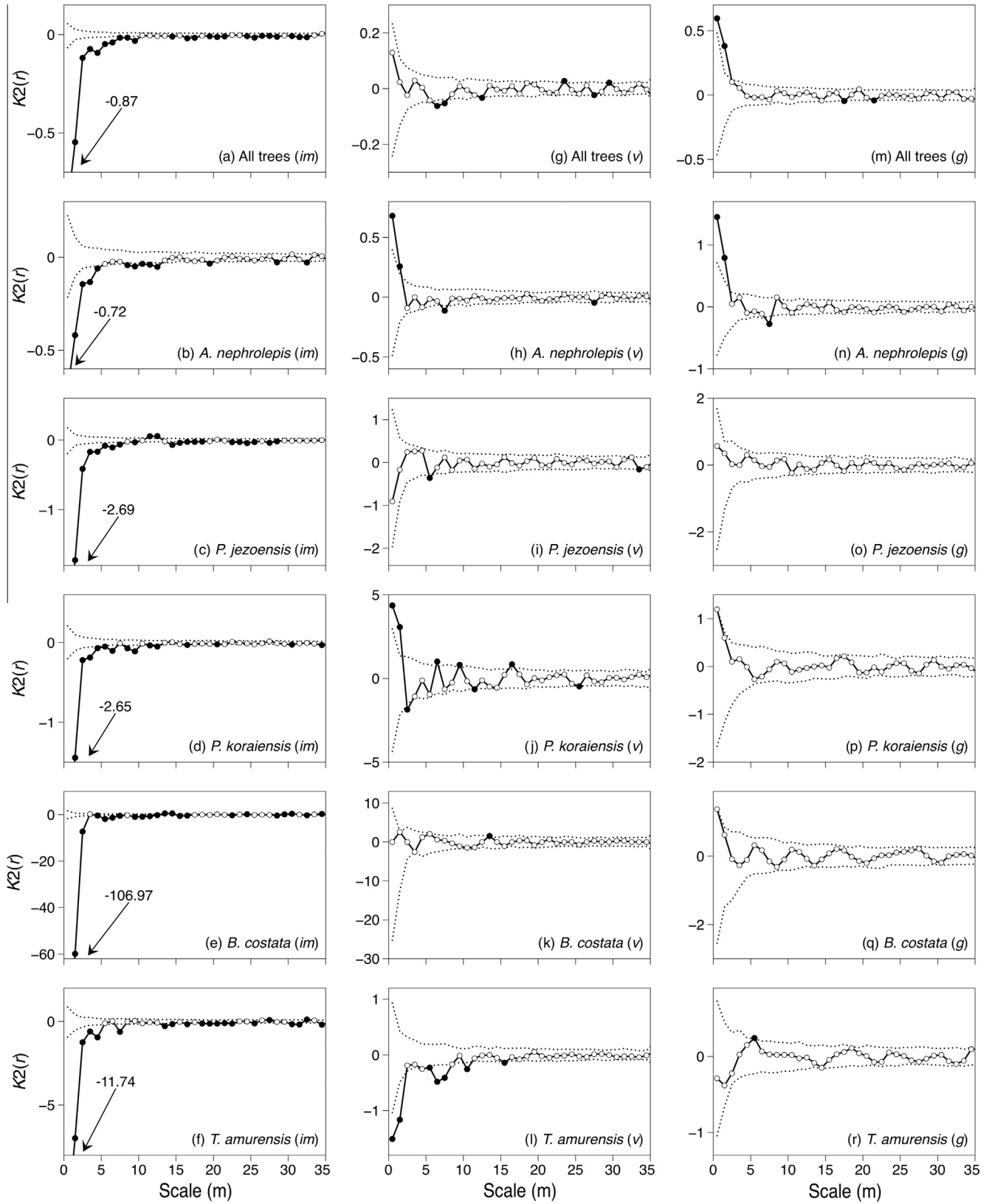


Fig. 7. Univariate point pattern analyses of five dominant species using $K2(r)$ function. The insets show the analyses of point patterns of different ontogeny stages (*im* – immature trees, *v* – virginal trees, *g* – generative trees); Solid line indicate ring statistic $K2(r)$, dashed lines indicate the upper and lower limits of 99% simulation envelope, circles and black dots represent points inside and outside simulation envelopes respectively. Points below lower the envelope indicate aggregation, within the envelopes random placement, above envelope – hyperdispersion.

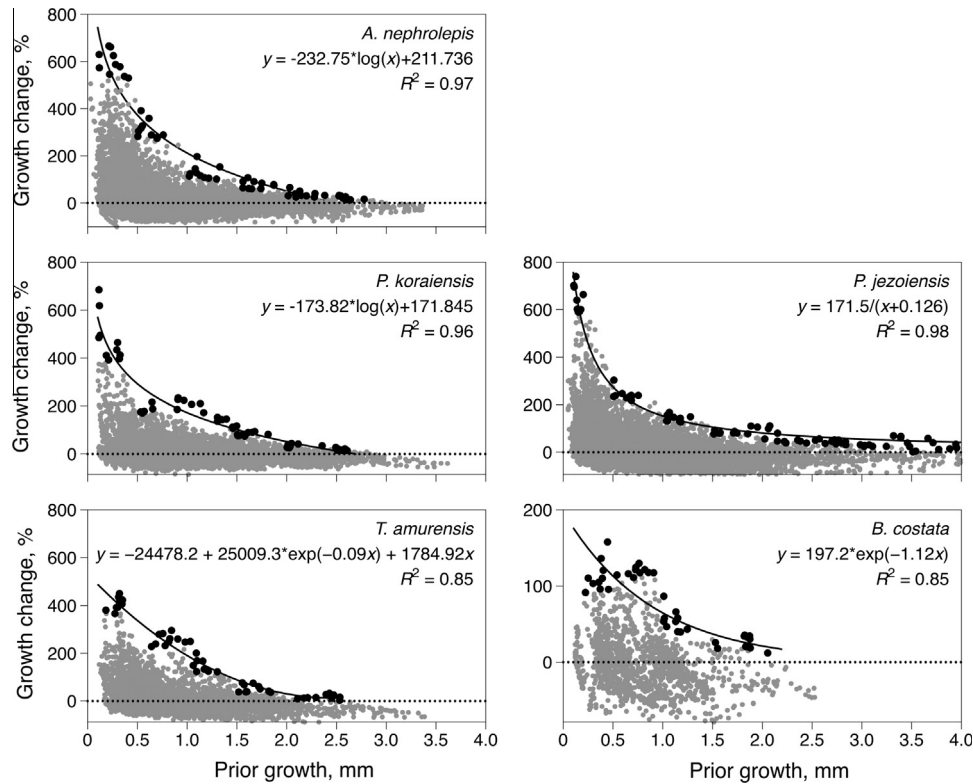


Fig. A1. Boundary line functions for five dominant species in an old-growth Korean pine-broadleaved forest. Gray points – percentage of growth change vs. prior growth, black points – ten maximum values of percentage growth change within each 0.5 mm interval of prior growth, solid line – boundary line function (corresponding equations are in insets).

be 50–200 m². In their studies conducted at Changbai Mountain, Zhao et al. (2006) demonstrated that the gaps formed by wind disturbance events are typically less than 250 m² in size.

4.2. Forest composition response to the disturbance regime

The forest stand under study is formed by 12 woody species; five (including the Korean pine) are dominant (Table 2). The remaining seven species are represented by significantly smaller number of trees and even individual trees, but seedlings, saplings, and the adult trees of these species were simultaneously detected in the plot. It is clear that although the five species are dominant and no severe disturbance events have occurred over the past two centuries, special conditions that allow regeneration and the co-existence of all 12 species occur periodically. This implies that the species composition that currently exists and the contribution of each species to the community depend on the historic disturbance regime.

Because the accumulation of undergrowth under the canopy plays a crucial role in gap dynamics at the building phase (Ukhvatkina et al., 2011; Omelko and Ukhvatkina, 2012), one can assume that species composition and stand structure start forming as seeds germinate. The waves of *P. jezoensis* regeneration begin the decade following growth release peaks (1811–1820, 1841–1850, 1881–1890, and 1951–1960) (Fig. 5q). Two regeneration waves of *A. nephrolepis* also begin the next decade after the peak in growth release (1881–1890 and 1951–1960) (Fig. 5r). We believe that the partially decayed windthrown trees are needed for the seeds of these two species to germinate (Komarova, 1986), i.e., many seeds will be able to germinate on the windthrown trees sometime after the trees die. Thus, taking into account the shifts between growth release peaks and regeneration

waves, we can assume that partial decomposition of windthrown trees takes at least a decade. Once a windthrown tree has decomposed, the regeneration wave subsides (e.g., as was observed during the 1921–1960s) (Fig. 5q and r). The regeneration waves of *P. koraiensis* are less obvious and do not always clearly coincide with the growth release peaks (Fig. 5p), which can be explained by the fact that the regeneration of *P. koraiensis* depends to a greater extent on a mast seed production whose average periodicity is 4 and 10 years (Orekhova, 2005) and on the dispersal of seeds by animals (Zakharov, 1992; Bromlei and Kostenko, 1974; Hutchins et al., 1996; Omelko et al., 2007). No specific substrate is required for *P. koraiensis* seeds to germinate, but the significant shade tolerance of *P. koraiensis* in the undergrowth (Usenko, 1968) ensures the vitality of the germlings and the subsequent juvenile and immature plants that emerge under the canopy. All of these events significantly smooth the *P. koraiensis* regeneration waves. The presence of partially decomposed windthrown trees is also important for the germination of *B. costata* seeds (Komarova, 1986), but *T. amurensis* seeds can germinate on various substrates (Komarova, 1986; Usenko, 1968). Approximately 80% of the immature coniferous trees currently present in the plot emerged after the disturbance events of 1951–1960s (Fig. 5p–r). Immature deciduous trees are younger (Table 2); almost all immature plants are suppressed, and their distribution is non-uniform (Fig. 7b–f), which seems to be due to the significant heterogeneity of the microenvironment. We believe that this heterogeneity is caused by two main factors. The first factor is the non-uniform distribution of light under the stand canopy (i.e., light penetrating through gaps of different sizes). Despite the fact that immature plants can survive while being suppressed for a long time, they still require a certain amount of light to grow and develop. Hence, they are expected to survive and be accumulated to a greater extent in

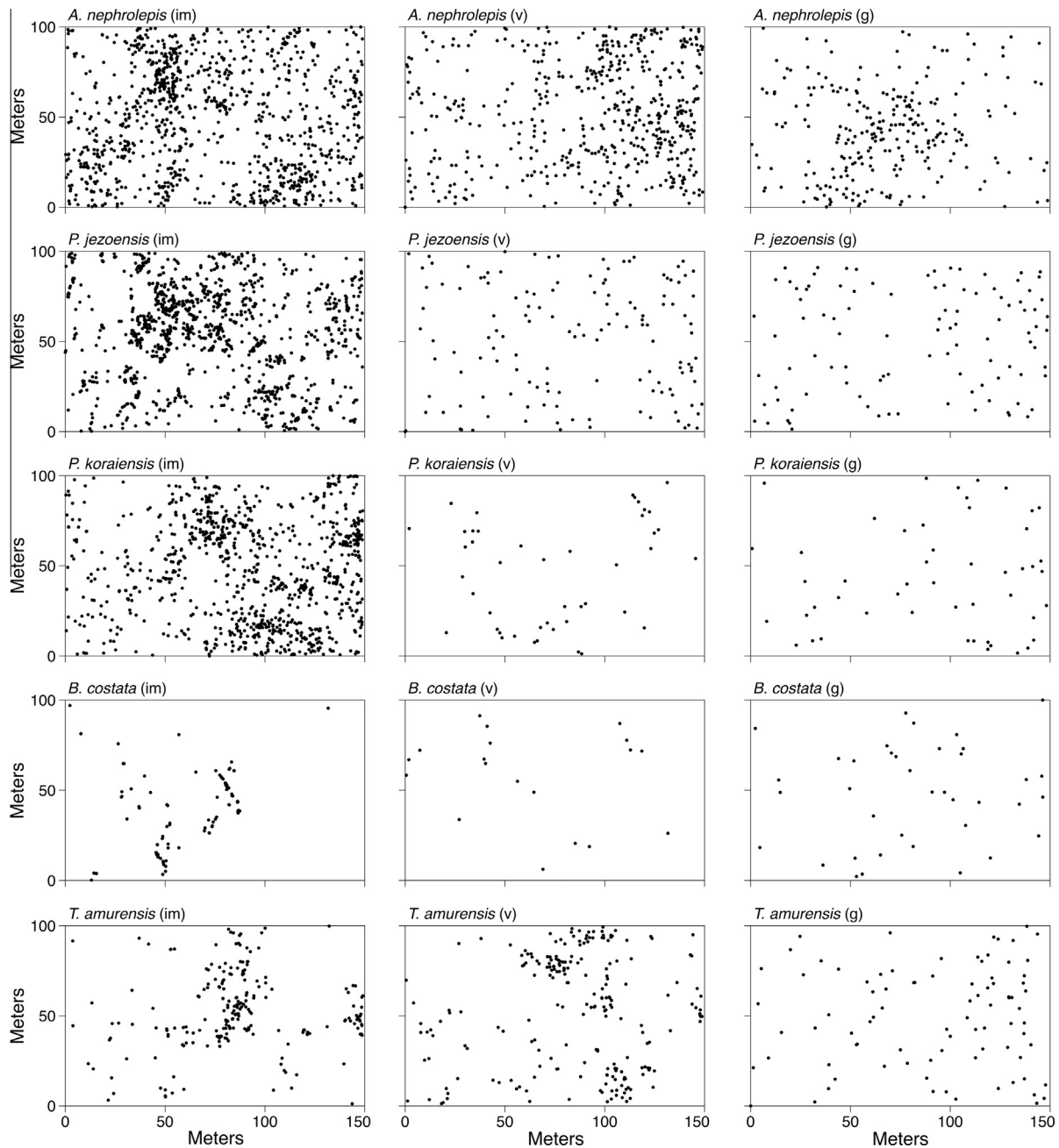


Fig. A2. Spatial distribution of five dominant tree species within the study plot: *im* – immature trees, *v* – virginal trees, *g* – generative trees.

better-illuminated areas, whereas there will be virtually no immature plants in the areas where the light level has been reduced for a long time. The second factor is the heterogeneity of the distribution of the substrate required for the survival of germlings and the development of juvenile and immature plants.

These factors have different effects on different species, which results in the formation of complex patterns of immature plants. Immature *P. jezoensis*, *A. nephrolepis* and *B. costata* plants only develop on partially decomposed stumps and windthrown trees (Komarova, 1986); otherwise, the plants will not survive even under favorable light conditions. For example, *B. costata* germinates in large numbers on windthrown trees but does not tolerate long-term suppression, as evidenced by the relatively small range of absolute ages of immature plants (Table 2), so this species forms small, dense aggregates (Fig. 7e). Individuals of *P. jezoensis*

germinate in smaller numbers and can tolerate suppression, so their aggregates are larger (Fig. 7d). The different levels of aggregation levels of immature plants in this case can be attributed to the fact that windthrown trees and tree stumps are distributed non-uniformly. According to our observations, *A. nephrolepis* plants do not require large windthrown trees and stumps as small, partially decomposed plant parts (e.g., branches and small trunk fragments) are sufficient. Meanwhile, this species is very shade-tolerant (Usenko, 1968), so significant accumulation of immature plants takes place (Fig. 3). Because *P. koraiensis* plants do not depend on the substrate, their aggregation is most likely to be caused by heterogeneous light distribution under the canopy and the pattern of the gaps that have formed over at least 100 years (Fig. 5p, Table 2). Immature *T. amurensis* plants “point to” the gaps and well-illuminated areas under the canopy that have existed for less

Table A1

Point pattern analysis: number of plants of five dominant tree species in different ontogenetic stages (n) and results of the GoF test (rank, p).

Species	Stage	n	rank	p
<i>Abies nephrolepis</i>	im	1019	200	0.005
	v	584	198	0.015
	g	202	200	0.005
<i>Picea jezoensis</i>	im	1162	200	0.005
	v	96	142	0.295
	g	152	25	0.880
<i>Pinus koraiensis</i>	im	1040	200	0.005
	v	45	197	0.020
	g	55	159	0.210
<i>Betula costata</i>	im	136	200	0.005
	v	21	154	0.235
	g	41	85	0.580
<i>Tilia amurensis</i>	im	236	200	0.005
	v	224	200	0.005
	g	82	178	0.115
All trees	im	3593	200	0.005
	v	970	172	0.145
	g	532	200	0.005

than 30–40 years, as evidenced by their maximal age (Table 2). Identical *B. costata* plants, immature *T. amurensis* plants do not tolerate suppression and quickly die after the canopy gap closes.

When a gap is formed above an accumulation of immature plants, a growth release event occurs and the plants reach the virginal ontogenetic state (Ukhvatkina et al., 2011). Because virginal plants require a relatively greater amount of light to grow compared to immature plants (Evstigneev, 1991; Lebedev and Chumachenko, 2002), the composition of virginal plants directly depends on the size of the canopy gap. Only single virginal plants survive because of the increasing competition within the groups of immature plants (especially coniferous trees), which explains their uniform or near-uniform distribution (Fig. 7h–k). *T. amurensis* is the only exception (Fig. 7l); the virginal and immature plants of this species are aggregated due to the rapid development of plants within the canopy gap. This is also explaining the virtually equal number of individual trees at the immature and virginal ontogenetic stages (Fig. 3).

The vitality of virginal plants varies considerably depending on whether they grow under the canopy or within the canopy gap. Virginal plants of all species with normal vitality only occur within the canopy gaps or at their periphery (Fig. 6), and the different ratios between the number of plants under the canopy and within the canopy gaps for coniferous and deciduous species indicate how well the plants of different species can tolerate suppression. Coniferous species (*A. nephrolepis*, *P. jezoensis* and to a lesser extent, *P. koraiensis*) can tolerate suppression for a long time and increase their growth again after conditions became more favorable (Ukhvatkina et al., 2011). Deciduous trees cannot tolerate suppression for a long time, so plants with low vitality are expected to die quickly. Our findings demonstrate that *B. costata* exhibits the lowest suppression tolerance as almost no *B. costata* plants were found under the stand canopy. Thus, the vitality analysis demonstrates that virginal plants of all species, both the light-demanding deciduous and the significantly more shade-tolerant coniferous ones, require canopy gaps for further development. The presence of a large number of suppressed conifer plants under the canopy suggests that they may require several releases to reach the canopy if small-scale disturbances predominate rather than undergoing continuous development (Ishikawa et al., 1999; Zhang et al., 2014). The results also documented multiple releases for not only *P. koraiensis*, as reported in other studies (Wang and Zhao, 2011; Zhang et al., 2014), but for all of the other species as well.

Because almost all plants require multiple releases to reach the generative stage, only some can survive to reach the stand canopy (Fig. 3). The ontogenetic spectra demonstrate that only a few immature plants reach the generative stage, so the distribution patterns of generative plants of most species are uniform (Fig. 7o and r) or even tend to hyperdispersion at small scales because generative plants have large crowns (Fig. 7p and q). Generative plants are expected to be non-uniformly distributed because of the factors affecting the plants at a large scale (Liu and Jin, 2012), but the heterogeneity of these factors does not manifest itself at the scale of a 1.5-ha plot.

Medium-scale disturbances provide favorable conditions for the development of virginal coniferous plants (*P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*) and their transition to the generative stage. In particular, a significant number of virginal plants became generative due to the disturbance events from 1951–1960s, which is evidenced by the fact that the absolute age of most virginal plants of all three species virtually coincides with the age of the young generative plants (Fig. 5d–f, g–i). In our previous studies (Ukhvatkina et al., 2011; Omelko and Ukhvatkina, 2012), we described the transition of coniferous species from the virginal to the generative stage, during which tree height and diameter increased abruptly. The stunted virginal trees that remain under the stand canopy will be suppressed and become the so-called buffer proportion of a population (East-European forests (Russia), 2004).

The gradual and continuous replacement of dead trees with new ones creates an uneven-aged stand (Fig. 5p–r). Meanwhile, trees with different absolute ages can be in one ontogenetic stage, and conversely, trees with the same absolute age can be in different ontogenetic stages. In particular, trees of the same age can be characterized as being in both the virginal and middle-aged generative ontogenetic stages (Fig. 5f, i and l) because the death of individual trees due to small-scale disturbances, as opposed to severe ones, may improve conditions for only some plants. As a result, even if immature (or virginal) plants are of virtually the same age, only those that used to grow near the newly formed gap and were not damaged during its formation will proceed to the virginal (or generative) ontogenetic stage. The remaining immature and virginal plants will be suppressed until another gap is formed.

The bimodality of the ontogenetic spectra of dominant species (namely, the presence of two population peaks, one of which corresponds to immature plants while the other one corresponds to middle-aged generative plants (Fig. 3) is caused for the following reasons. When plotting the spectra, we counted all of the plants regardless of their vitality, but suppressed individuals are predominant among immature and virginal plants. When the accumulation of immature plants takes place, some of them can be 100 years old and even older (Table 2), which is why there is the peak corresponding to the number of immature plants. Subsequently, intense thinning takes place, so the number of virginal and young generative plants is reduced. Middle-aged generative plants accumulate again because they have remained at this ontogenetic stage for a long time. Only a few plants reach the old generative stage, so their number decreases.

The populations of the five dominant species are generally stable within the study plot, as evidenced by the inverse J-shaped ontogenetic spectra and the presence of plants at all ontogenetic stages (Fig. 3) (Smirnova et al., 2002). The presence of virginal plants is particularly important because individuals reach the canopy during the virginal stage, and it indicates the occasional existence of disturbances that enable plants to reach the canopy layer in the stand. However, because the overall gap size during the study period was small (50–200 m²), greater-light-demanding species (Usenko, 1968), which require larger gaps for successful regeneration (*A. mono*, *A. tegmentosum*, *C. maximowiczii*, and *S. amurensis*, *U. laciniata*), are currently represented by single plants.

4.3. Implications for conservation and management

Korean pine-broadleaved forests have remained intact only in the Northeast China and Southeast Russia (Krestov, 2003). These unique forests have complicated spatial and vertical structure (Kolesnikov, 1956), which explains the presence of a variety of habitat conditions. Therefore, the Korean pine-broadleaved forests are featured by a high level of biodiversity. In addition, these forests provide habitat for rare species of plants and animals, such as ginseng (*Panax ginseng* C.A. Mey.), Japanese yew (*Taxus cuspidata* Siebold et Zucc. ex Endl.) and Amur tiger (*Panthera tigris altaica* Temminck).

Our studies have shown that populations of dominant tree species sustainably coexist in the stand due to small and medium scale disturbances. We have found no evidence that over the last two centuries this stand has been affected by severe disturbances such as strong windfalls and fires. Similar results have been obtained for the Korean pine-broadleaved forests in other parts of their range in the Southeast Russia (Ishikawa et al., 1999).

Our results also emphasize the fact that most dominant species require a very long period for reaching maturity (e.g. 300–600 years for *P. koraiensis* and 120–240 years for *B. costata*). This means that Korean pine-broadleaved forests are sensitive to severe disturbances, as it takes a long time for the plants to regain their place in community.

At present, wood is harvested in the Korean pine-broadleaved forests using methods that are common to Russia as a whole (Forest Code of Russian Federation, 2007). In particular, the interval between selective loggings on a given site is 40 years. Thus, this interval is several times shorter than the time required for the dominant tree species to reach maturity (7.5 times for *P. koraiensis*, 5 times for *P. jezoensis* and 3 times for *T. amurensis* and *B. costata*). Also, up to 30–40% of the total stand wood volume are harvested per one time, which means severe disturbance takes place every 40 years.

Thus, once again our results have shown that the use of the Korean pine-broadleaved forests for wood harvesting should be limited, since trees regeneration takes a very long time. These forests also require the development of specific forest management regime that should mimic the natural disturbance regime (predominance of small and medium scale disturbances), which is necessary for successful regeneration of all tree species. Otherwise, stand is rapidly degraded because frequent loggings promote regeneration of pioneer tree species, while long-lived tree species do not have enough time for the development. Industrial logging in the Korean pine-broadleaved forests in Russia began about 150 years ago, and now their area has almost halved (Koryakin, 2007).

Acknowledgments

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Appendix A

(See Figs. A1 and A2, Table A1).

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