Journal of Vegetation Science 10: 439-448, 1999
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Disturbance history and tree establishment in old-growth *Pinus koraiensis*-hardwood forests in the Russian Far East

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Abstract. Dendro-ecological studies were undertaken to document the disturbance history in two old-growth mixed *Pinus koraiensis*-hardwood forests in the southern part of the Sikhote-Alin mountains in the Russian Far East. Establishment of four common canopy conifers, *Abies holophylla*, *A. nephrolepis*, *P. koraiensis* and *Picea ajanensis*, and three common canopy hardwoods, *Acer mono*, *Betula costata* and *Tilia amurensis*, were also inferred from population age structures and spatial dispersion patterns.

Growth releases on increment cores suggested that peak periods of growth releases indicating partial canopy disturbances have repeatedly occurred over the past 230 yr at intervals from ca. 35 to 100 yr. Slight releases and suppressions other than the peak releases occurred in many years of both histories, suggesting the formation of smaller-scale canopy gaps. Despite the predominance of anthropogenic fires in Primorskiy Kray at present, destructive fires had not affected either forest. Wind disturbances and low intensity fires are likely factors controlling the dynamics of the forests. Under the disturbance regime, *P. koraiensis* has maintained its populations through its dependence on canopy gaps for establishment. Age distribution and gap dependence of *P. ajanensis*, *A. nephrolepis* and *A. mono* suggested continuous establishment of these species under a closed canopy, whereas occasional establishment of *T. amurensis* was derived largely from vegetative reproduction. Restricted establishment of *A. holophylla* and *B. costata* suggested a variety in kinds of disturbance throughout the histories. Continuous habitation of the study area by *P. koraiensis* is likely under the disturbance regime without destructive fires.

Keywords: Age structure; Canopy gap; Dendro-ecology; Dispersion pattern; Fire; Primorskiy Kray; Sikhote-Alin mountains; Wind disturbance.

Nomenclature: Kharkevich (1985-1991)

Abbreviations: SAR = Sihkote-Alinskiy Reserve plot ; UR = Ussuriskiy Reserve plot.

Introduction

The genus *Pinus* occurs in an enormous area of the northern Hemisphere, from the Equator to 75° N, and plays an important ecological role (Mirov 1967). Pines are basically drought- and light-enduring trees (Mirov 1967; Kramer & Kozlowski 1979), and the colonization of denuded areas by *Pinus* is related to disturbances such as fire and wind (Ahlgren 1974, 1976; Habeck & Mutch 1973; Heinselman 1973, 1981; Rowe & Scotter 1973; Gauthier et al. 1993; Thanos et al. 1996; Bergeron et al. 1997; Flannigan & Bergeron 1998; Kuuluvainen & Juntunen 1998). However, some *Pinus* species can live longer, attain a larger size, take part in old-growth forests, and thus have greater effects on the forest.

Pinus koraiensis (Korean pine), with a maximum age near 500 yr (Kolesnikov 1956; Anon. 1982), can grow as scattered canopy individuals in mixed conifer-hardwood forests in northeast China, northern Korea, and the Russian Far East. Mixed *P. koraiensis*-hardwood forest is one of the principal forest types here (Kolesnikov 1956; Wang 1961; Anon. 1980, 1982; Ishikawa 1996). Despite its dominance in the forest, the establishment process and disturbance regime have not been fully understood. Scattered canopy individuals of *P. koraiensis* in the forests suggest that this species may persist as a gap-phase species (Kolesnikov 1956; Okitsu 1996), whereas stand devastating fires sometimes cause the regeneration of *P. koraiensis* (Anon. 1982; Komarova 1992; Namikawa & Wang 1996). Furthermore, large numbers of saplings are also observed under the closed canopy of some forests (Anon. 1980).

A variety of establishment processes in *P. koraiensis* forest and of disturbances may be common in other *Pinus* species with longer longevity and larger size than pioneer pines. In the hemlock-*Pinus strobus*-northern hardwood region of eastern North America (Braun 1950), *P. strobus* (white pine) forms both monospecific stands and a tall emergent supercanopy in mixed species stands. The former stands are initiated by catastrophic canopy clearance by fires or wind (Heinselman 1973; Ahlgren 1976; Foster 1988), whereas *P. strobus* regenerates after small-scale canopy disturbances in the latter stands (Hibbs 1982; Quinby 1991; Kearsley & Jackson 1997). Similar disturbance and regeneration patterns have been described for mature *Pinus sylvestris* forest (e.g. Engelmark et al. 1998). This variety of regeneration processes have been explained by site parameters, stand structure or disturbance history (Hibbs 1982; Carleton et al. 1996).

In view of the wide distribution range of *P. koraiensis*, contradicting views on regeneration processes and disturbance regimes may partly result from a variation in site parameters and disturbance history. However, they may also result from the lack of detailed data on tree age and growth rate. Unlike the intensive dendro-ecological studies in the *P. strobus* forests in eastern North America (Foster 1988; Abrams & Orwig 1994), few studies on the history of natural disturbances have been conducted in old-growth mixed *P. koraiensis*-hardwood forests of the Asian Far East. Here, we use data from two old-growth mixed *P. koraiensis*-hardwood forests in the Sikhote-Alin mountains. The specific objectives of the present study are (1) to clarify the histories of disturbances controlling forest dynamics by examining tree ring width sequences, and (2) to cast light on the establishment processes of common tree species in the forests on the basis of age structures, along with the spatial dispersion pattern of trees in relation to the disturbances.

Study sites

The present study was conducted in the Sikhote-Alinskiy Biosphere Reserve and in the Ussuriskiy Reserve of the Vladivostok Institute of Biology and Pedology, both of which are located in the southern part of the Sikhote-Alin mountain system in the Primorskiy Kray region north of Vladivostok in the Russian Far East. The mountain system is 1200 km long and runs from 42° 50' N, 132° 20' E to 51° 20' N, 140° 30' E. It consists of mountain ranges with an average height of 1500 - 1700 m a.s.l. Mean annual temperature at Terney, just outside of the Sikhote-Alinskiy Reserve, is 2.3 °C; August is usually the warmest month (mean 17.4 °C), and January the coldest (– 14.0 °C); mean annual rainfall at Terney is 813 mm. Mean annual temperature at Suputinka near the Ussuriskiy Reserve is 2.6 °C, with August (20.3 °C) warmer, January (– 19.5 °C) colder and mean annual rainfall (719 mm) lower than at Terney. Soils are predominantly brown forest soils with a thin litter layer in the area covered with mixed *Pinus koraiensis*-hardwood forests in the mountain system (Ivanov 1964).

Mixed *P. koraiensis*-hardwood forests in the mountain system have been divided into northern, central and southern types (Kolesnikov 1956). The first two are prevalent in the Sikhote-Alinskiy Reserve, whereas the third is typical of the Ussuriskiy Reserve. *Pinus koraiensis*, *Picea ajanensis* and *Abies nephrolepis* are common coniferous species in the whole area. Common hardwood species include *Acer mono*, *Betula costata*, *B. lanata*, *Tilia amurensis* and *Quercus mongolica*. Understorey shrubs are more abundant in the Ussuriskiy Reserve than in the Sikhote-Alinskiy Reserve; they include *Corylus mandshurica*, and *Syringa amurensis*, common in both reserves, and *Acer barbinerve*, *Carpinus cordata*, *Eleutherococcus senticosus* and *Euonymus pauciflora* only in the Ussuriskiy Reserve. Common herbs and ferns are *Carex siderosticta*, *Maianthemum bifolium*, *Oxalis acetosella*, *Thalictrum filamentosum*, *Dryopteris expansa* and *D. bushiana* (Kurentsoba 1968; Krestov 1996).

Methods

Sampling methods

In the summer of 1995, two permanent plots, one of 0.6 ha (50 m × 120 m) in the Sikhote-Alinskiy Reserve, (SAR) and one of 1.0 ha (50 m × 200 m) in the Ussuriskiy Reserve (UR), at 280 km distance, were sampled (Table 1). Both plots were located in the middle part of a mountain slope with mesic conditions. All living stems ≥ 2 m in height were identified, marked with numbered vinyl tags, and measured for DBH (diameter at breast height, at 1.3 m above ground level) and height in both plots. Dead standing stems ≥ 2 m in height were also marked and measured if they could be identified. The position of all the living and the dead stems was recorded to the nearest 0.1 m. Three size classes were defined: (1) canopy tree (DBH ≥ 30 cm); (2) subcanopy tree (30 cm > DBH ≥ 10 cm); and (3) saplings (DBH < 10 cm and H ≥ 2 m).

In both plots, increment core samples for age determination of trees and disturbance history analysis were extracted at heights from 0.3 m to 1.1 m from live canopy and subcanopy trees, and saplings. Two cores were taken from each canopy tree ≥ 50 cm DBH, but only one core from each sapling, subcanopy tree and canopy tree < 50 cm DBH. For each species, the number

Table 1. Location and topographic features of the plots in the Sikhote-Alinskiy (SAR) and the Ussuriskiy (UR) Reserves.

Site	Location	Aspect	Inclination (°)	Plot size (ha)	Elevation (m)
SAR	45°08'N, 135°52'E	NW	10 - 18	0.6	600
UR	43°39'N, 132°27'E	SSW	5 - 12	1	240

of cored trees was nearly in proportion to its contribution to each of the three size classes. Although the cored trees were arbitrarily selected, we tried to scatter them uniformly over each plots. The numbers of trees cored in the Sikhote Alin plot and in the Ussuri plot were 322 and 309, respectively. Some trees could not be age-determined – due to a severely rotten pith – and were excluded from the analysis. Cores were used from 258 trees (83 % of the cored trees) in SAR and from 273 trees (89 %) in UR. Almost all cores were taken from *A. holophylla*, *A. nephrolepis*, *P. ajanensis*, *P. koraiensis*, *A. mono*, *B. costata*, and *T. amurensis*, the common species in the two plots (Table 2, below).

These cores were air-dried and prepared with a razor blade to maximize visual resolution, and then the numbers of rings on the cores were counted under a binocular zoom microscope. Ring widths were also measured to the nearest 0.01 mm using a micrometer. If coring missed the pith, the number of rings to the pith was estimated geometrically (Baker 1992). Samples that did not reach the central 10-yr portion of the tree were not included in the age distributions of the sampled plots, but were used to examine tree ring width sequences. The number of years for trees to reach coring height was estimated by using age-height regressions obtained from saplings harvested at the ground level for conifers and hardwoods, respectively.

Plot disturbance history

Evidence of past disturbances in a forest may be found both in the population structure of the forest and in the anatomy of the trees growing in the forest (Lorimer 1985; Lusk & Ogden 1992). Age structure of a population suggests the establishment process of the population, reflecting disturbance history on the population. There are, however, two lines of evidence which are independent of the population structure:

1. Abrupt changes in growth rate in the rings of trees which have survived disturbance events. Not only growth 'release' but also growth 'suppression' may occur in the trees after the disturbances.
2. Scars visible on increment cores, resulting from the destruction of the cambium on part of the circumference, either by tree falls, rock falls, avalanches, or by fires.

The more or less simultaneous occurrence of the two phenomena in many trees can be considered evidence of some past disturbance at that date. Not only canopy-, but also subcanopy trees and saplings, were used to reconstruct disturbance histories of the two plots, because it is advisable to use even smaller trees in detailed analysis of the disturbance history in a few plots (Lorimer & Frerich 1989). A growth release was defined by the following two criteria: (1) a doubling of a moving average of ring width in a certain 5-yr period to that in the previous five years, and (2) continued doubling for at least 10 yr. Trees which experienced initial rapid growth, reflecting establishment under relatively open conditions, were also counted as 'release'. Such trees in each species were identified by their consistently wide rings (at least 2 × the mean ring width for each species) over the initial 10 yr of growth. This definition of growth release is essentially the same as used by Foster (1988), Lorimer & Frelich (1989), Lusk & Ogden (1992) and Veblen et al. (1994). A growth suppression was defined inversely to a growth release. Release and suppression data were summarized as the percentage of those trees surviving to 1995 that showed a release or a suppression in a given year. Release and suppression frequencies were only plotted if the total number of sampling trees living in a given year exceeded 10 individuals.

Spatial pattern of saplings

Clumping of saplings at different scales may result from a species' mode of establishment and/or regeneration. We used Morisita's (1959) index of spatial dispersion to determine the departure from a random distribution:

$$I_\delta = q\sum_{i=1}^{q} n_i(n_i - 1)/(N - 1) \tag{1}$$

where q = number of quadrats, n_i = number of stems of a species in the ith quadrat, and N = the total number of stems of the species in all quadrats. In the present study, the index was calculated not by individuals but by stems because clumping of stems in an individual may reflect an important regeneration mode: stump or stem sprout.

The index, I_δ, equals 1.0 when the population is randomly distributed. If stems are clumped, I_δ is > 1.0, and if regularly distributed, I_δ is < 1.0. Each index value was tested to determine whether it varied significantly from that expected from a random distribution by using an F-test (Morisita 1959). When the number of individuals is small, I_δ can vary erratically, and thus it was computed only for species ≥ 15 saplings.

A variant of the nested-quadrat method (Kershaw & Looney 1985) was used to detect the scale of the pattern. In SAR, the scale of the spatial dispersion pattern was computed in the central 4608 m^2 (48 m × 96 m) portion of the plot. First, the portion was divided into 512 square quadrats (3 m × 3 m), and then I_δ was calculated for each species. Next, the size of the quadrat was duplicated up to 2304 m^2, and I_δ was calculated in each quadrat size. If the shape of quadrats was rectangular, two indices were calculated for both direction of the rectangle and averaged to avoid fluctuations of I_δ as a result of block shape (Pielou 1977). Clump size was analysed for different species by using the $I_{\delta(s)} / I_{\delta(2s)}$ method (Morisita 1959), where $I_{\delta(s)}$ is the I_δ value of the quadrat size s, and $I_{\delta(2s)}$ is that of the quadrat size $2s$. A peak $I_{\delta(s)} / I_{\delta(2s)}$ value coincides well with the size of the clump or with the size of an aggregation of clumps. In UR, the central 9216 m^2 (48 m × 192 m) portion was first divided into 1024 square quadrats (3 m × 3 m), and the size of the quadrats was then duplicated up to 4608 m^2. I_δ was calculated in each plot size for each species.

Gap dependence of saplings

To clarify the establishment conditions of common species after disturbance, we compared the number of saplings between two different canopy states, i.e., under closed canopy and in canopy gaps. The analysis was carried out in the same central portions of both plots as in the analysis of the spatial dispersion pattern. A canopy gap was defined as a group of square quadrats (3 m × 3 m) where no crowns of canopy and subcanopy trees showed any cover. The numbers of saplings under closed canopy and in canopy gaps were compared by the G-test (Sokal & Rohlf 1973) for each common species.

Results

Basal area and density

The total basal areas of living trees in the Sikhote Alin plot (SAR) and the Ussuri plot (UR) were very similar, nearly 42 m^2/ ha (Table 2). The total basal areas of standing dead trees in SAR and UR were 7.5 m^2/ ha and 6 m^2/ha, respectively. In each of these plots, about three-fourths of the basal area for standing dead trees was composed of large *Pinus koraiensis* trees (> 40 cm DBH). The total density of trees in SAR was ca. 2 × that in UR. This resulted partly from the larger numbers of stems of the shrub species *Acer ukurunduense* and *Corylus mandshurica*, and partly from abundant saplings of *P. koraiensis* and *Abies nephrolepis*. The total numbers of tree and shrub species in both plots were 17 and 28, respectively.

In SAR, *P. koraiensis* was dominant regarding basal area, but *A. nephrolepis* had the greatest density. *Betula costata* and *Tilia amurensis* acounted for ca. 10 % in relative basal area. In UR, *P. koraiensis* shared the basal area more equally with *Picea ajanensis*, *T. amurensis*, *A. nephrolepis*, *Abies holophylla,* and *A. mono* than in SAR. *A. holophylla* was observed only in UR, which was located within the distribution range of the species (< 44° N). We defined these seven tree species as common species, and analysed their age structures and dispersion patterns. The shrub species *Acer barbinerve*, *A. ukurunduense*, *Carpinus cordata* and *C. mandshurica*, though abundant were excluded from the analyses.

Table 2. Basal area, Ba (m^2 /ha) and density D (stems/ha) of the common tree and shrub species; **a.** Sikhote Alin plot (SAR); **b.** Ussuri plot (UR).

	Ba		Ba %		D		D %	
Species	live	dead	live	dead	live	dead	live	dead
a.								
Pinus koraiensis	17.02	5.50	40.5	73.6	612	73	18.46	18.34
Abies nephrolepis	8.78	0.46	20.9	6.2	1103	115	33.26	28.89
Betula costata	4.87	< 0.01	11.6	< 0.1	47	5	1.42	1.26
Tilia amurensis	3.81	0.09	9.1	1.2	115	2	3.47	0.50
Picea ajanensis	2.15	1.00	5.1	13.4	165	15	4.98	3.77
Acer mono	1.45	0.02	3.4	0.3	217	7	6.54	1.76
Acer ukurunduense	0.92	0.09	2.2	1.2	223	23	6.72	5.78
Corylus mandshurica	0.26	0.06	0.6	0.8	597	120	18.00	30.15
Other species	2.75	0.25	6.5	3.3	237	38	7.15	9.55
Total	42.01	7.47	100	100	3316	398	100	100
b.								
Picea ajanensis	8.35	0.56	19.9	9.3	251	17	15.72	7.46
Pinus koraiensis	7.83	4.52	18.7	75.1	64	15	4.01	6.58
Tilia amurensis	6.04	0.01	14.4	0.2	49	2	3.07	0.88
Abies nephrolepis	4.93	0.26	11.8	4.3	216	27	13.35	11.84
Abies holophylla	4.83	0	11.5	0	16	0	1.00	0
Acer mono	2.96	0.28	7.1	4.6	129	21	8.08	9.21
Betula costata	0.99	0.13	2.4	2.2	28	4	1.75	1.75
Carpinus cordata	0.66	0.02	1.6	0.3	117	4	7.33	1.75
Acer barbinerve	0.37	0.07	0.9	1.2	372	75	23.29	32.89
Other species	4.95	0.17	11.8	2.8	355	63	22.33	27.63
Total	41.91	6.02	100	100	1597	228	100	100

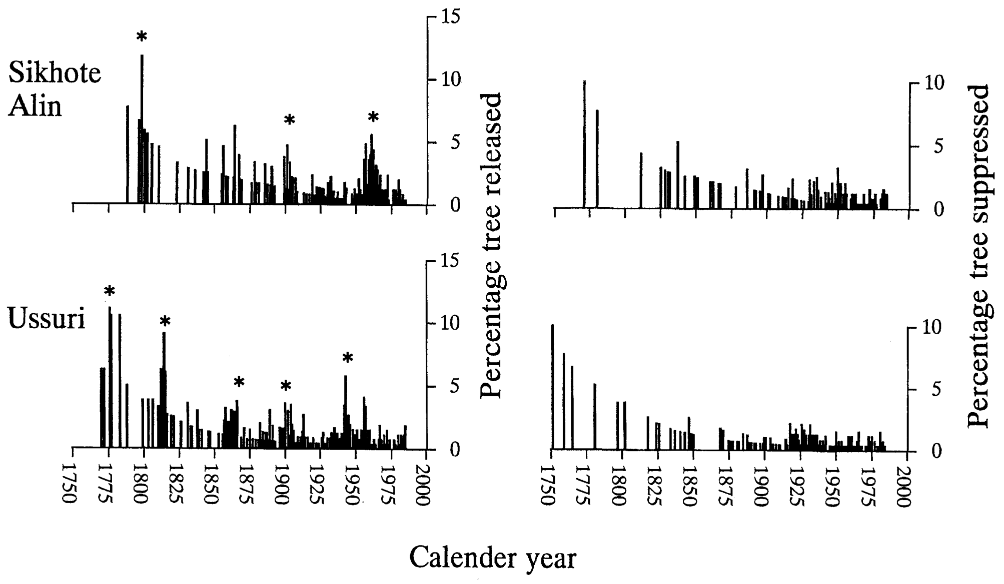

Fig. 1. Distributions of growth releases (left) and suppressions (right) in the Sikhote Alin (SAR) and Ussuri (UR) plots. Asterisks indicate peak years of major growth releases.

Plot disturbance history

All species were grouped together because of the insufficient number of cores for older trees ≥ 200 yr. The disturbance history in SAR could be dated back to 1765 (230 yr ago), and that in UR to 1750 (245 yr ago) (Fig. 1). Thus the part common to the two histories, 230 yr, was considered. The 230-yr histories of disturbances in both plots were characterized by several peak periods of growth 'release'. In this study, a major release (or suppression) of growth was tentatively defined as a period when more than 20 % of trees living in 1995 showed growth releases (or suppressions) in the consecutive 10 yr. The peak year in a major release (or suppression) of growth, indicating disturbance events, was defined as a year having the maximum percentage value in the period.

There were three peak years of growth release in SAR: 1798, 1901 and 1961. The intervals of these peaks were 103 and 60 yr. In UR we recognized five peak years of growth release: 1776, 1814, 1866, 1900 and 1942 with intervals from 34 to 52 yr. Except for the major release periods, minor releases have repeatedly occurred in most of the histories. No peak periods of growth suppression were observed in both plots, but slight suppressions have occurred in many years.

No fire scars were observed either on a total of 371 increment cores in SAR, or on a total of 397 cores in UR. No fragments of burned branches, stems and stumps were found on the soil surface of the two plots.

Age-height relation

Age-height relations were analysed only for trees established before 1950, because few saplings < 5 cm DBH could be sampled for age (Figs. 2 and 3). *P. koraiensis, P. ajanensis* and *A. holophylla* reached heights of ca. 35 m and became emergent trees, towering above the surrounding coniferous and hardwood trees. *Tilia amurensis* and *B. costata* reached at most 30 m and formed a canopy with the above-mentioned conifers, whereas the maximum heights of *A. nephrolepis* and *A. mono* were not more than 25 m.

Figs. 2 and 3 also indicate the age structure of both plots. In each plot, the population of *P. koraiensis* was composed of at least two age groups. In SAR, most canopy trees of *P. koraiensis* were established between 1740 and 1820, while another peak period of establishment occurred between 1860 and 1940. In UR, peak periods of establishments occurred between 1690 and 1780 and between 1840 and 1900.

In *P. ajanensis* and *A. mono*, the age distributions of trees confirmed that their establishments have been continuous in both plots. The establishment of *A. nephrolepis* occurred intermittently from 1810-1860 and 1890-1950 in SAR, but rather continuously in UR. Occasional establishment of *T. amurensis* occurred in both plots throughout most of the 250-yr period from ca. 1750 onwards. In UR, the establishment of *A. holophylla* was restricted to the period 1790 - 1840. In *B. costata*, the age distribution was also discontinuous in UR, whereas it was unclear in SAR – because of insufficient age samples.

Spatial pattern of saplings

Saplings of *P. ajanensis* and *A. nephrolepis* had clumped distributions in almost all quadrat sizes (Table 3). Each of the two species had the same clump size of

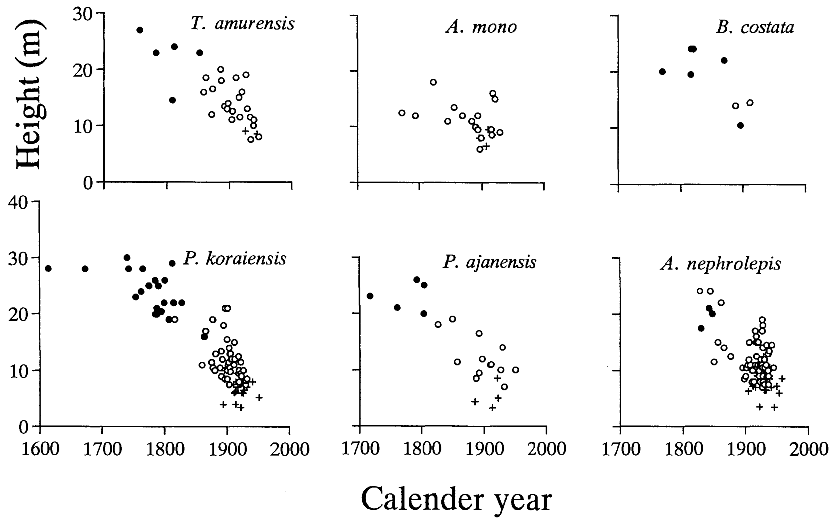

Fig. 2. Age-height relationships for the six common tree species in the Sikhote Alin plot (SAR). Saplings < 5 cm DBH were not included because of the difficulty in sampling increment cores. Solid and open circles, and crosses indicate canopy tree, subcanopy tree, and sapling, respectively.

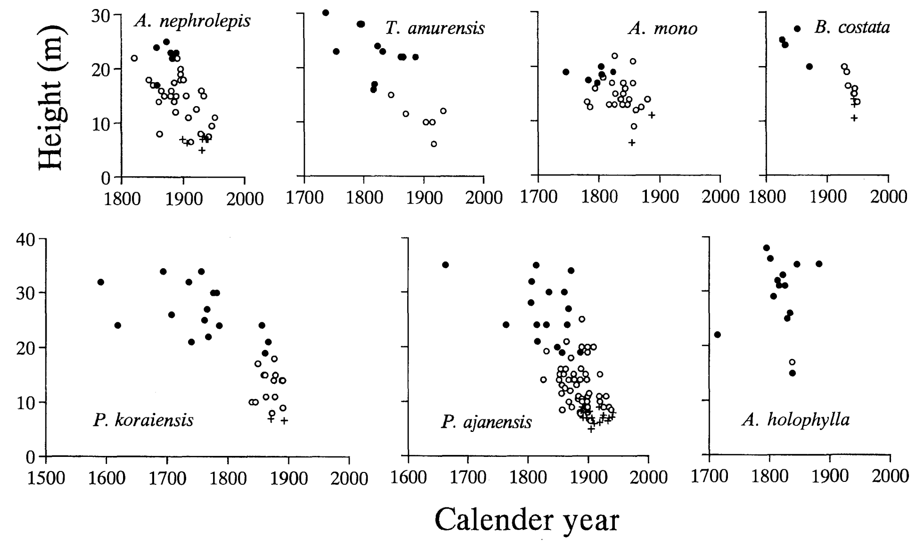

Fig. 3. Age-height relationships for the seven common tree species in the Ussuri plot (UR). Saplings < 5 cm DBH were not included in the figure, because of the difficulty in sampling increment cores. Symbols as in Fig. 2.

saplings in both plots: *P. ajanensis*, 36 m^2, and *A. nephrolepis*, 72 m^2. In SAR, saplings of *P. koraiensis* also had a clumped distribution, but the clump sizes of the saplings were estimated to be 18 m^2 and 144 m^2. In UR, however, the pattern was not determined because there were few *P. koraiensis* saplings (n = 14).

Saplings of *T. amurensis*, including both seedlings and sprouts, had a clumped distribution in SAR, and their clump size was 18 m^2. Saplings of *A. mono* showed a different pattern from those of the above species. They had a more or less clumped distribution in the larger quadrats. Dispersion patterns of saplings of *B. costata* and *A. holophylla* were not determined because of the very few saplings in both plots.

Gap dependence of saplings

1056 m^2 (22.9 %) was occupied by canopy gaps in the central 4608 m^2-portion of SAR, and 1368 m^2 (14.8 %) in the central 9216 m^2-portion of UR (Table 4). In both plots, saplings of *P. ajanensis* and *A. nephrolepis* were abundant, and there were no statistically significant differences in their distributions between under closed canopy and in canopy gaps. In contrast, few saplings of *B. costata* and *T. amurensis* were distributed under either closed canopy or in canopy gaps, despite their predominance in the canopy layer. Saplings of *P. koraiensis* were also few in UR, but tended to grow in canopy gaps in SAR. Although no difference in sapling distribution was observed in UR, *A. mono* showed more saplings under a closed canopy than in canopy gaps in SAR.

Table 3. Spatial dispersion pattern and clump size of saplings for the common canopy species in (a) the Sikhote Alin plot (SAR) and (b) the the Ussuriskiy plot (UR). Values significantly different from 1.0 ($P < 0.05$, F-test) in bold. Asterisks indicate clump sizes by $I_{\delta\,(s)} / I_{\delta\,(2s)}$ analysis.

	Quadrat size (m^2)									
Species	9	18	36	72	144	288	576	1152	2304	4608
a.										
Pinus koraiensis	**1.52**	**1.42** *	**1.32**	**1.31**	**1.26** *	**1.14**	**1.10**	**1.08**	**1.05**	-
Abies nephrolepis	**1.38**	**1.33**	**1.28**	**1.26** *	**1.20**	**1.16**	**1.10** *	**1.03**	1.00	-
Tilia amurensis	**9.75**	**6.10** *	**3.66**	**3.35**	**2.44**	1.52	1.07	1.05	0.93	-
Picea ajanensis	**2.86**	**3.13**	**3.31** *	**2.10**	**1.70**	**1.42**	**1.21**	**1.11**	0.98	-
Acer mono	1.60	1.60	**1.40**	1.25	1.16	1.13	**1.11**	**1.14**	**1.16**	-
b.										
Picea ajanensis	**2.30**	**2.18**	**2.08** *	**1.73**	**1.49**	**1.38**	**1.31** *	**1.17**	**1.08**	0.99
Abies nephrolepis	**3.82**	**3.73**	**3.30**	**2.85** *	**2.20**	**1.71**	**1.50**	**1.34**	**1.26**	**1.06**
Acer mono	2.16	1.89	1.89	**2.03**	**1.69**	**1.59**	**1.44**	**1.34**	**1.21**	0.99

Discussion

Although there are several differences in climate and tree composition between the Sikhote Alin plot (SAR) and the Ussuri plot (UR), the results of both plots are discussed together because of the similarities in total basal area (Table 2) and in their vertical and horizontal structure (Figs. 2 and 3, Tables 3 and 4). In both plots, continuous establishment of *P. koraiensis* under a closed canopy (Anon. 1980) has not occurred, nor was there any important influence of stand-devastating fires (Anon. 1982; Komarova 1992; Namikawa & Wang 1996). Rather, its establishment originated from disturbances with a smaller impact. Evidence for this can be derived from the all-age structures and the growth release patterns of both plots, and the gap dependence of *P. koraiensis*.

The age structures of both plots (Figs. 2 and 3) apparently showed that both plots have not been affected by stand-devastating fires since ca. 1600. In fact, no evidence of fires was found on soil profiles in, and around, SAR (M. Gromyko pers. comm.). Of eight peak-years of growth releases in both plots, two peak years (1814 and 1942) in UR coincided well with the restricted establishment of *B. costata* (Figs. 1 and 3). *Betula costata* is probably one of the least shade-tolerant species in the forests, as *Betula* species are generally intolerant to shade or less shade-tolerant (Kramer & Kozlowski 1979; Koike 1988). This is also supported by the scantiness of saplings of *B. costata* under a closed canopy (Table 4). In addition, similar values of percentage trees released were reported after partial canopy disturbances by snow avalanches, fire or wind (Foster 1988; Veblen et al. 1994). Thus, it seems likely that the major releases were initiated by partial canopy removals. Considering this, it is further concluded that the slight releases and suppressions in other years than the major release periods were caused by slighter disturbances forming small canopy gaps.

Wind disturbance has been the most likely cause of the releases and suppressions of tree growth during the 230-yr period in both forests. Although no wind damage was recorded in the Sikhote-Alin mountains, typhoons have frequently landed on Hokkaido, northern Japan, at the opposite shore of the Sea of Japan (Anon. 1992), and have played an important role in the disturbance and subsequent regeneration of forests (Ishikawa & Ito 1989; Osawa 1992; Namikawa et al. 1997). Furthermore, the predominance in height of *P. koraiensis* (Figs. 2 and 3) itself may accelerate the susceptibility of old canopy

Table 4. Comparison of the numbers of saplings between under closed canopy and in canopy gap in SAR and UR. Asterisks indicate significant differences ($P < 0.05$, G-test). Numerals in bold indicate that the number of saplings in one canopy state is statistically larger than that in the other canopy state.

		Sikhote Alin plot			Ussuriskiy plot		
Species	Canopy/gap Area (m^2)	Canopy 3552	Gap 1056	G-value	Canopy 7848	Gap 1368	G-value
Picea ajanensis		44	10	0.60	101	26	2.91
Abies nephrolepis		314	75	3.03	95	9	3.62
Pinus koraiensis		109	**47**	4.31*	10	4	1.72
Acer mono		**65**	7	8.54*	33	11	3.09
Tilia amurensis		13	2	0.88	5	1	0.02
Betula costata		5	5	3.48	5	**4**	4.48*

trees to disturbances, because the effects of wind disturbances are most severe on trees towering above the surrounding trees (Brewer & Meritt 1978; Oliver 1981). However, low-intensity fires leaving no fire scars on stems may have also affected the forests. Small and low intensity ground-level fires promote seedling establishments of pines by exposing mineral soils in North America (Heinselman 1981). Insect outbreaks can initiate regeneration of trees in some coniferous forests in North America (Baker & Veblen 1990; Veblen et al. 1994), and outbreaks of *Ips* spp. have been observed in Primorskiy Kray (Kurentsov 1941). However, Kurentsov (1941) also pointed out that they prefer to attack dead conifer woods, indicating that these outbreaks are not a cause, but the result of disturbances. Direct observations are needed on the establishments of trees after particular disturbances.

The populations of *P. koraiensis* in both plots have been maintained by the above disturbance regime characterized by considerable canopy removals at intervals of several decades, and by frequent formation of small canopy gaps. Saplings of *P. koraiensis* tended to grow in canopy gaps (Table 4) in SAR, and they had a clumped distribution with clump sizes of 18 and 144 m^2 (Table 3). Although the causal factor of the former clump size is unclear, the latter one is equivalent to a circle of 13.5 m diameter, and this circle is similar to maximum canopy diameters of *P. koraiensis* and hardwoods in old-growth mixed *P. koraiensis*-hardwood forests (Krylov 1974; Okitsu 1996). In addition, the age ranges of the cohorts of *P. koraiensis* (Figs. 2 and 3) were apparently wider than the duration of the major releases (Fig. 1). This indicates that *P. koraiensis* had been established not only by canopy removals at the major releases but also in small gaps formed in many years in the past. It is therefore concluded that the removal of one or a few canopy trees by slight disturbances or senescence provides suitable sites for the establishment of *P. koraiensis* – which has been mentioned by Kolesnikov (1956) and Okitsu (1996).

The analyses of age distribution and spatial dispersion patterns suggested that the establishment of *P. ajanensis*, *A. nephrolepis*, and *A. mono* occurred continuously beneath closed canopy. Okitsu et al. (1982) and Kubota et al. (1995) found continuous size and age distributions of *Picea jezoensis* (a synonym for *Picea ajanensis*) and *Abies sachalinensis*, a species closely related to *A. nephrolepis* (Liu 1971) in subalpine coniferous forests in Hokkaido. *Acer mono* is a late successional species with a high net photosynthetic rate under low light intensity (Koike 1988). This ability enables its seedlings to be established under closed canopy, resulting in the continuous age distributions in both plots. *Tilia amurensis* showed continuous, but limited establishments throughout most of the 230-yr histories of both plots (Figs. 2 and 3). Of 31 individuals of *T. amurensis* growing in the canopy layers of both plots, seven (22.6 %) were multi-stemed with an average of 1.4 sprouting stems in an individual. The percentage of sprouting and the average number of sprouting stems were highest among hardwood tree species in the forests, and imply a relatively high sprouting ability of this species. This sprouting ability is also supported by the fact that the clump size of saplings in *T. amurensis* was 18 m^2 in SAR (Table 4). Occasional establishments of *T. amurensis* result largely from this sprouting ability.

Betula costata and *A. holophylla* showed establishment processes different from the above-mentioned five species. In *B. costata*, most cored trees were established toward the two peak years of major growth releases, 1814 and 1942, in UR (Fig. 3). In addition, saplings were rarely observed in both plots (Table 4). The ages of the most cored trees of *A. holophylla* coincided with the 1814 peak in UR. The absence of establishments of both species in the remaining peak years may indicate a variety in kinds of disturbances.

Conclusion

Most fires in the last 250 years in the Russian Far East have originated from human activities (Sheshukov et al. 1992; Sheingauz 1996). Considering this, we can conclude that low-intensity disturbances have been more important factors controlling the dynamics of mixed *P. koraiensis*-hardwood forests before the onset of mass colonization by Europeans (in the 17th century) than in recent centuries. Under the disturbance regime without destructive fires, continuous habitation of the study area by *P. koraiensis* has been likely due to its gap dependence at establishment.

The vertical structure of mixed *P. koraiensis*-hardwood forests is similar to that of *P. strobus*-northern hardwood forests in eastern North America: *P. strobus* is an emergent tree reaching above surrounding hardwoods (Raup 1966). In addition, *P. strobus* is moderately shade tolerant (Kramer & Kozlowski 1979; Foster et al. 1992), which may be equivalent to the gap dependence of *P. koraiensis* found in the present study. The variety of establishment processes of *P. strobus* in eastern North America (Heinselman 1973; Ahlgren 1976; Hibbs 1982; Foster 1988; Quinby 1991; Abrams & Orwig 1996) require further studies on the dynamics of mixed *P. koraiensis*-hardwood forests in interior parts of the Asian Continent where a different disturbance regime may prevail.

Acknowledgements. We thank Dr. V.P. Velkholat (Institute of Biology and Pedology, Russia), I.A. Kolomeiets (Sikhote-Alinskiy Biosphere Reserve), S. Prokopenko and T. Kuznetsova (Far Eastern State University) for taking part in the field work. We also thank Drs. S. Okitsu (Chiba University, Japan), Eddy van der Maarel and three anonymous reviewers for their helpful comments on the manuscript. M. Gromyko (Sikhote-Alinskiy Biosphere Reserve) provided data on the fire history of the reserve. This work was partly supported by a grant from the Japan Private School Promotion Foundation.

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Received 8 July 1997;
Revision received 4 August 1998;
Final version received 11 November 1998;
Accepted 11 November 1998.